Principles of
Animal Behavior

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PREFACE

The purpose of this book is to help students understand the fundamental concepts of this discipline. It is designed to motivate students to learn and prosper. I am grateful for the support of my colleagues. I would also like to acknowledge the encouragement of my family.

The scientific study of animal behavior is conducted under the domain of ethology. It primarily focuses on the behavior of animals under natural conditions and views it as an evolutionary adaptive trait. It generally focuses on behavioral processes instead of particular animal groups. Understanding of animal behavior plays an important role in animal training. Some of the learning characteristics which are studied within this field are habituation, associative learning, imprinting and observational learning. Ethology also studies animal communication and emotions in animals. Communication in animals refers to the transfer of information from a single animal or a group of animals to one or more animals. Such information generally affects the current or future behavior of the receivers. This book unfolds the innovative aspects of animal behavior which will be crucial for the holistic understanding of the subject matter. Some of the diverse topics covered in this book address the varied branches that fall under this category. It will serve as a valuable source of reference for those interested in this field.

A foreword for all the chapters is provided below:

Chapter – Introduction

The scientific study of the different ways in which animals interact with each other, with the environment and with other living beings is called animal behavior. It is also known as ethology. This chapter has been carefully written to provide an easy understanding of the varied facets of ethology as well as its branches.

Chapter – Approaches to Animal Behavior

A few of the different approaches to animal behavior are adaptation, animal cognition and mobbing. Some of the types of adaptation are physiological, structural and behavioral. This chapter closely examines these key concepts related to these approaches of animal behavior to provide an extensive understanding of the subject.

Chapter – Evolutionary Basis of Animal Behavior

Animal behavior is often considered to be an evolutionarily adaptive trait. Some of the concepts in animal behavior which are studied in the context of evolution are natural selection, behavior mutation and biological altruism. The topics elaborated in this chapter will help in gaining a better perspective about the evolutionary basis of animal behavior.

Chapter – Animal Migration and Communication

The relatively long distance movement of individual animals is called animal migration. Animal communication refers to the transfer of information from a single animal or a group of animals to one or more animals such that it affects the behavior of the receivers in the present or the future. The diverse aspects of animal migration and communication have been thoroughly discussed in this chapter.

Chapter – Reproductive Behavior in Animals

The reproductive behavior of animals refers to the actions and events which are involved in the process where an organism produces one or more than one replacement of itself. Some of the activities which are displayed by animals as a part of their reproductive behavior are mating calls, courtship display and lordosis behavior. This chapter has been carefully written to provide an easy understanding of these facets of reproductive behavior in animals.

Chapter – Feeding Behavior in Animals

The actions of an animal for procurement of nutrition are termed as feeding behavior. Some of the commonly observed behavior in animals related to feeding are hoarding, predation and cannibalism. This chapter closely examines these feeding behaviors in animals to provide an extensive understanding of the subject.

Samantha Morales

Introduction

1 CHAPTER

The scientific study of the different ways in which animals interact with each other, with the environment and with other living beings is called animal behavior. It is also known as ethology. This chapter has been carefully written to provide an easy understanding of the varied facets of ethology as well as its branches.

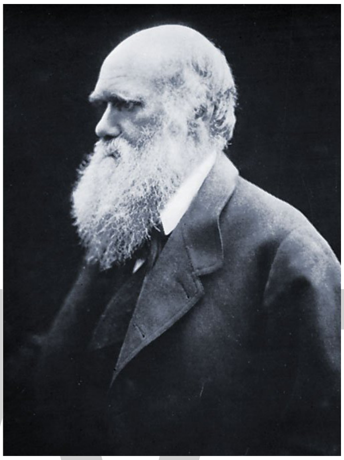
ANIMAL BEHAVIOR

Animal behavior is a concept referring to everything animals do, including movement and other activities and underlying mental processes. Human fascination with animal behavior probably extends back millions of years, perhaps even to times before the ancestors of the species became human in the modern sense. Initially, animals were probably observed for practical reasons because early human survival depended on knowledge of animal behavior. Whether hunting wild game, keeping domesticated animals, or escaping an attacking predator, success required intimate knowledge of an animal's habits. Even today, information about animal behavior is of considerable importance. For example, in Britain, studies on the social organization and the ranging patterns of badgers (Meles meles) have helped reduce the spread of tuberculosis among cattle, and studies of sociality in foxes (Vulpes vulpes) assist in the development of models that predict how quickly rabies would spread should it ever cross the English Channel. Likewise in Sweden, where collisions involving moose (Alces alces) are among the most common traffic accidents in rural areas, research on moose behavior has yielded ways of keeping them off roads and verges. In addition, investigations of the foraging of insect pollinators, such as honeybees, have led to impressive increases in agricultural crop yields throughout the world.

Even if there were no practical benefits to be gained from learning about animal behavior, the subject would still merit exploration. Humans (Homo sapiens) are animals themselves, and most humans are deeply interested in the lives and minds of their fellow humans, their pets, and other creatures. British ethologist Jane Goodall and American field biologist George Schaller, as well as British broadcaster David Attenborough and Australian wildlife conservationist Steve Irwin, have brought the wonders of animal behavior to the attention and appreciation of the general public. Books, television programs, and movies on the subject of animal behavior abound.

Darwin's Influence

The origins of the scientific study of animal behavior lie in the works of various European thinkers of the 17th to 19th centuries, such as British naturalists John Ray and Charles Darwin and French naturalist Charles LeRoy. These individuals appreciated the complexity and apparent purposefulness of the actions of animals, and they knew that understanding behavior demands long-term observations of animals in their natural settings. At first, the principal attraction of natural history studies was to confirm the ingenuity of God. The publication of Darwin's On the Origin of Species in 1859 changed this attitude. In his chapter on instinct, Darwin was concerned with whether behavioral traits, like anatomical ones, can evolve as a result of natural selection. Since then, biologists have recognized that the behaviors of animals, like their anatomical structures, are adaptations that exist because they have, over evolutionary time (that is, throughout the formation of new species and the evolution of their special characteristics), helped their bearers to survive and reproduce.



Charles Darwin.

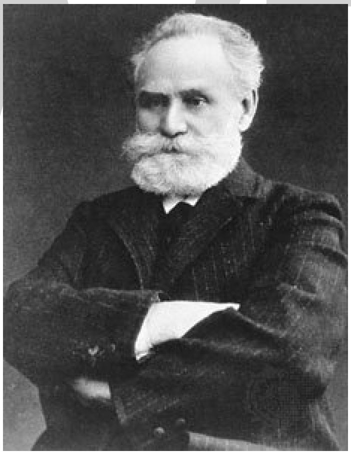
Furthermore, humans have long appreciated how beautifully and intricately the behaviors of animals are adapted to their surroundings. For example, young birds that possess camouflaged colour patterns for protection against predators will freeze when the parent spots a predator and calls the alarm. Darwin's achievement was to explain how such wondrously adapted creatures could arise from a process other than special creation. He showed that adaptation is an inexorable result of four basic characteristics of living organisms:

1. There is variation among individuals of the same species. Even closely related individuals, such as parent and offspring or sibling and sibling, differ considerably. Familiar human examples include differences in facial features, hair and eye colour, height, and weight.
2. Many of these variations are inheritable—that is, offspring resemble their parents in many traits as a result of the genes they share.
3. There are differences in numbers of surviving offspring among parents in every species. For example, one female snapping turtle (family Chelydridae) may lay 24 eggs; however, only 5 may survive to adulthood. In contrast, another female may lay only 18 eggs, with 1 of her offspring surviving to adulthood.
4. The individuals that are best equipped to survive and reproduce perpetuate the highest frequency of genes to descendant populations. This is the principle known colloquially as "survival of the fittest," where fitness denotes an individual's overall ability to pass copies of his genes on to successive generations. For example, a woman who rears six healthy offspring has greater fitness than one who rears just two.

An inevitable consequence of variation, inheritance, and differential reproduction is that, over time, the frequency of traits that render individuals better able to survive and reproduce in their present environment increases. As a result, descendant generations in a population resemble most closely the members of ancestral populations that were able to reproduce most effectively. This is the process of natural selection.

Ecological and Ethological Approaches to the Study of Behavior

The natural history approach of Darwin and his predecessors gradually evolved into the twin sciences of animal ecology, the study of the interactions between an animal and its environment, and ethology, the biological study of animal behavior. The roots of ethology can be traced to the late 19th and early 20th centuries, when scientists from several countries began exploring the behaviors of selected vertebrate species: dogs by the Russian physiologist Ivan Pavlov; rodents by American psychologists John B. Watson, Edward Tolman, and Karl Lashley; birds by American psychologist B.F. Skinner; and primates by German American psychologist Wolfgang Köhler and American psychologist Robert Yerkes. The studies were carried out in laboratories, in the case of dogs, rodents and pigeons, or in artificial colonies and laboratories, in the case of primates. These studies were oriented toward psychological and physiological questions rather than ecological or evolutionary ones.



Ivan Petrovich Pavlov.

It was not until the 1930s that field naturalists—such as English biologist Julian Huxley, Austrian zoologist Konrad Lorenz, and Dutch-born British zoologist and ethologist Nikolaas Tinbergen studying birds and Austrian zoologist Karl von Frisch and American entomologist William Morton Wheeler examining insects—gained prominence and returned to broadly biological studies of animal behavior. These individuals, the founders of ethology, had direct experience with the richness of the behavioral repertoires of animals living in their natural surroundings. Their "return to nature" approach was, to a large extent, a reaction against the tendency prevalent among psychologists to study just a few behavioral phenomena observed in a handful of species that were kept in impoverished laboratory environments.

The goal of the psychologists was to formulate behavioral hypotheses that claimed to have general applications (e.g., about learning as a single, all-purpose phenomenon). Later they would proceed using a deductive approach by testing their hypotheses through experimentation on captive animals. In contrast, the ethologists advocated an inductive approach, one that begins with observing and describing what animals do and then proceeds to address a general question: Why do these animals behave as they do? By this they meant “How do the specific behaviors of these animals lead to differential reproduction?” Since its birth in the 1930s, the ethological approach—which stresses the direct observation of a broad array of animal species in nature, embraces the vast variety of behaviors found in the animal kingdom, and commits to investigating behavior from a broad biological perspective—has proved highly effective.

One of Tinbergen’s most important contributions to the study of animal behavior was to stress that ethology is like any other branch of biology, in that a comprehensive study of any behavior must address four categories of questions, which today are called “levels of analysis,” including causation, ontogeny, function, and evolutionary history. Although each of these four approaches requires a different kind of scientific investigation, all contribute to solving the enduring puzzle of how and why animals, including humans, behave as they do. A familiar example of animal behavior—a dog wagging its tail—serves to illustrate the levels of analysis framework. When a dog senses the approach of a companion (dog or human), it stands still, fixates on the approaching individual, raises its tail, and begins swishing it from side to side. Why does this dog wag its tail?

With respect to causation, it becomes important to identify the physiological and cognitive mechanisms that underlie the tail-wagging behavior. For example, the way the dog’s hormonal system adjusts its responsiveness to stimuli, how the dog’s nervous system transmits signals from its brain to its tail, and how the dog’s skeletal-muscular system generates tail movements need to be understood. Causation can also be addressed from the perspective of cognitive processes (that is, knowing how the dog processes information when greeting a companion with tail wagging). This perspective includes determining how the dog senses the approach of another individual, how it recognizes that individual as a friend, and how it decides to wag its tail. The dog’s possible intentions (for example, receiving a pat on the head), feelings, and awareness of self become the focus of the investigation.

With respect to ontogeny, the focus here is on investigating the underlying developmental mechanisms that lead to the occurrence of the behavior. The answer derives from understanding how the sensory-motor mechanisms producing the behavior are shaped as the dog matures from a puppy into a functional adult animal. Both internal and external factors can shape the behavioral machinery, so understanding the development of the dog’s tail-wagging behavior requires investigating the influence of the dog’s genes and its experiences.

With respect to function: The focus of this question is rooted in the subfield called behavioral ecology; the answer requires investigating the effects of tail wagging on the dog’s survival and reproduction.

Lastly, with respect to evolutionary history, scientists must hypothesize evolutionary antecedent behaviors in ancestral species and attempt to reconstruct the sequence of events over evolutionary time that led from the origin of the trait to the one observed today. For example, an antecedent behavior to tail wagging by dogs might be tail-raising and tail-vibrating behaviors in ancestral wolves. Perhaps when a prey animal was sighted, such behaviors were used to signal other pack members that a chase was about to begin.

Both the biological and the physical sciences seek explanations of natural phenomena in physicochemical terms. The biological sciences, however, have an extra dimension relative to the physical sciences. In biology, physicochemical explanations are addressed by Tinbergen’s questions on causation and ontogeny, which taken together are known as “proximate” causes. The extra dimension of biology seeks explanations of biological phenomena in terms of function and evolutionary history, which together are known as “ultimate” causes. In biology, it is legitimate to ask questions concerning the use of this life process today (its function) and how it came to be over geologic time (its evolutionary history). More specifically, the words use and came to be are applied in special ways, namely “promoting genetic success” and “evolved by means of natural selection.” In physics and chemistry, these types of questions are out of bounds. For example, questions concerning the use of the movements of a dog’s tail are reasonable, whereas questions regarding the use of the movements of an ocean’s tides are more metaphysical.

Causation

Sensory-motor Mechanisms

At this level of analysis, questions concern the physiological machinery underlying an animal’s behavior. Behavior is explained in terms of the firings of the neural circuits between reception of the stimuli (sensory input) and movements of the muscles (motor output). Consider, for example, a worker honeybee (Apis mellifera) flying back to her hive from a field of flowers several kilometres away. The sensory processes the bee employs, the neural computations she performs, and the patterns of muscular activity she uses to make her way home constitute some of the mechanisms underlying the insect’s impressive feat of homing. In the course of exploring these mechanisms and those underlying other forms of animal behavior, physiologists have learned an important lesson regarding the mechanisms underlying behavior: they are special-purpose adaptations tailored to the particular problems faced by an animal, but they are not all-purpose solutions to general problems faced by all animals. Linked to this lesson is the realization that the physiology of a species will have limitations and biases that reflect individuals’ need to deal only with certain behavioral problems and only in specific ecological contexts. In behavior, as in morphology, an animal’s capabilities are matched to its expected environmental requirements, because the process of natural selection shapes organisms as if it were always addressing the question of how much adaptation is enough.

Honeybee (Apis mellifera).

Consider first the sensory abilities of animals. All actions (such as body movements, detection of objects of interest, or learning from others in a social group) begin with the acquisition of information. Thus, an animal’s sense organs are exceedingly important to its behavior. They constitute a set of monitoring instruments with which the animal gathers information about itself and its environment. Each sense organ is selective, responding only to one particular form of energy; an instrument that responds indiscriminately to multiple forms of energy would be rather useless and similar to having none at all. The particular form of energy to which a sense organ responds determines its sensory modality. Three broad categories of sensory modalities are familiar to humans: chemoreception (exemplified by the senses of taste and smell but also including specialized receptors for pheromones and other behaviorally important molecules), mechanoreception (the basis for touch, hearing, balance, and many other senses, such as joint position), and photoreception (light sensitivity, including form and colour vision).

The capabilities of an animal's sense organs differ depending on the behavioral and ecological constraints of the species. In recognition of this fact and of the equally important fact that animals perceive their environments differently than do humans, ethologists have adopted the word Umwelt, a German word for environment, to denote an organism's unique sensory world. The umwelt of a male yellow fever mosquito (Aedes aegypti), for example, differs sharply from that of a human. Whereas the human auditory system hears sounds over a wide range of frequencies, from 20 to about 20,000 Hz, the male mosquito's hearing apparatus has been tuned narrowly to hear only sounds around 380 Hz. Despite its apparent limitations, a male mosquito's auditory system serves him perfectly well, for the only sound he must detect is the enchanting wing-tone whine of a female mosquito hovering nearby, a sound all too familiar to anyone who lingers outdoors on a midsummer's evening.

Pit vipers, colubrid snakes from the subfamily Crotalinae, which include the well-known rattlesnakes, provide another example of how the umwelt of a species serves its own ecological needs. Pit vipers possess directionally sensitive infrared detectors with which they can scan their environment while stalking mammalian prey, such as mice (Mus) and kangaroo rats (Dipodomys), in the dark. A forward-facing sensory pit, located on each side of the snake's head between the eye and the nostril, serves as the animal's heat-sensing organ. Each pit is about 1 to 5 mm (about 0.04 to 0.2 inch) deep. A thin membrane, which is extensively innervated and exquisitely sensitive to temperature increases, stretches from wall to wall inside the pit organ, where it functions like the film in a pinhole camera, registering any nearby source of infrared energy.

Human umwelt is not without its own limits and biases. Human eyes do not see the flashy advertisements to insects that flowers produce by reflecting ultraviolet light, and human ears do not hear the infrasonic calls of elephants or the ultrasonic sounds of bats. Furthermore, human noses are limited relative to those of many other mammals. Moreover, humans completely lack the sense organs for the detection of electric fields or of Earth's geomagnetic field. Sense organs for the former occur in various species of electric fishes (such as electric eels and electric catfish), which use their sensitivity to electric fields for orientation, communication, and prey detection in murky jungle streams, while the latter exist in certain birds and insects, including homing pigeons and honeybees, which use them to navigate back to the home loft or hive. At the same time, unlike most animals, humans are endowed with superb visual acuity and colour vision as a result of having evolved large, high-performance, single-lens eyes.

Each species' nervous system is an assemblage of special-purpose devices with species-specific and sometimes sex-specific capabilities. These capabilities become even more apparent when investigating how animals use their sense organs to acquire information for solving behavioral problems, such as territory defense or prey capture. Although an animal may possess diverse sensory organs that enable it to receive a great deal of information about the environment, in performing a particular behavioral task, it often responds to a rather small portion of the stimuli perceived. Moreover, only a subset of available stimuli reliably provides the information needed to perform a particular task. Ethologists call the crucial stimuli in any particular behavioral context “sign stimuli.”

A classic example of sign stimuli comes from the behavior of male three-spined sticklebacks (Gasterosteus aculeatus) when these fish defend their mating territories in the springtime against intrusions from rival male sticklebacks. The males differ from all other objects and forms of life in their environment in a special way: they possess an intensely red throat and belly, which serve as signals to females and other males of their health and vigour. Experiments using models of other fish species have shown that the red colour is the paramount stimulus by which a territory-holding male detects an intruder. Models that accurately imitated sticklebacks but lacked the red markings were seldom attacked, whereas models that possessed a red belly but lacked many of the other characteristics of the sticklebacks, or even of fish in general, were vigorously attacked.

Three-spined stickleback (Gasterosteus aculeatus).

Similarly, the brain cells of some toads (Bufo) are tuned to pick out those features of the environment that reliably match the toads’ natural prey items (such as earthworms). Experiments were conducted in which a hungry toad was presented with cardboard models moving horizontally around the individual at a constant distance and angular velocity. The research revealed that just two stimuli, the elongation of the object (that is, making the cardboard model longer to increase resemblance to prey) and movement in the direction of the elongation, were sufficient to initiate the toad’s prey-catching behavior. Subsequently, the toad jerked its head after the moving model in order to place it in its frontal visual field. Other stimuli, such as the colour of the model and its velocity of movement, did not influence the toad’s ability to distinguish worms from non-worms, even though toads possess good colour and form vision. Even the broadly tuned human sensory system operates in a highly selective, yet adaptive, manner. For instance, a person hunting white-tailed deer seeks the prey almost exclusively by watching closely for deerlike movements amid the stationary trees of a forest, not by straining to sense the deer’s shape, smell, or sound.

As with sensory systems, the neural mechanisms by which animals compute solutions to behavioral problems have not evolved to function as general-purpose computers. Rather, the central nervous system (that is, the brain and spinal cord of a vertebrate or one of the segmental ganglia of an invertebrate) performs specific computations associated with the particular ecological challenges that individuals face in their environment. A helpful illustration of this point is the startle response of goldfish (Carassius auratus). If a hungry predatory fish strikes from the side, the goldfish executes a brisk swivelling movement that propels its body sideways by about one body length to dodge the predator’s attack. How does the goldfish’s central nervous system process information from the sense organs to instantaneously decide the correct direction (right or left) to move? The key neural element in the startle response of the goldfish is a single bilateral pair of neurons, called the Mauthner neurons, located in the goldfish's hindbrain. Each neuron on the left or right receives input from the lateral line system (a row of small pressure sensors that are triggered by the disturbances caused by nearby moving objects) located on the left or right side of the goldfish's body. Each neuron sends output to neurons that activate the musculature on the opposite side of the body. There is strong, mutual inhibition between the left and right Mauthner neurons; should the left one fire in response to a mechanical stimulus from the left side of the body, for example, the right one is inactivated. Inactivation prevents it from interfering with the crucial, initial contractions of the trunk muscles on the goldfish's right side. The net effect is that 20 milliseconds after sensing danger the goldfish assumes a C-like shape with the head and tail bent to the same side and away from the attacker. This reaction is followed 20 milliseconds later by muscle contractions on the other side of the body so that the tail straightens and the fish propels itself sideways, away from the danger. Thus, the two Mauthner neurons of the goldfish's nervous system function exquisitely for processing information regarding predator attacks, and solving this crucial behavioral problem appears to be the only task that they perform.

Small-brained creatures, such as fishes, are not the only species whose nervous systems have evolved to solve tasks in a limited—but ecologically sufficient—way that turns difficult problems of computation into more tractable ones. For example, take the task of a human computing an interception course with a flying object, such as when a baseball player runs to catch a fly ball. In principle, the task could be solved with a set of differential equations based on the observed curvature and acceleration of the ball. What happens instead, evidently, is that the fielder finds a running path that maintains a linear optical trajectory for the ball. In other words, the player adjusts the speed and direction of his movement over the baseball field so that the trajectory of the ball appears to be straight. Unlike the more complicated differential equation approach, the linear trajectory approach does not tell the player when or where the ball will land. Consequently, the player cannot run to the point where the ball will fall and wait for it. If he did, complicating factors such as wind gusts diverting the ball might mean that he would end up in the wrong place. Instead, the player simply keeps his body on a course that will ensure interception.

Once an animal has received information about the world from its sense organs and has computed a solution to whatever behavioral problem it currently faces, it responds with a coordinated set of movements—that is, a behavior. Any particular movement reflects the patterned activity of a specific set of muscles that work on the skeletal structures to which they are attached. The activity of these muscles is controlled by a specific set of motor neurons that in turn are controlled by sets of interneurons connected to the animal's brain. Thus, a given behavior is ultimately the result of a specific pattern of neural activity.

Sometimes neural control takes the form of a simple sensory reflex, in which the activity in the motor neurons is triggered by sensory neurons. This activity can be achieved directly or via one or two interneurons. Other times, as in the case of rhythmic behavior (such as with birds flying or insects walking), a central pattern generator located in the central nervous system produces rhythms of activity in the motor neurons. Central pattern generators do not depend on sensory feedback. Feedback, however, commonly occurs to modulate and reset the rhythm of the motor output after a disturbance to the animal's behavior, as in the case of air turbulence disrupting the wing movements of a flying bird.

Most commonly, the neural control of behavior takes the form of a motor command in which the initiation and modulation of activity in the motor neurons is produced by interneurons descending from the animal's brain. The animal's brain is where inputs from multiple sensory modalities are integrated. In this way, a sophisticated tuning of the animal's behavior in relation to its internal condition and its external circumstances can occur. Often the control of an animal's movements involves an intricate synthesis of all three forms of neural control: patterned neural activity, simple sensory reflex, and motor command. As in all aspects of behavioral physiology, an immense diversity exists among animal species and behavior patterns in the way the components of behavioral machinery have been linked over time by natural selection.

Cognitive Mechanisms

Cognitive psychology proposes yet another way to study the causal mechanisms of animal behavior. The aim of cognitive psychology is to explain an animal's behavior in terms of its mental organization for information processing (that is, how the animal acquires, stores, and acts on information present in its world). By studying cognitive mechanisms of an animal, one may study how the animal perceives, learns, memorizes, and makes decisions.

Consider, for example, crows (Corvus brachyrhynchos) that crack walnuts open by dropping them from heights of 5 to 10 metres (about 16 to 33 feet) or more onto rocks, roads, or sidewalks. The birds generally avoid dropping the nuts onto soil, where they would be unlikely to break open. Remarkably, the crows can discriminate between black and English walnuts, for they drop the harder black walnuts from greater heights. In addition, when a crow drops a nut, it takes into account the likelihood that a fellow crow might steal the contents before it can be retrieved. If fewer competing crows are perched nearby, the crow carries a nut higher into the air before releasing it. Thus, numerous processes of perception, learning, and decision-making activity underlie the crows' nut-cracking behavior.

Each of these processes may be analyzed. For example, how do crows judge the height from which to drop nuts? Do they have to learn to adjust the dropping height in relation to the type of walnut? When faced with the conflicting conditions of having a hard-shelled black walnut and seeing a number of other crows nearby, how do they decide what drop height to use?

Until the 1970s, students of animal cognition eschewed speculation about the unobservable processing of information, limiting themselves to explaining behaviors in terms of quantifiable relationships between stimuli and responses. Today, however, they make use of behavior as a window into how an animal's nervous system processes information. Students of cognition also emphasize the investigation of behaviors in which the animal does not simply respond to immediate stimuli but relies on stored representations of objects and events. For some investigators, mental representations of the environment are the essence of cognition. According to this view, known as the computational-representational approach, the experience of an animal results in the formation in the brain of isomorphisms between brain processes and events in the world. The brain then performs computations on these representations that are ultimately converted to behavioral outputs. For example, a bird assessing the availability of berries on a bush might store information about the time at which it finds each berry as it searches the bush. It might then convert this information, through a brain process equivalent to division, into a representation of the rate of berry collection.

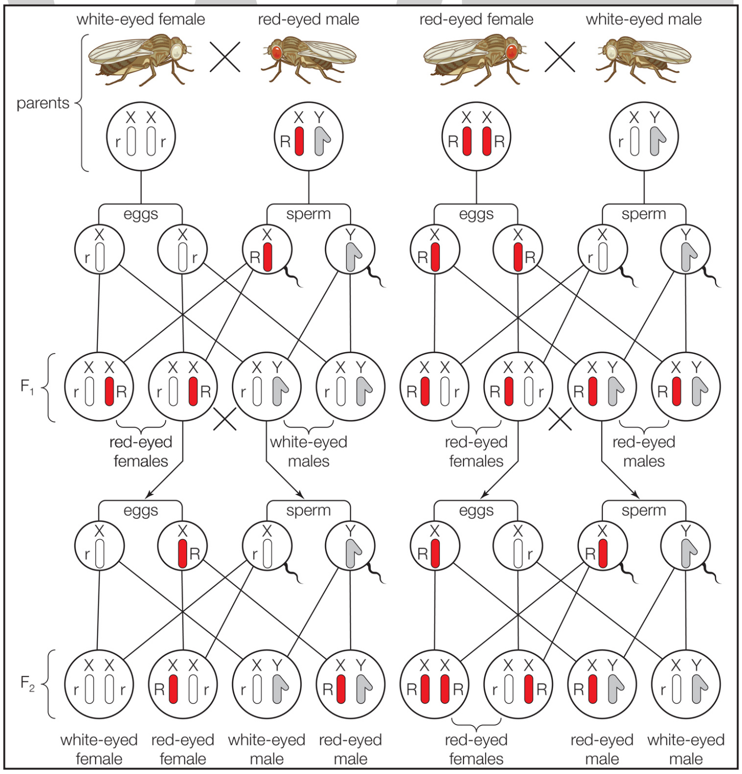
It is possible, however, that the computational-representational approach exaggerates the richness and detail of animals' representations and the complexity of the brain processes operating on them. A good illustration comes from studies of the mechanisms by which ants (Cataglyphis fortis) living in the Sahara desert navigate home after conducting a circuitous search for food (mainly dead insects). Such a search can take these ants 100 metres (about 330 feet) or more (equivalent to 10,000 body lengths) from the entrance of their underground nest. To get back home, the ants rely on landmarks as visual signposts to show the way. Originally, it was assumed that these ants and other insects that orient using landmarks are able to store their knowledge of the nest environs in maplike internal representations called “cognitive maps.” Doing so would give an ant tremendous flexibility in homing: equipped with a bird’s-eye knowledge of the terrain over which it travels, an ant could return even from points where it had never before been. The mental representation used by these ants in landmark guidance is, however, actually somewhat simpler. Experiments have revealed that each ant stores a two-dimensional visual template—a kind of snapshot—of the landmark array it saw when it left its nest. When returning to its nest, the ant moves so as to match the current visual image as closely as possible with the memorized template. The snapshot-matching mechanism, unlike the cognitive-map one, enables an ant to steer its way home only from points it has recently visited, as opposed to novel sites to which it might be displaced by an experimenter. Although this mental mechanism provides a less complete and less flexible solution to the problem of finding home, it is entirely sufficient for the problems that desert ants routinely face.

An unseen and therefore largely unappreciated aspect of behavior is the use of decision-making rules or “Darwinian algorithms.” Organisms rely on these rules to process information from their physical and social environments and result in particular behavioral outputs that guide key behavioral and life-history decisions. Darwinian algorithms are made up of the sensory and cognitive processes that perceive and prioritize cues within an individual’s perceptual range. These inputs are then translated into motor outputs. A Darwinian algorithm may involve a stimulus threshold (such as “when the day-length exceeds 10 hours, migrate north”) or may depend on the occurrence of a cue that is normally associated with a fitness-enhancing outcome (such as “build nests in dense vegetation where chick survival is predictably high”). Darwinian algorithms are shaped through evolutionary time by the specific selective regime of each population. Which cues are relied upon depends on the certainty with which a cue can be recognized, the reliability of the relationship between the cue and the anticipated environmental outcome, and the fitness benefits of making a correct decision versus the costs of making an incorrect decision. In general, Darwinian algorithms underlying behavioral and life-history decisions are only as complex as is necessary to yield adaptive outcomes under a species’ normal environmental circumstances but not so complex as to cover all experimentally or anthropogenically induced contingencies.

An intriguing question in the study of animal cognition is the role of consciousness. Humans easily distinguish between merely responding to objects and being conscious of them. For example, while driving along a highway deep in thought or conversation, the driver may suddenly realize that he has not been conscious of the road for the past several miles. Indeed, it is well documented that humans can effectively perceive, memorize, process, and even act on objects and events without the kind of awareness that underlies a verbal report of consciousness. It is possible, therefore, that the behavior of animals occurs without conscious awareness. However, given that humans have consciousness, it seems reasonable to suppose that individuals in other species, especially social species (such as primates), also experience at least a rudimentary form of consciousness. To think otherwise would be to presume an evolutionary discontinuity between humans and all other forms of life. Thus, the possibility that at least some of the behavior of animals is accompanied by conscious thinking seems reasonable.

Although most students of animal behavior accept the idea that animal consciousness is a likely possibility, some argue that it is not yet possible to know whether any particular animal experiences consciousness because it is a private, subjective, and, ultimately, unknowable state. In contrast, cognitive ethologists (a separate group of animal behaviorists), most notably American biophysicist and animal behaviorist Donald Griffin, argue that animals are undoubtedly conscious, since individuals from a wide variety of species behave with apparent intentions of achieving certain goals. For example, chimpanzees (Pan troglodytes) stalking a monkey high above them in the treetops will distribute themselves among the trees that would otherwise provide the monkey with an escape route and attack the creature simultaneously. Similarly, groups of female lions (Panthera leo) fan out widely and then coordinate their attacks on ungulate prey. In another example, a raven (Corvus corax), when presented with the novel situation of a meat morsel dangling from a long string tied to a perch, will study the situation briefly before it acts. Subsequently, the raven will quickly procure the meat by repeatedly pulling up a length of the string with its beak and clamping each length pulled up with its feet while sitting on the perch. Studies of the states and mechanisms of animal consciousness represent important frontiers of future research.

Behavioral Genetics



Sex-linked inheritance of white eyes in Drosophila flies.

The evidence is now compelling that genes influence behavior in all animals, including humans. Indeed, an increasing share of biomedical research is devoted to the hunt for genes involved in human behavioral maladies such as alcoholism, obesity, schizophrenia, and Alzheimer disease. Often these studies are pursued using animal models with subjects that include mice, rats, and dogs with behavioral symptoms resembling those of humans. The principal point of confusion arises from equating genetic influence on behavior with genetic determination of behavior. To do so is to mistakenly believe that identifying genes “for” a behavior implies that the gene controls, fully and inevitably, this behavior. In actuality, to say that there are genes “for” a particular behavior means only that within a population of individuals there exists genetic variation underlying some of the differences in this specific behavior. To cite an example involving a morphological trait, the statement that there are genes for coat colour in guinea pigs (Cavia porcellus) or horses (Equus caballus) means that genetic variation in the guinea pig or horse population is responsible for some of the variation in coat colour.

Furthermore, identifying a gene that influences a behavior does not imply that the behavior is inevitable; there is considerable variation among behaviors in the relative importance of the individual’s genetic constitution and its environment to the expression of the behavior. Occasionally, the possession of a particular form of a gene does consistently result in the individual having a particular form of a behavior; more frequently, however, the form of the behavior is due to a complex interaction between genes and environment.

The strength of the influence of genes on a particular behavior is quantified by a genetic measure called “heritability.” Heritability is defined as the fraction of the total variation in a trait among individuals in a population that is attributable to the genetic variation among those individuals. The remaining source of the variation is, of course, the environment. Values of heritability range between zero and one. The smaller the environmental variation experienced by the individuals in a population, the greater will be the fraction of the total variation in the behavior that is the result of genetic variation.

One way to measure the heritability of a behavioral trait is to determine the average values of the behavior for the parents and offspring in a sample of families within a population and calculate the linear relationship between offspring values and parental values. The slope of this line reveals the heritability of the behavioral trait in that population. For example, the heritability of the calling behavior that male crickets (Gryllus integer) use to attract females has been measured. In any one population, some males chirp away for many hours each night, others call for just a few hours, and still others almost never call. The heritability of calling duration for one Canadian population that was studied was 0.53. The value indicates that slightly more than half of the variation in calling duration arose because males differed genetically and slightly less than half arose from environmental differences. (For example, the more parasites a cricket had acquired, the less food he had obtained, and thus the less he might be able to call on a given night).

The degree of genetic influence on a particular behavior is not a fixed characteristic. Rather, heritability can vary greatly depending on how much environmental variation is experienced by individuals in the specific population being studied. Thus, regarding the calling behavior of male crickets, if every male fed well, thereby eliminating several environmental influences on calling, the numerical value of heritability would be considerably higher.

Numerous studies involving diverse species, including humans, have detected some level of heritability for every trait that has ever been examined. For example, the mean value of heritability for morphological traits, such as body and wing length, is 0.46; for life history traits, such as fecundity and life span, is 0.26; and for behavioral traits, such as calling duration and fighting stamina, is 0.30. Thus, the genetic influence on the characteristics of individual animals falls generally between 30 and 50 percent for most traits.

Instinctive Learning

An animal adjusts its behavior based on experience—that is, it learns—when experience at one time provides information that will be useful at a later time. Viewed in this light, learning is seen as a tool for survival and reproduction because it helps an animal to adjust its behavior to the particular state of its environment. An animal needs to know such things as what food is good to eat, when and where to find it, whom to avoid and approach, with whom to mate, and how to find its way home. When these things are not genetically preprogrammed—because they depend on the particular circumstances of an individual's time and place—the animal must learn them.

Consider, for example, a female digger wasp called the bee wolf (Philanthus triangulum) who has finished excavating a tunnel in a sandy bank. She then digs a small outpocket where one of her young will develop, and she stocks this cell with worker honeybees (Apis mellifera), which she has paralyzed by stinging and which will serve to provision her young. After laying an egg on one of the bees, she closes off the cell with sand and starts work on a new cell. To provision the cell, she must fly out to hunt more honeybees; however, after crawling out of her nest burrow, closing its entrance hole, and launching into flight, she does not immediately depart the area. Instead, she hovers just over her nest site, inspecting the ground and flying in wider and wider arcs to scan an ever-increasing area. During this elaborate departure flight, the wasp memorizes the specific configuration of landmarks—sticks, tufts of grass, and trees—around her burrow. Later, when she returns, she will use the information to pinpoint her nest's location. Her genes cannot provide her with knowledge of the landmark array around her nest, so she must learn it.

One of the clearest indications of the falseness of the old dichotomy between innate and learned behavior is the fact that in most cases animals are genetically predisposed to acquire only specific information in developing their behavior. One might say that most of the learning performed by animals is instinctive learning. This phenomenon is conspicuous in the flower-learning behavior of honeybees (A. mellifera). Since at least the time of the Greek philosopher and scientist Aristotle (384–322 BCE), it has been known that worker bees show "flower constancy," a specialization by individual bees on a single species of flower. Flower constancy occurs in spite of the fact that honeybees are generalist foragers capable of exploiting many flower species. The flowers have much to gain from bees that remain faithful to them; specialist bees will be carrying the appropriate species of pollen. Therefore, the colours and odours of flowers probably evolved as conspicuous signals for the bees to learn. In turn, specialization benefits the bees by reducing flower-handling time and facilitating the collection of nectar.

Early in the 20th century, Austrian biologist Karl von Frisch demonstrated experimentally that honeybees are able to learn and distinguish a single floral odour from among at least 700 others. In addition, he found that they could distinguish colour from yellow into the ultraviolet across the electromagnetic spectrum. One striking feature of this type of colour and odour learning is the rigid programming of the timing. Research has revealed that a bee learns the flower's colour only during the final few seconds before beginning to feed, and odour learning occurs during feeding. It is as if bees possess a set of switches that turn colour and odour learning on and off at specific times during the foraging process. The time course of this learning program is highly adaptive, being restricted to times when a bee is alighted on a rewarding flower. In this manner, its learning is focused on the colour and odour of the flowers of this rewarding species rather than on the hues and scents of any nearby flowers of unrewarding species.

Until the mid-1960s, psychologists generally believed so. Studying mainly birds and mammals, they developed an approach known as “general process learning theory,” which attempted to account for learning with a single set of principles, namely unconstrained “associative learning” as studied in instrumental (operant) conditioning and classical (Pavlovian) conditioning. Associative learning is said to occur when an animal changes its behavior upon forming an association between an environmental event and its own response to the event. In operant conditioning, the animal learns to associate a voluntary activity with specific consequences. In classical conditioning, the animal learns to associate a novel (conditioned) stimulus with a familiar (unconditioned) one. For example, in his study of classical conditioning, Russian physiologist Ivan Petrovich Pavlov demonstrated that by consistently exposing a dog to a particular sound (novel stimulus) and simultaneously placing meat powder (familiar stimulus) in its mouth the dog could be made to salivate upon hearing the sound even without the meat stimulus. Initially, salivation was the unconditioned response, whereas the food stimulus was the unconditioned stimulus. Once the dog learned to associate the sound stimulus with the food stimulus, salivation became the conditioned stimulus to sound—that is, a stimulus that previously did not trigger a response.

The popularity of general process learning theory peaked in the 1940s and ’50s. In the mid-1960s, however, American psychologist John Garcia discovered several puzzling phenomena that indicated adaptive limits on learning and contradicted the supposedly general principles of conditioning. One of the most important of these anomalies was flavour aversion learning. When rats (Rattus norvegicus) and many other vertebrates, including humans, sample a flavour and later become ill, they learn to avoid consuming that flavour in the future. This phenomenon has two remarkable properties. First, it occurs despite delays of several hours between experiencing the flavour (the conditioned stimulus, or CS, in the Pavlovian conditioning paradigm) and experiencing the illness (the unconditioned stimulus, or US); it does not require the brief delay specified by the general principles of conditioning. Second, in rats, learning with the US being illness is limited to flavours. This response was revealed in an experiment in which rats experienced a flash of light and the sound of a buzzer each time they took a drink from a tube of flavoured water (hence “bright noisy tasty water” became the CS). Some of the rats were made ill (nauseous) after drinking (hence illness became the US for them), whereas others were shocked through the feet shortly after they began drinking (hence pain became the US for them). After conditioning, the rats were tested with the noise plus the light alone or with the flavour alone. Those rats that had been made ill avoided drinking only the “tasty water,” whereas the rats that had been shocked avoided drinking only the “bright noisy water.” In other words, the rats could learn to associate a taste with an illness but not a visual and auditory stimulus. Conversely, the rats could learn to associate a visual and auditory stimulus, but not a taste, with pain.

These findings attracted tremendous skepticism when they were first reported because both the long delay between CS and US and the CS-US specificity contradicted the idea of general laws of learning. Both findings, however, make considerable sense in light of the problems faced by rats living in nature. If they consume a new food and become ill even hours later, they will not eat the food again and thus not suffer the illness associated with the food. Moreover, it is adaptive that rats learn to associate a taste cue, not an auditory or visual cue, with illness-causing food because rats discriminate foods best using chemical cues sensed by taste, olfaction, or both. In contrast, something that causes pain is best recognized from a safe distance. Therefore, it is adaptive that rats learn to associate auditory and visual cues with painful experiences. Thus, these “anomalies” for general process learning theory can be understood by considering the functions that the rats' learning has evolved to serve.

There is now compelling evidence that humans also possess adaptive predispositions in learning abilities. Consider, for example, the curious anthropological discovery made in 1926 by Finnish sociologist Edward Westermarck that arranged marriages between children that grow up together (whether biological siblings or not) are far more likely to fail than arranged marriages between individuals not raised together. The failures most often result from sexual incompatibilities. Evidently, children are genetically guided to learn to treat as siblings all individuals with whom they are raised together. And because siblings tend to avoid sexual contact, presumably due to a long evolutionary history of detrimental consequences associated with inbreeding, marriages between these individuals tend to fail.

Today it is widely recognized that the general-purpose psychological approach to learning had overlooked its biological significance and that animals possess learning mechanisms that are specialized for solving the problems they face in the natural world. This view of learning explains the psychologists' observations of the limits of learning by animals in laboratory settings. It also makes sense of ethological reports of special forms of learning, such as imprinting (that is, the rapid identification of parents by newborn animals triggered by following the first object they see moving away from them), which have been studied in naturalistic settings. To a large extent, this picture of instinctive learning has brought a constructive end to the centuries-old debate about whether "nature" (genes) or "nurture" (experiences) is the source of adaptive behavior of animals. Animals are shaped by their experiences; however, the interpretation of each experience is governed by a collection of rules (Darwinian algorithms) set by the genes in each species.

The general-purpose view of learning that prevailed during most of the 20th century was based on two assumptions: (1) the ability to learn is always beneficial, and (2) animal learning abilities are like human learning abilities, which seem to be of completely general and unlimited applicability. Neither assumption is correct.

First, there are costs as well as benefits to learning, so learning abilities will be beneficial, and favoured by natural selection, only when the benefits outweigh the costs. The costs include those involved in building and maintaining the required neural circuitry and also the time and mistakes involved in learning while the animal is fine-tuning its behavior to the current or likely future state of its environment. When learning is a matter of life or death—as in geese (Anser and Branta), sheep (Ovis), and antelopes (family Antilopinae), where newborn young must keep up with mobile parents—the advantage of rapid learning (that is, staying together) and the danger of slow learning (that is, lagging behind) are both extremely high. By considering both the fitness costs and the benefits of different forms of learning, one can readily appreciate the reasons why imprinting occurs in these species, rather than the slower process of trial-and-error learning.

Second, as described earlier, the learning abilities of animals, including humans, are not completely general; learning abilities are adaptively specialized so that, in any particular context, animals take in only the most relevant information. Late in his career, Lorenz referred to "the innate schoolmarm," a phrase that picturesquely expresses the reality that animals possess adaptive predispositions in their learning.

Function

In studying the function of a behavioral characteristic of an animal, a researcher seeks to understand how natural selection favours the behavior. In other words, the researcher tries to identify the ecological challenges, or “selection pressures,” faced by a species and then investigates how a particular behavioral trait helps individuals surmount these obstacles so that they can survive and reproduce.

Until the mid-1960s, functional interpretations of animal behavior were usually made in terms of how a behavior was “good for the species.” Social behaviors that excluded some individuals from reproducing (such as territorial defense and courtship displays) were seen as adaptations for regulating animal populations at levels that would prevent overpopulation, environmental destruction, and extinction of the species. This view was based on the observation of ecological phenomena—such as the overgrazing of grassland by cattle, leading to the starvation of the animals. American evolutionary biologist George C. Williams and British ornithologist David Lack, however, revealed the underlying theoretical problem with the view that animals behave in ways that limit their reproduction for the good of their species. Williams noted that individuals who maximize their own reproduction will have greater genetic success than those who behave in ways that limit their reproduction. Thus, over time, in subsequent generations, reproduction-reducing behaviors will be replaced by reproduction-enhancing ones. Therefore, it has become evident that it is incorrect to interpret the behavior of animals as having evolved to function “for the good of the species.” Instead, the appropriate interpretation is how a behavior has evolved for the “good of the individual.”

Williams’s theoretical argument was bolstered by Lack’s long-term study of the reproductive behavior of the European, or common, swift (Apus apus). At first glance, swifts appear to voluntarily restrict their own reproduction. When Lack removed the eggs laid each day from a pair’s nest he discovered that the female could lay up to 72 or more eggs in a season. Yet, surprisingly, she usually lays just two or three eggs. Are chimney swifts regulating their egg production to avoid overpopulation, or does the number of eggs laid equal the number of young they can successfully rear each year? Lack answered this question by performing the experiment of adding one or two nestlings to the nests of certain pairs so that, instead of the normal two or three young, they would have to rear four or five. He then compared the reproductive success of these pairs to those that were left rearing the normal number. Lack found that the birds with four or five young were less successful (that is, rearing fewer young to fledging) than those in a control group who reared a normal-sized brood. Therefore, chimney swifts, in rearing just two or three offspring, are not withholding reproduction for the good of their species or local population; instead, they are producing as many young as they can successfully rear given a limited food supply, thereby maximizing their own reproduction.

Chimney swifts provide just one example of a pattern that has been found repeatedly by biologists studying the behavior and reproduction of animals. They have found that individuals are “selfish,” behaving in ways that benefit their own reproduction regardless of its long-term effect on the survival of their species. Sometimes, however, animals engage in apparent altruism (that is, they exhibit behavior that increases the fitness of other individuals by engaging in activities that decrease their own reproductive success). For example, American zoologist Paul Sherman found that female Belding’s ground squirrels (Spermophilus beldingi) give staccato whistles that warn nearby conspecifics of a predator’s approach but also attract the predator’s attention to the caller. Likewise, worker honeybees (Apis mellifera) perform suicidal attacks on intruders to defend their colony, and female lions (Panthera leo) sometimes nurse cubs that are not their own (although some authorities note that such cubs suckle the lioness when she is asleep).

The key insight to understanding the evolution of such self-sacrificial behavior was provided by British evolutionary biologist William D. Hamilton in the mid-1960s. He argued that natural selection favours genetic success, not reproductive success per se, and that individuals can pass copies of their genes on to future generations. Genes are passed from direct parentage (the rearing of offspring and grand-offspring) and by assisting the reproduction of close relatives (such as nieces and nephews), a concept referred to as "inclusive fitness" or "kin selection."

Hamilton devised a formula—now called Hamilton's rule—that specifies the conditions under which reproductive altruism evolves:

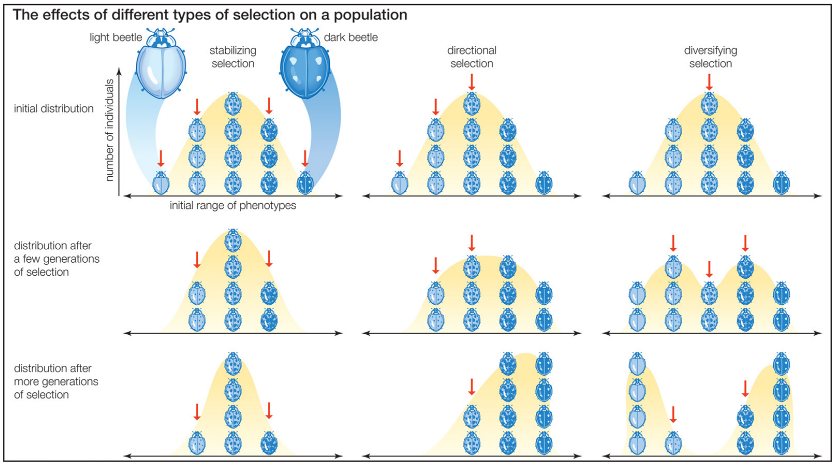
$$r \times B > C$$

where B is the benefit (in number of offspring equivalents) gained by the recipient of the altruism, C is the cost (in number of offspring equivalents) suffered by the donor while undertaking the altruistic behavior, and r is the genetic relatedness of the altruist to the beneficiary. Relatedness is the probability that a gene in the potential altruist is shared by the potential recipient of the altruistic behavior. Altruism can evolve in a population if a potential donor of assistance can more than make up for losing C offspring by adding to the population B offspring bearing a fraction r of its genes. For example, a female lion with a well-nourished cub gains inclusive fitness by nursing a starving cub of a full sister because the benefit to her sister (B = one offspring that would otherwise die) more than compensates for the loss to herself (C = approximately one quarter of an offspring), since the survival probability of her own, non-starving cub is only slightly reduced. Given that the average genetic relatedness (that is, r) between two full sisters is 0.5, then according to Hamilton's rule $(0.5 \times 1) > 0.25$. In essence, genes for altruism spread by promoting aid to copies of themselves.

According to this view, which was popularized by British zoologist Richard Dawkins, the most appropriate way of viewing natural selection is from a gene-selection perspective, as embodied in Hamilton's rule. Genes that are best able to guide the organisms that bear them to propagate successfully will persist and proliferate over generations. Consequently, an explanation of the function of a particular behavior should include how the behavior promotes the success of the genes that underlie the behavior. Of course, since an animal's behavior almost always promotes genetic success by helping the animal survive and reproduce its genes, investigations of behavioral function typically address the survival and reproductive value of the behavior.

Natural Selection in Action

The most straightforward way to study the function of a behavior is to see how natural selection operates on it under current conditions by studying differential reproduction. Often this kind of investigation can be conducted by exploiting the naturally occurring variation among individuals, such as in a particular phenotypic (observable) trait in a population. Sometimes, however, the researcher must experimentally enhance behavioral variation where too little exists in nature. The experimental approach may have the disadvantage of involving unnatural variants, but it has the advantage of revealing how differences among individuals, even in a single trait, can cause variation in reproductive fitness. Either way, a study of natural selection acting on behavior requires that the researcher be able to observe natural populations and obtain detailed information on each individual's survival, its ability to attract a mate, its fertility, and so forth. All of this information is essential to assess an animal's success in passing on its genes.



Three types of natural selection, showing the effects of each on the distribution of phenotypes within a population. The downward arrows point to those phenotypes against which selection acts. Stabilizing selection (left column) acts against phenotypes at both extremes of the distribution, favouring the multiplication of intermediate phenotypes. Directional selection (centre column) acts against only one extreme of phenotypes, causing a shift in distribution toward the other extreme. Diversifying selection (right column) acts against intermediate phenotypes, creating a split in distribution toward each extreme.

An investigation of why male titmice, or great tits (Parus major), woodland birds of Europe, sing multiple songs serves to illustrate how a behavioral function can be studied by exploiting naturally existing variation. Each great tit male has a repertoire of one to eight songs that he uses to advertise his presence on a territory. Investigators can acquire detailed information on the breeding biology of these birds because great tits are cavity nesters that readily accept man-made nest boxes. In one experiment on a wooded estate near Oxford, Eng., English zoologist John Krebs and his colleagues installed and regularly inspected nest boxes during the breeding season. The researchers recorded the singing behavior of each breeding male in order to determine repertoire size. They also recorded the egg-laying date, the clutch size (number of eggs), the brood size (number of young), and the fledgling weight for the nests of numerous males. It was possible to monitor the survival of each male's young to the time of its own breeding, because all the young were banded before they fledged and most fledglings returned to the same woods to breed themselves.

The researchers found that individual tits had different repertoire sizes. Males with larger repertoires had chicks that were heavier at fledging, and more of these chicks survived to breed than offspring of males with smaller repertoires. Thus male repertoire size and reproductive success were correlated. The underlying mechanism is that males with larger song repertoires were able to acquire superior territories—specifically, ones with better food. Previous studies had shown that size and survival of young tits depend on body weight at time of fledging: the bigger and heavier the fledgling, the greater its chances of survival to maturity. Thus, the function of a great tit male's singing multiple songs is to help him secure a top-quality breeding territory and mate. So why do all males not sing multiple songs? Perhaps songs are learned over time, so that only the oldest males can possess a large repertoire. Alternatively, perhaps there are costs (such as time away from foraging or increased vulnerability to predators) to singing multiple songs, and only the biggest, strongest males can sing many songs and still survive.

Direct comparisons of individuals of the same species exhibiting natural variation in behavior is a revealing way to study behavioral function. However, when appropriate natural variations do not exist, experimental manipulations can provide the needed variation in the behavior. The variant forms are then studied in the field to determine how well extreme forms of the behavior do in the face of natural selection. Using this method, American biologist Thomas Seeley investigated nest site choice in a species of Southeast Asian honeybee, Apis florea. Colonies build their nests of beeswax combs amid dense foliage, suspended from the branches of bushes and understory trees. Moreover, if a colony's nest loses its cover during the dry season when many trees shed their leaves, the colony will build its new nest in another leafy site. What is the function of this behavior of nesting in dense vegetation? Is it to prevent the nest from overheating under the strong tropical sun, or to conceal the nest from predators, or both?

To test the antipredator hypothesis, pairs of naturally occurring colonies were identified. Within each pair the vegetation around the nest of one colony, which served as the experimental unit, was removed, leaving only enough to provide shade but rendering it conspicuous to predators. The vegetation surrounding the nest of the second colony, which served as the control, was not removed. Measurements of nest site temperatures one day later revealed no significant differences between the two nests. Within one week, however, four of the seven experimental colonies had been discovered and destroyed by predators (probably monkeys and tree shrews) whereas none of the control nests had suffered any damage. Thus, it appears that A. florea colonies choose dense vegetation as nesting sites primarily to conceal their nests from predators.

Another example of a well-controlled field experiment on the function of behavior is Dutch-born British zoologist and ethologist Nikolaas Tinbergen's pioneering study of eggshell removal by black-headed gulls (Larus ridibundus). In a matter of hours after their eggs hatch, they pick up the empty eggshells, fly off, and drop them well away from the nest. Why should a gull engage in this behavior? One hypothesis was that the sharp edges of the shells might injure the chicks, a danger that is well known to poultry breeders. Another hypothesis was that the white insides of broken shells might attract predators, such as crows and herring gulls flying overhead, and so endanger the brood. To test the latter hypothesis, Tinbergen and his colleagues distributed single gull decoy eggs around the dunes where the black-headed gulls nest, and placed broken eggshells near some of the decoy eggs while leaving others isolated. The investigators found that the eggs near broken shells were preyed upon sooner than the isolated, less conspicuous eggs. Evidently, the removal of broken eggshells from the nest by gulls helps to maintain the camouflage of the brood, thereby reducing predation.

ETHOLOGY

Ethology is a branch of zoology concerned with the study of animal behavior. Ethologists take a comparative approach, studying behaviors ranging from kinship, cooperation, and parental investment, to conflict, sexual selection, and aggression across a variety of species. Today ethology as a disciplinary label has largely been replaced by behavioral ecology and evolutionary psychology. These rapidly growing fields tend to place greater emphasis on social relationships rather than on the individual animal; however, they retain ethology's tradition of fieldwork and its grounding in evolutionary theory.

The study of animal behavior touches upon the fact that people receive joy from nature and also typically see themselves in a special role as stewards of creation. Behavior is one aspect of the vast diversity of nature that enhances human enjoyment. People are fascinated with the many behaviors of animals, whether the communication "dance" of honeybees, or the hunting behavior of the big cats, or the altruistic behavior of a dolphin. In addition, humans generally see themselves with the responsibility to love and care for nature.

The study of animal behavior also helps people to understand more about themselves. From an evolutionary point of view, organisms of diverse lineages are related through the process of descent with modification. From a religious point of view, human also stand as "microcosms of nature". Thus, the understanding of animals helps to better understand ourselves.

Ethologists engage in hypothesis-driven experimental investigation, often in the field. This combination of lab work with field study reflects an important conceptual underpinning of the discipline: behavior is assumed to be adaptive; i.e., something that makes it better suited in its environment and consequently improves its chances of survival and reproductive success.

The egg-rolling behavior of the greylag goose is a widely cited example of a fixed-action pattern, one of the key concepts used by ethologists to explain animal behavior.

Ethology emerged as a discrete discipline in the 1920s, through the efforts of Konrad Lorenz, Karl von Frisch, and Niko Tinbergen, who were jointly awarded the 1973 Nobel Prize in Physiology or Medicine for their contributions to the study of behavior. They were in turn influenced by the foundational work of, among others, ornithologists Oskar Heinroth and Julian Huxley and the American myrmecologist (study of ants) William Morton Wheeler, who popularized the term ethology in a seminal 1902 paper.

Important Concepts

One of the key ideas of classical ethology is the concept of fixed action patterns (FAPs). FAPs are stereotyped behaviors that occur in a predictable, inflexible sequence in response to an identifiable stimulus from the environment.

For example, at the sight of a displaced egg near the nest, the greylag goose (Anser anser) will roll the egg back to the others with its beak. If the egg is removed, the animal continues to engage in egg-rolling behavior, pulling its head back as if an imaginary egg is still being maneuvered by the underside of its beak. It will also attempt to move other egg-shaped objects, such as a golf ball, doorknob, or even an egg too large to have been laid by the goose itself.

Kelp Gull chicks peck at a red spot on their mother's
beak to stimulate the regurgitating reflex, another example of a fixed action pattern.

Another important concept is filial imprinting, a form of learning that occurs in young animals, usually during a critical, formative period of their lives. During imprinting, a young animal learns to direct some of its social responses to a parent or sibling.

Despite its valuable contributions to the study of animal behavior, classical ethology also spawned problematic general theories that viewed even complex behaviors as genetically hardwired (i.e., innate or instinctive). Models of behavior have since been revised to account for more flexible decision-making processes.

Methodology

Tinbergen's four Questions for Ethologists

The practice of ethological investigation is rooted in hypothesis-driven experimentation. Lorenz's collaborator, Niko Tinbergen, argued that ethologists should consider the following categories when attempting to formulate a hypothesis that explains any instance of behavior:

- Function: How does the behavior impact the animal's chance of survival and reproduction?
- Mechanism: What are the stimuli that elicit the response? How has the response been modified by recent learning?
- Development: How does the behavior change with age? What early experiences are necessary for the behavior to be demonstrated?
- Evolutionary history: How does the behavior compare with similar behavior in related species? How might the behavior have arisen through the evolutionary development of the species, genus, or group?

The four questions are meant to be complementary, revealing various facets of the motives underlying a given behavior.

Using Fieldwork to Test Hypotheses

As an example of how an ethologist might approach a question about animal behavior, consider the study of hearing in an echolocating bat. A species of bat may use frequency chirps to probe the environment while in flight. A traditional neuroscientific study of the auditory system of the bat would involve anesthetizing it, performing a craniotomy to insert recording electrodes in its brain, and then recording neural responses to pure tone stimuli played from loudspeakers. In contrast, an ideal ethological study would attempt to replicate the natural conditions of the animal as closely as possible. It would involve recording from the animal's brain while it is awake, producing its natural calls while performing a behavior such as insect capture.

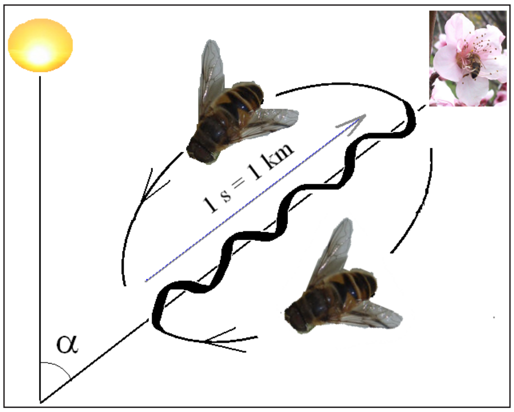
Key Principles and Concepts

Behaviors are Adaptive Responses to Natural Selection

Because ethology is understood as a branch of biology, ethologists have been particularly concerned with the evolution of behavior and the understanding of behavior in terms of the theory of natural selection. In one sense, the first modern ethologist was Charles Darwin, whose book The Expression of the Emotions in Man and Animals has influenced many ethologists. (Darwin's protégé George Romanes became one of the founders of comparative psychology, positing a similarity of cognitive processes and mechanisms between animals and humans).

Note, however, that this concept is necessarily speculative. Behaviors are not found as fossils and cannot be traced through the geological strata. And concrete evidence for the theory of modification by natural selection is limited to microevolution—that is, evolution at or below the level of species. The evidence that natural selection directs changes on the macroevolutionary level necessarily involves extrapolation from these evidences on the microevolutionary level. Thus, although scientists frequently allude to a particular behavior having evolved by natural selection in response to a particular environment, this involves speculation as opposed to concrete evidence.

Animals use Fixed Action Patterns in Communication



The honeybee's figure-eight dance is a fixed-action pattern that communicates information to other members of the group: the angle from the sun indicates the direction of a food source; the duration signifies its distance.

As mentioned above, a fixed action pattern (FAP) is an instinctive behavioral sequence produced by a neural network known as the innate releasing mechanism in response to an external sensory stimulus called the sign stimulus or releaser. Once identified by ethologists, FAPs can be compared across species, allowing them to contrast similarities and differences in behavior with similarities and differences in form (morphology).

An example of how FAPs work in animal communication is the classic investigation by Austrian ethologist Karl von Frisch of the so-called "dance language" underlying bee communication. The dance is a mechanism for successful foragers to recruit members of the colony to new sources of nectar or pollen.

Imprinting is a type of Learning Behavior

Imprinting describes any kind of phase-sensitive learning (i.e., learning that occurs at a particular age or life stage) during which an animal learns the characteristics of some stimulus, which is therefore said to be "imprinted" onto the subject.

The best known form of imprinting is filial imprinting, in which a young animal learns the characteristics of its parent. Lorenz observed that the young of waterfowl such as geese spontaneously followed their mothers from almost the first day after they were hatched. Lorenz demonstrated how incubator-hatched geese would imprint on the first suitable moving stimulus they saw within what he called a critical period of about 36 hours shortly after hatching.

Sexual imprinting, which occurs at a later stage of development, is the process by which a young animal learns the characteristics of a desirable mate. For example, male zebra finches appear to prefer mates with the appearance of the female bird that rears them, rather than mates of their own type. Reverse sexual imprinting has also observed: when two individuals live in close domestic proximity during their early years, both are desensitized to later sexual attraction. This phenomenon, known as the Westermarck effect, has probably evolved to suppress inbreeding.

Relation to Comparative Psychology

In order to summarize the defining features of ethology, it might be helpful to compare classical ethology to early work in comparative psychology, an alternative approach to the study of animal behavior that also emerged in the early 20th century. The rivalry between these two fields stemmed in part from disciplinary politics: ethology, which had developed in Europe, failed to gain a strong foothold in North America, where comparative psychology was dominant.

Broadly speaking, comparative psychology studies general processes, while ethology focuses on adaptive specialization. The two approaches are complementary rather than competitive, but they do lead to different perspectives and sometimes to conflicts of opinion about matters of substance:

- Comparative psychology construes its study as a branch of psychology rather than as an outgrowth of biology. Thus, where comparative psychology sees the study of animal behavior in the context of what is known about human psychology, ethology situates animal behavior in the context of what is known about animal anatomy, physiology, neurobiology, and phylogenetic history.
- Comparative psychologists are interested more in similarities than differences in behavior; they are seeking general laws of behavior, especially relating to development, which can

then be applied to all animal species, including humans. Hence, early comparative psychologists concentrated on gaining extensive knowledge of the behavior of a few species, while ethologists were more interested in gaining knowledge of behavior in a wide range of species in order to be able to make principled comparisons across taxonomic groups.

- Comparative psychologists focused primarily on lab experiments involving a handful of species, mainly rats and pigeons, whereas ethologists concentrated on behavior in natural situations.

Since the 1970s, however, animal behavior has become an integrated discipline, with comparative psychologists and ethological animal behaviorists working on similar problems and publishing side by side in the same journals.

Cognitive Ethology

Cognitive ethology is the comparative, evolutionary, and ecological study of nonhuman animal (hereafter animal) minds including thought processes, beliefs, rationality, information-processing, and consciousness. It is a rapidly growing interdisciplinary field of science that is attracting much attention from researchers in numerous and diverse disciplines including those interested in animal welfare. Cognitive ethology can trace its beginnings to the writings of Charles Darwin, an anecdotal cognitivist, and some of his contemporaries and disciples. Their approach incorporated appeals to evolutionary theory, interests in mental continuity, concerns with individual and intraspecific variation, interests in the worlds of the animals themselves, close associations with natural history, and attempts to learn more about the behavior of animals in conditions that are as close as possible to the natural environment where selection has occurred. They also relied on anecdote and anthropomorphism to inform and to motivate more rigorous study. In addition, cognitive ethologists are frequently concerned with the diversity of solutions that living organisms have found for common problems. They also emphasize broad taxonomic comparisons and do not focus on a few select representatives of limited taxa. Many people inform their views of cognitive ethology by appealing to the same studies over and over again (usually those done on nonhuman primates), and ignore the fact that there are many other animals who also show interesting patterns of behavior that lend themselves to cognitive studies.

Comparative cognitive ethology is an important extension of classical ethology because it explicitly licenses hypotheses about the internal states of animals in the tradition of classical ethologists such as Nobel laureates Niko Tinbergen and Konrad Lorenz. However, although ethologists such as Lorenz and Tinbergen used terms such as “intention movements,” they used them quite differently from how they are used in the philosophical literature. “Intention movements” refers to preparatory movements that might communicate what action individuals are likely to do next, and not necessarily to their beliefs and desires, although one might suppose that the individuals did indeed want to fly and believed that if they moved their wings in a certain way they would fly. This distinction is important to mark because the use of such terms does not necessarily add a cognitive dimension to classical ethological notions, although it could.

In his early work Tinbergen identified four overlapping areas with which ethological investigations should be concerned - namely, evolution (phylogeny), adaptation (function), causation, and development (ontogeny), and his framework also is useful for those interested in animal cognition. The methods for answering questions in each of these areas vary, but all begin with careful observation and description of the behavior patterns that are performed by the animals under study. The information afforded by these initial observations allows a researcher to exploit the animal's normal behavioral repertoire to answer questions about the evolution, function, causation, and development of the behavior patterns that are performed in various contexts.

Donald R. Griffin and Modern Cognitive Ethology

The modern era of cognitive ethology and its concentration on the evolution and evolutionary continuity of animal cognition is usually thought to have begun with the appearance of Griffin's major concern was to learn more about animal consciousness, and then, as now, Griffin wanted to come to terms with the difficult question of "what is it like to be a particular animal?" While Griffin was mainly concerned with the phenomenology of animal consciousness, it is only one of many important and interesting aspects of animal cognition. Indeed, because of its broad agenda and wide-ranging goals, many view cognitive ethology as being a genuine contributor to cognitive science in general. For those who are anthropocentrically minded, it should be noted that studies of animal cognition can also inform, for example, inquiries into human autism.

Methods of Study

Ethologists interested in animal minds favor research in conditions that are as close as possible to the natural environments in which natural selection occurred or is occurring. When needed, research on captive animals also can inform the comparative study of animal cognition, but cognitive ethologists are resistant to suggestions that (i) field studies of animal cognition are impossible (difficult, yes, but certainly not impossible), (ii) they should give up in their attempts to study animal minds under natural conditions, and (iii) studies of learning and memory are all that are needed to learn about animal cognition. Naturalizing the study of animal cognition and animal minds in the laboratory and in the field should lead to a greater appreciation for the cognitive skills of animals living under natural conditions. Animal minds can be studied rigorously using methods of natural science and will not ultimately have to be reduced or eliminated.

The tractability of cognitive questions involves application of a diverse set of comparative methods in order to draw inferences about cognitive states and capacities. Cognitive research may include staged social encounters, playback of recorded vocalizations, the presentation of stimuli in different modalities, observation of predator-prey interactions, observation of foraging behavior, neurobiological techniques, and studies of social and other sorts of learning. Computer analyses also are useful for those who want to learn what kind of information must be represented in an adequate computational model.

There are no large differences between methods used to study animal cognition and those used to study other aspects of animal behavior. Differences lie not so much in what is done and how it is done, but rather how data are explained. Allen and Bekoff argue that the main distinction between cognitive ethology and classical ethology lies not in the types of data collected, but in the understanding of the conceptual resources that are appropriate for explaining those data.

Perhaps one area that will contribute more to the study of animal minds than it does to other areas of comparative ethology is neurobiology and behavior. Those interested in the cellular or neural bases of behavior and animal cognition and consciousness may use techniques such as positron emission tomography (PET) that are also employed in other endeavors. In general, studies using brain imaging have provided extremely valuable data for humans engaged in various sorts of activities, whereas the use of these and other imaging techniques on animals has not been pursued rigorously for individuals engaged in activities other than learning or memory in captivity. Furthermore, while neurobiological studies are extremely important to those interested in animal cognition, there remains an explanatory gap between neurophysiological processes and behavior.

Behavioral studies usually start with the observation, description, and categorization of behavior patterns that animals perform. The result of this process is the development of an ethogram, or behavioral catalogue, of these actions. Ethograms present information about an action's form or morphology and its code name. Descriptions can be based on visual information (what an action looks like), auditory characteristics (sonograms, which are pictures of sounds), or chemical constituents (output of chromatographic analyses of glandular deposits or urine or feces, for example). It is essential that great care be given to the development of an ethogram, for it is an inventory that others should be able to replicate without error. Permanent records of observations allow others to cross-check their observations and descriptions against original records. The number of actions and the breadth of categories that are identified in a behavioral study depends on the questions at hand, but generally it is better to split rather than to lump actions in initial stages, and lump when questions of interest have been carefully laid out.

In studies of behavior it is important to know as much as possible about the sensory world of the animals being studied. Experiments should not be designed that ask animals to do things that they cannot do because they are insensitive to the experimental stimuli or unmotivated by the stimuli. The relationships between normal ecological conditions and differences between the capabilities of animals to acquire, process, and respond to information is the domain of a growing field called "sensory ecology". A good ethologist asks "what is it like to be the animal under study" and develops an awareness of the senses that the animals use singly or in combination with one another. It is highly unlikely that individuals of any other species sense the world the same way we do, and it is unlikely that even members of the same species sense the world identically all of the time, and it is important to remain alert to the possibility of individual variation.

Stimulus Control and Impoverished Environments

While carefully conducted experiments in the laboratory and in the field often are able to control for the influence of variables that might affect the expression of behavioral responses, it is usually the case that there is a possibility that the influence of some variables cannot be accounted for. Field studies may be more prone to a lack of control because the conditions in which they are conducted are inherently more complex and less controllable.

An illustration of the concern for undercontrol is found in the excellent cognitive ethological field research of Cheney and Seyfarth on the behavior (e.g. communication and deception) and minds of vervet monkeys. In their studies of the attribution of knowledge by vervets to each other, Cheney and Seyfarth played back vocalizations of familiar individuals to other group members. These researchers were, however, concerned about their inability to eliminate "all visual or auditory evidence of the familiar animal's physical presence". Actually, this inability may not be problematic if the goal is to understand "how monkeys see the world." Typically, in most social situations the physical presence of individuals and access to stimuli from different modalities may be important to consider. Vervets, other nonhumans, and humans may attribute mental states using a combination of variables that are difficult to separate experimentally. Negative or inconclusive experimental results concerning vervets' or other animals' attribution of mind to other individuals may stem from impoverishing their normal environment by removing information that they normally use in attribution. Researchers might also be looking for complex mechanisms involved in the attribution of minds to others and might overlook relatively simple means for doing so. Just because an animal does not do something does not mean that it cannot do it (assuming that what we are asking the animal to do is reasonable, that is within their sensory and motor capacities). Thus, insistence on absolute experimental control that involves placing and maintaining individuals in captivity and getting them accustomed to test situations that may be unnatural may greatly influence results. And these sorts of claims, if incorrect, can wreak havoc on discussions of the evolutionary continuity of animal cognitive skills. Cheney and Seyfarth recognize some of these problems in their discussion of the difficulties of distinguishing between alternative explanations maintaining either that a monkey recognizes another's knowledge or a monkey monitors another's behavior and adjusts his own behavior to the other.

Although control may be more of a problem in field research than in laboratory work, it certainly is not the case that cognitives ethologist should abandonfield work. Cognitive ethologists and comparative or cognitive psychologists can learn important lessons from one another. On the one hand, cognitive psychologists who specialize in highly controlled experimental procedures can teach something about the importance of control to those cognitive ethologists who do not peform such research. On the other hand, those who study humans and other animals under highly controlled and often contrived and impoverished laboratory conditions can broaden their horizons and learn more about the importance of more naturalistic methods: they can be challenged to develop procedures that take into account possible interactions among stimuli within and between modalities in more naturalistic settings. For example, among those who are interested in important and "hot" questions about animal minds that are typically studied in controlled captive conditions (e.g. inquiries into the possibility of self-recognition) there is a growing awareness that more naturalistic approaches are needed. The use of single tests relying primarily on one modality, for example vision, for comparative studies represents too narrow an approach. Ultimately, all types of studies should be used to exploit the behavioral flexibility or versatility of the animals under study, a criterion for attributions of complex information processing or consciousness.

Some Criticisms of Cognitive Ethology

A balanced view of cognitive ethology requires consideration of critics' points of view. Criticisms of cognitive ethology come in many flavors but usually center on: (i) the notion that animals do not have minds; (ii) the idea that (many, most, all) animals are not conscious, or that so little of their behavior is conscious (no matter how broadly defined) that it is a waste of time to study animal consciousness; (iii) the inaccessibility to rigorous study of animal mental states (they are private) and whatever (if anything) might be contained in them; (iv) the assumption that animals do not have any beliefs because the content of their beliefs are not similar to the content of human beliefs; (v) the rigor with which data are collected; (vi) the lack of large empirical data bases; (vii) the nature of the (merely instrumental) “soft,” nonparsimonious, yet complex explanations that rely heavily on theoretical constructs (e.g. minds, mental states) that are offered for the behavioral phenotype under study (they are too anthropomorphic, too folk psychological, or too “as if-fy” - animals act “as if” they have beliefs or desires or other thoughts about something; and (viii) the heavy reliance on behavior for motivating cognitive explanations (but this is not specific only to cognitive inquiries).

While most criticism comes from those who ignore the successes of cognitive ethology, those who dismiss it in principle because of strong and radical behavioristic leanings, or those who do not understand basic philosophical principles that inform cognitive ethology, it should be pointed out that more mechanistic approaches to the study of animal cognition are not without their own faults. For example, comparative psychologists often disregard how relevant a study is to the natural existence of the animals under study and pay too much attention to the logical structure of the experiments being performed without much regard for more naturalistic approaches. Noncognitive mechanistic “rules of thumb” also can be very cumbersome, nonparsimonious, and often appeal to hard-to-imagine past coincidences. Furthermore, it is not clear if the differences between noncognitive rules of thumb and cognitive explanations are differences in degree rather than differences in kind. Both noncognitive and cognitive explanations can be “just-so” stories (just like many evolutionary explanations) that rely on hypothetical constructs, and neither applies in all situations.

Neuroethology

Neuroethology refers to the study of the neural basis of natural behavior in animals. It attempts to understand how sensory organs and central structures process behaviorally relevant stimuli, and how this information is integrated by the central nervous system to produce the behavioral output observed under natural conditions. Many of the concepts and techniques of neuroethology are derived from other biological disciplines, including ethology, neurophysiology, neuroanatomy, neuroendocrinology, and biological cybernetics. A characteristic overall goal of neuroethology is to understand, from mechanistic and evolutionary points of view, both specialization and diversity of neural control among different species.

Neuroethology is a multidisciplinary area of study that emerged as an independent scientific discipline in the 1970s and 1980s. This rather late development contrasts with the history of its two foundation disciplines, neurobiology and ethology. The beginnings of modern neurobiology can be dated back to the end of the nineteenth century after the histological studies of Santiago Ramón y Cajal had provided experimental evidence in favor of the cell theory as an adequate description of the organization of the nervous system. Ethology was formally established between the 1930s and 1950s, particularly through the work of Konrad Lorenz and Niko Tinbergen.

One reason for the late development of neuroethology lies in the lack of proper methodology and suitable model systems. Traditionally, neurobiologists have worked on anesthetized animals, or isolated parts of nervous tissue, or even single cells. The species is typically chosen based on technical considerations, such as the ease by which a favorable preparation can be obtained. For example, the classical investigations in the late 1940s and early 1950s of Alan Lloyd Hodgkin and Andrew Fielding Huxley of the physicochemical factors that define the resting potential of neurons, their excitation, and the generation and propagation of the action potential, were possible only by using preparations of particularly large, and readily accessible, axons, such as the squid giant axon.

By contrast, ethologists employ a whole-animal approach. Often, they study the behavior of an animal in its natural habitat, avoiding disturbance by the experimenter as much as possible. If investigations in the laboratory are performed, the animal is kept under conditions mimicking those in the natural habitat as closely as possible. Many of the behaviors studied are rather complex, often occurring in the context of social interactions between conspecifics.

Obviously, combination of these two rather diametric approaches has been difficult, and continues to be challenging. For example, to explore the involvement of certain, anatomically defined brain areas in the control of specific behaviors it was reasonable to stimulate neurons of these areas electrically via electrodes implanted in the brain of awake, freely moving animals. This became possible after Walter Rudolf Hess developed in the late 1920s the focal brain stimulation technique to examine how regions within the diencephalon control vegetative functions in cats. First successful attempts to employ such an approach in an ethological context were made by Franz Huber and Erich von Holst in the time period between the mid 1950s and early 1960s. Huber had learned the focal brain stimulation technique from Hess, and he applied this approach to the brains of crickets. By stimulation of brain structures in the protocerebrum, he succeeded in eliciting and inhibiting complex behaviors, including calling, courtship, and aggressive songs, and associated motor patterns. Similarly, by stimulation of discrete areas in the hypothalamus of alert chicken Erich von Holst was able to evoke specific, and sometime even quite complex, behavioral patterns, and to study the interactive structure of behavioral motivations.

Besides ethology and neurophysiology, other scientific disciplines eased the birth of neuroethology. In the 1950s, major advances were made in the development of methods to trace neural connections using silver staining of degenerating axons. In the 1970s, these methods were replaced by more powerful techniques based on anterograde and retrograde transport of tracers, enabling neuroethologists to study pathways in the central nervous system involved in neural control of specific behavioral patterns. In the 1960s, the field of chemical neuroanatomy was established with the introduction of the Falck-Hillarp fluorescence method for identification of monoamine neurons. This step was followed in the 1970s and 1980s by novel immunohistochemical approaches based on indirect labeling techniques. These techniques offered, among others, the exciting opportunity to chemically characterize neurons involved in sensory processing of behaviorally relevant information or in the motor control of behavioral output. Other milestones in the historical development of neuroethology included in the 1960s the advent of techniques that allowed investigators to correlate morphological and physiological data by combining intracellular recording and tracer injection techniques.

These breakthroughs in neuroanatomy and neurophysiology were paralleled by the emergence of biological cybernetics. Starting in the 1950s, Bernhard Hassenstein and Werner Reichardt pioneered the study of information processing and modeling by using the visual system of the beetle Chlorophanus, and later particularly the housefly Musca, as model systems. Based on experimental behavioral data, Hassenstein, Reichardt and others developed computational models that produced the observed behavioral output after sensory stimulation. Non-trivial predictions inferred from these models could be tested in experiments incorporating behavioral, neuroanatomical, neurophysiological, and computational approaches. A milestone of this work was the development of the Reichardt correlator, a autocorrelation scheme that made predictions about the algorithm employed by visual systems to detect motion. This and other models had a major influence on computational studies in neuroethology, with applications reaching as far as the design of integrated circuits modeled after neural networks.

An important step toward the establishment of neuroethology as an independent discipline was the focus on rather simple behaviors. However, especially in the early stages of neuroethology, these behaviors were often part of vegetative functions, instead of being displayed in a social context, so that they were largely ignored by ethologists. For example, neuroethologists have intensively studied rhythmic movements of internal organs such as the crustacean foregut and heart. Although few ethologists would attend to such motor activities, their study has provided valuable insights into a number of important neurobiological phenomena, such as central pattern generators and neuromodulation.

As a rough guide, the major questions of neuroethology focus on the neural basis of; (i) identification of a behaviorally relevant stimulus; (ii) localization of such a stimulus in space; (iii) motivation underlying a specific behavior; (iv) generation of a behavioral pattern; and (v) modulation of a neural circuit mediating a stimulus-response. Such modulations are defined, among other factors, by the endocrine status of the animal and include the formation of memory. In this context, specific questions are addressed, including those regarding the mode of neural information processing.

Choice of Suitable Model Systems

As in many other biological disciplines, neuroethological research crucially depends on the choice of suitable model systems. Ideally, the behavior under scrutiny should be simple, robust, readily accessible, and ethologically relevant. Thus, such behaviors are exhibited not only under natural conditions, but they can also be evoked without much difficulty, and even on repeated occasions, upon presentation of an adequate stimulus under standardized laboratory conditions. Furthermore, these behavioral patterns are clearly defined so that quantitative analysis is possible. The animal displaying such behaviors should be inexpensive and suitable for maintenance and breeding in the laboratory. Furthermore, the neural network underlying the behavior should be relatively simple in the sense that the nervous system consists of a rather small number of neurons, representing a minimal number of different classes of nerve cells.

Because of the difficulty of obtaining neurophysiological recordings from moving animals, often the only way to monitor the neural activity associated with the perception of sensory stimuli relevant for eliciting a given behavior, or with the generation of the corresponding motor activity, is to employ reduced preparations. Such preparations can be obtained by removing muscles or, most commonly, by immobilizing the animal through blocking synaptic transmission at the neuromuscular junction. Immobilized awake animals can still perceive and process sensory stimuli, and may still be able to generate the neural activity associated with the production of the motor action. These fictive behaviors approximate the real behavior and can be measured with relative ease. For example, tadpoles of the clawed-toad (Xenopus laevis) produce a well-characterized behavior called escape swimming upon sensory stimulation during the first day after hatching. The neural activity of the circuitry in the spinal cord that controls this behavior can be studied in animals that are immobilized by blocking synaptic transmission at the neuromuscular junction with alpha-bungarotoxin (a constituent protein of the venom of the Southeast Asian Krait, Bungarus multicinctus). The study of such fictive swimming in tadpoles has enabled investigators to identify universal mechanisms that control rhythmic motor patterns in vertebrates.

Classical Model Systems in Neuroethology

In contrast to biomedically oriented disciplines, which typically focus on a few model organisms, neuroethology is distinguished by the diversity of taxa studied. The wealth of data obtained through investigations that ask similar questions but are conducted in different species offers the opportunity to examine evolutionary aspects by employing a comparative approach. For example, in gastropod molluscs, similarities and differences in feeding behavior among different species have been linked to anatomical, physiological, and pharmacological properties of the underlying neural network. Neuroethological investigations in African mormyrid fishes have examined the role of sexual signal evolution in relation to morphological and ecological divergence during species radiation. Comparative studies in weakly electric fishes have provided the basis for a phylogenetic comparison of neural systems specialized for time coding.

The following brief description of four classical model systems aims at exemplifying neuroethological research.

- Recognition of prey and predators in toads: This was one of the first major neuroethological research endeavors, led by Jörg-Peter Ewert in the 1960s. It was aimed at the question whether there are neurons that respond selectively to specific features of prey- or predator-like stimuli (so-called feature detectors). By combination of behavioral and physiological experiments, neurons were found in the thalamic-pretectum and the optic tectum, each of which receives visual input from retinal ganglion cells. A specific subpopulation of neurons in the thalamic-pretectum responds best to predator-like features, and electrical stimulation of this area activates escape behavior. On the other hand, a specific subpopulation of neurons in the optic tectum responds best to prey-like features, and stimulation of the brain region evokes prey-catching behavior in toads. Applying a sophisticated method, records of action potentials from freely moving toads showed that the efficiency in prey detection and predator detection are ensured by pretecto-tectal inhibitory interactions. After lesioning pretectal connections to the optic tectum, both prey-selective neurons (recorded by a microelectrode) and prey-catching behavior were disinhibited. After such treatment, these neurons can be activated by any moving object, including predator-like stimuli.

- The neural basis of acoustic communication in crickets: In crickets, communication is largely carried by acoustic signals that are produced by males and transmitted to females or other males. Calling songs, for example, are generated to attract sexually receptive females. A female cricket that is in the state of copulatory readiness responds to these songs by flying or walking toward the source of sound, until she reaches the male (positive phonotaxis). Behavioral experiments have shown that the phonotactic response of female crickets is best elicited by a sound of the carrier frequency and the syllable rate matching those of natural songs produced by the male. This behavioral preference to certain sound parameters is reflected by the tuning to the carrier frequency of the tympanal membrane of the cricket's ear, and an optimal response of certain auditory interneurons to syllable repetition rates in the range that best elicits phonotaxis in females in behavioral tests. These neurons evidently function as recognition neurons.

- The jamming avoidance response of the weakly electric fish of the genus Eigenmannia. A central theme of neuroethology is based on the question of how sensory information is integrated with motor programs to produce a specific, ethologically relevant behavior in response to an adequate stimulus. The first behavior for which a comprehensive answer to this question could be provided was the jamming avoidance response of the weakly electric fish Eigenmannia sp. This behavior consists of shifting the frequency of the fish's electric-organ discharge away from the neighbor's frequency to avoid 'jamming', which would impair the fish's ability to electrolocate objects in its vicinity. Using this model system, it has been possible to identify the entire neural chain underlying this behavior — from the sensory receptors to the effector organ and including the major behavioral and neural rules that govern the sensory processing and the generation of the behavioral output. An important discovery made in the course of the investigations was that different physical parameters of the external electric stimulus triggering the jamming avoidance response are, at lower levels of central processing, analyzed separately (parallel processing), but converge at higher brain levels.

- Neuromodulation of the stomatogastric ganglion *of decapod crustaceans*. Neural networks are rarely static. Instead, they often exhibit the potential for neural plasticity. This phenomenon forms the basis for behavioral plasticity. Endogenous control of plastic changes in behavior is evident in cases in which stimuli arising from the environment are held constant. The mechanisms that mediate such changes have been studied in great detail in the stomatogastric ganglion of decapod crustaceans. Using this model system, it has been shown that the mode of function of the ganglion is determined by the actual modulatory environment — the anatomical network provides only a physical backbone upon which neuromodulators, particularly neuropeptides and monoamines, can operate. This makes it possible that a single neural network can produce multiple variations in behavioral output under different conditions.

Approaches to Animal Behavior

CHAPTER 2

A few of the different approaches to animal behavior are adaptation, animal cognition and mobbing. Some of the types of adaptation are physiological, structural and behavioral. This chapter closely examines these key concepts related to these approaches of animal behavior to provide an extensive understanding of the subject.

Animal behavior theory is all about modeling adaptive behavior of animals and seeing whether they have a relationship with human behavior. The theory explores the mechanisms and evolution of animal behavior, including neural, hormonal, and genetic substrates of behavior; foraging; anti-predator defenses; mating systems and sexual selection; social behavior; communication; parental care; kin selection and recognition; and territoriality in relations to human conflict patterns.

Factors that Guides Animal Theory

1. Neural, Endocrine, and Genetic Mechanisms: Causes that explain how a behavior is elicited and coordinated. What are the anatomical or physiological mechanisms that underlie the behavior? The behavior is present because the nervous system makes it happen. It includes a search for the impact of genetic components, physiological mechanisms, environmental conditions needed, and hormones on behavior.
2. Ontogeny and Development: How does the behavior develop and change during the lifespan of a single individual? The behavior is present because the individual developed an ability to do it this way.
3. Survival Value: Explanations are phrased as ultimate causes that explain why a behavior has evolved. Selection ought to favor individuals with behaviors that help it increase its reproductive success. The behavior is present because the individual inherited them from parents who were historically successful with this behavior. This includes a search for functional significance or adaptiveness of behavior.
4. Phylogeny, Evolution: What were the macro evolutionary patterns of changes that lead to the behavior today? Phylogeny is the study of evolutionary relatedness among groups of organisms as it treats a species as a group of lineage-connected individuals over time. It attempts to historically characterize the branching processes in which breeding populations have changed over time. The ethologist's view holds that behavioral characteristics, which receive at least a partial genetic contribution, and can be viewed in a phylogenetic perspective like any other morphological trait. The behavior is present because the individual is an offspring from ancestors that had the behavior.

Guiding Modeling Adaptive Behavior

It is a daunting (or impossible) task to study behavior by simultaneously considering all significant factors and interactions that may impact it. An alternative method attempts to reduce the associated complexities by wrapping ones expectations into a set of mathematical abstractions based on a reduced number of significant variables. Resulting quantitative predictions are necessarily incomplete but are often less ambiguous and easier to test. The goal is to model an animal's rational decisions of what action to take, given some information about the world. The player then faces consequences for the decision as a function of the action, the actions of others (if applicable), and the state of the surrounding environment. The player is expected to be rational by maximizing the expected utility.

1. Optimality Model for Animal Adaptive Behavior: Optimality models quantitatively predict the consequences for a particular animal to behave in a certain way when pitted against the environment. It assumes that animals should behave so as to maximize their fitness. Optimality models consider separate, dependent, fitness benefits (B) and fitness costs (C) over a given range of values in a decision variable (i.e., the variable of interest). The solution to an optimality model attempts to find the point where the net benefits (i.e., B-C) are maximized. Individual solutions consider the consequences for a focal animal regardless of what strategies other individuals are relying on. Optimality models use calculus and logic to solve for a minimum or a maximum in a specific function f(x).

2. Predator-prey Population Cycles for Animal Adaptive Behavior: In order to study predation and population oscillations, Huffaker used mite species, one being the predator and the other being the prey. By modifying the spatial structure of the habitat, he could manipulate the population dynamics and allow the overall survival rate for both species to increase. He did this by altering the distance between the prey and oranges (their food), establishing barriers to predator movement, and creating corridors for the prey to disperse. These changes increased habitat patches and in turn provided more areas for the prey to seek temporary protection. When the prey would go extinct locally at one habitat patch, they were able to reestablish by migrating to new patches before being attacked by predators. This habitat spatial structure of patches allowed for coexistence between the predator and prey species and promoted a stable population oscillation model.

3. Optimal Foraging Theory for Animal Adaptive Behavior: OFT examines the choice of food items. Such prey models (even though the prey doesn't necessarily have to be another animal) look at decisions of basic diet selection. The animal searches for food, and finds potential prey items one at a time. It has to decided whether it should stop searching and eat the food it has found, or whether to ignore the food and keep searching. We assume that the animal is trying to maximize its currency (i.e., rate of energy intake measured in calories) in a particular time period. Each type of food takes a different amount of time to handle it during consumption. For instance, Northwestern Crows search along the water line during low tide for large molluscs called whelks. When it finds one, it flies upward and drops it on the rocks to break it open. Smaller whelks are harder to break, and need to be dropped from a greater hight, so they may be ignored. Also the content of certain kinds of nuts is more difficult to access than that of others.

4. Marginal value theorem for Animal Adaptive Behavior: The MVT considers an optimally foraging creature that exploits patchy resources as it must decide when to move on to the next patch. As it attempts to optimize a cost/benefit ratio individual will stay longer as the distance between patches increases or when the environment as a whole is less profitable.
5. Deal Free Distribution for Animal Adaptive Behavior: An ideal free distribution describes the way in which animals distribute themselves among several patches of resources. The theory states that individual animals will aggregate in various patches proportionately to the amount of resources available in each. So for example, if patch A contains twice as much food as patch B, there will be twice as many individuals foraging in patch A as in patch B.

ADAPTATION

All living beings need to adapt to their environment to survive. These environments are as wide ranging as life itself, whether underwater, in a desert or even in the body of another living being. Helping to better understand these types of adaptations, we can place them all in three major categories:

1. Physiological
2. Structural
3. Behavioral

The adaptation of animals to their environment is a series of varied biological processes with varying purposes, but the general purpose is the continued survival of the species. This is key to the difference between an animal's adaptation and ability. Many animals are able to engage in certain behaviors which have no discernible function and may not be a part of adaptation.

As stated above, behavioral changes are not the only processes in which animals take par as a form of adaptation. It is neither solely behavior nor physical characteristics which allow animals to adapt to their environments. It is defined as:

> Any change in the structure or functioning of successive generations of a population that makes it better suited to its environment.

This means it is not just any physical trait or behavior. It has a purpose and that purpose is to survive.

Types of Adaptation in Animals

Some animals are much better able to adapt to their environment than others, but no species has survived intact. This is because the evolution of life on earth is a process. More precisely, it is a series of processes. Animals will adapt and change until they they barely resemble their forebears. The first bird had to sprout wings, the first mammal had lungs, etc. There are limits to the ability of science to trace back any organism, but it is believed that some species such as jellyfish have been able to last millions of years. However, the likelihood of any animal this old being exactly the same is very small.

It is likely that all life on earth originated in a single cell organism. This means all life is paradoxical. No animal alive today existed at the beginning of life on the planet. Yet all life that exists today existed in this single cell. The different forms this life takes is due to adaptation.

Although all animals are intrinsically adaptable, much of the specific adaptations happen for indeterminable reasons. Certain characteristics or behavioral traits have happened due to random mutations the genome. This doesn't mean that all failure of adaptation is due to genetics. Events such as climate change or natural catastrophes have resulted in the complete disappearance of many species on this planet.

Types of Adaptation

Physiological Adaptations

These types of adaptations are related to changes in the metabolism of different organisms. Some organs in an animal body function differently when certain changes occur in the environment. The two most well-known physiological adaptations are hibernation and estivation. These are two different types of inactivity where the metabolic rate slows down so much that the animal can survive without eating or drinking anything.

In both cases, temperature is usually a factor. While we often think of bears hibernating for the winter, it is not only when the temperature is low that these processes occur. When the temperature is below 0 °C or is above 40 °C and there is a relatively low humidity, certain animals can lower their basal metabolic rate for serious amounts of time.

Structural Adaptations

The external structures of animals can also help them to better adapt to their environment. Some of the most obvious examples to us might be an aquatic animal developing fins to swim or a mammal growing thicker fur to survive freezing climates. Some of the most attractive adaptations in nature occur for reasons of crypsis (e.g. camouflage) and mimicry.

Cryptic animals are those which camouflage perfectly with their environment and are almost impossible to detect. Certain reptiles and insects such as chameleons and stick insects may spring to mind as being particularly good at this type of animal adaptation. Another reason for this and many other adaptations is for evasion of predators. For example, the monarch butterfly is poisonous which leads to not having many predators. The viceroy has a very similar physical appearance, but is not poisonous. It is not often predated upon either.

Behavioral Adaptations

These adaptations lead the animals to develop certain behavioral characteristics to survive the individual or the species. Fleeing from a predator, hiding during sleep, seeking refuge from climate issues or moving to find different food sources are all behavioral adaptations. The two most characteristic forms of behavioral adaptations are probably migration and courtship. Migration allows the animals to find better resources or evade threat. Courtship is a set of behavioral patterns with the desired result of finding a mate and reproducing.

Examples of Adaptations in Animals

- Examples of Land Adaptation

Shells of certain animal embryos such as reptiles and birds are examples of adaptation to a terrestrial environment. The hard shell prevents the embryo from dying by providing physical protection outside of the body. Fur in mammals is another important adaptation as it allows them to protect their vital organs and maintain function in cold climates.

- Examples of Aquatic Adaptation

Fins and flippers on various types of fish and aquatic mammals have evolved as adaptations to better survive in water. Likewise, the interdigital membranes of amphibians and birds (the webbing between their ‘toes’) have the same adaptive purpose.

- Examples of Light Based Adaptation

Many nocturnal animals have developed eyeballs which allow them to see at night. The lack of light means they need this ability to avoid predators and find their own food sources. However, some animals have gone the other way. The golden mole has eyes, but they are completely covered as they spend all of their time underground and no longer have any use for them.

- Examples of Temperature Adaptation

The accumulation and maintenance of fat under the skin is a type of adaptation in cold climates According to Allen's rule, animals that live in cold areas have shorter extremities, ears, tails and snouts than animals that live in warmer areas. This is so then can preserve heat. In warmer climates, animals such as the fennec fox have larger ears for the opposite reason. These large appendages are used to cool down the body.

Limits to Animal Adaptation

Animal adaptations are various and extensive. They allow species to survive, but eventually something will come along to replace them. This is due to the limits of their adaptive abilities. However, many adaptations are not being allowed to happen naturally as humans are exerting such an influence in the world that they bypass natural selection.

Numbers of a species are key in their success of adaptation as does a range of genetic variation. Since humans have killed so many animals to near extinction, many species struggle to return their species to the numbers they once enjoyed. Also, the hazardous effects of climate change are making it difficult for animals to adapt in time to the rapidly changing environment.

ANIMAL COGNITION

Animal cognition describes the mental capacities of non-human animals and the study of those capacities. The field developed from comparative psychology, including the study of animal conditioning and learning. It has also been strongly influenced by research in ethology, behavioral ecology, and evolutionary psychology, and hence the alternative name cognitive ethology is sometimes used. Many behaviors associated with the term animal intelligence are also subsumed within animal cognition.

A crab-eating macaque using a stone tool to crack open a nut.

Researchers have examined animal cognition in mammals (especially primates, cetaceans, elephants, dogs, cats, pigs, horses, cattle, raccoons and rodents), birds (including parrots, fowl, corvids and pigeons), reptiles (lizards and snakes), fish and invertebrates (including cephalopods, spiders and insects).

Morgan's Canon

Coined by 19th-century British psychologist C. Lloyd Morgan, Morgan's Canon remains a fundamental precept of comparative (animal) psychology. In its developed form, it states that:

> In no case is an animal activity to be interpreted in terms of higher psychological processes if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development.

In other words, Morgan believed that anthropomorphic approaches to animal behavior were fallacious, and that people should only consider behavior as, for example, rational, purposive or affectionate, if there is no other explanation in terms of the behaviors of more primitive life-forms to which we do not attribute those faculties.

From Anecdote to Laboratory

The behavior of non-human animals has captivated human imagination from antiquity, and over the centuries many writers have speculated about the animal mind, or its absence. Speculation about animal intelligence gradually yielded to scientific study after Darwin placed humans and animals on a continuum, although Darwin's largely anecdotal approach to the topic would not pass scientific muster later on. Unsatisfied with the anecdotal method of Darwin and his protégé J. G. Romanes, E. L. Thorndike brought animal behavior into the laboratory for objective scrutiny. Thorndike's careful observations of the escape of cats, dogs, and chicks from puzzle boxes led him to conclude that what appears to the naive human observer to be intelligent behavior may be strictly attributable to simple associations. According to Thorndike, using Morgan's Canon, the inference of animal reason, insight, or consciousness is unnecessary and misleading. At about the same time, I. P. Pavlov began his seminal studies of conditioned reflexes in dogs. Pavlov quickly abandoned attempts to infer canine mental processes; such attempts, he said, led only to disagreement and confusion. He was, however, willing to propose unseen physiological processes that might explain his observations.

Behavioristic Half-century

The work of Thorndike, Pavlov and a little later of the outspoken behaviorist John B. Watson set the direction of much research on animal behavior for more than half a century. During this time there was considerable progress in understanding simple associations; notably, around 1930 the differences between Thorndike's instrumental (or operant) conditioning and Pavlov's classical (or Pavlovian) conditioning were clarified, first by Miller and Kanorski, and then by B. F. Skinner. Many experiments on conditioning followed; they generated some complex theories, but they made little or no reference to intervening mental processes. Probably the most explicit dismissal of the idea that mental processes control behavior was the radical behaviorism of Skinner. This view seeks to explain behavior, including "private events" like mental images, solely by reference to the environmental contingencies impinging on the human or animal.

Despite the predominantly behaviorist orientation of research before 1960, the rejection of mental processes in animals was not universal during those years. Influential exceptions included, for example, Wolfgang Köhler and his insightful chimpanzees and Edward Tolman whose proposed cognitive map was a significant contribution to subsequent cognitive research in both humans and animals.

Cognitive Revolution

Beginning around 1960, a "cognitive revolution" in research on humans gradually spurred a similar transformation of research with animals. Inference to processes not directly observable became acceptable and then commonplace. An important proponent of this shift in thinking was Donald O. Hebb, who argued that "mind" is simply a name for processes in the head that control complex behavior, and that it is both necessary and possible to infer those processes from behavior. Animals came to be seen as "goal seeking agents that acquire, store, retrieve, and internally process information at many levels of cognitive complexity".

Methods

The acceleration of research on animal cognition in the last 50 years or so has led to a rapid expansion in the variety of species studied and methods employed. The remarkable behavior of large-brained animals such as primates and cetacea has claimed special attention, but all sorts of mammals large and small, birds, fish, ants, bees, and others have been brought into the laboratory or observed in carefully controlled field studies. In the laboratory, animals push levers, pull strings, dig for food, swim in water mazes, or respond to images on computer screens in discrimination, attention, memory, and categorization experiments. Careful field studies explore memory for food caches, navigation by stars, communication, tool use, identification of conspecifics, and many other matters. Studies often focus on the behavior of animals in their natural environments and discuss the putative function of the behavior for the propagation and survival of the species.

These developments reflect an increased cross-fertilization from related fields such as ethology and behavioral ecology. Also, contributions from behavioral neuroscience are beginning to clarify the physiological substrate of some inferred mental process.

Some researchers have made effective use of a Piagetian methodology, taking tasks which human children are known to master at different stages of development, and investigating which of them can be performed by particular species. Others have been inspired by concerns for animal welfare and the management of domestic species: for example Temple Grandin has harnessed her unique expertise in animal welfare and the ethical treatment of farm livestock to highlight underlying similarities between humans and other animals. From a methodological point of view, one of the main risks in this sort of work is anthropomorphism, the tendency to interpret an animal's behavior in terms of human feelings, thoughts, and motivations.

The common chimpanzee can use tools.
This individual is using a stick to get food.

Human and non-human animal cognition have much in common. Of course, research in the two also differs in important respects. Notably, much research with humans either studies or involves language, and much research with animals is related directly or indirectly to behaviors important to survival in natural settings. Following are some of the major areas of research in animal cognition.

Perception

Animals process information from eyes, ears, and other sensory organs to perceive the environment. Perceptual processes have been studied in many species, with results that are often similar to those in humans. Equally interesting are those perceptual processes that differ from, or go beyond those found in humans, such as echolocation in bats and dolphins, motion detection by skin receptors in fish, and extraordinary visual acuity, motion sensitivity and ability to see ultraviolet light in some birds.

Attention

Much of what is happening in the world at any moment is irrelevant to current behavior. Attention refers to mental processes that select relevant information, inhibit irrelevant information, and switch among these as the situation demands. Often the selective process is tuned before relevant information appears; such expectation makes for rapid selection of key stimuli when they become available. A large body of research has explored the way attention and expectation affect the behavior of non-human animals, and much of this work suggests that attention operates in birds, mammals and reptiles in much the same way that it does in humans.

Selective Learning

Animals trained to discriminate between two stimuli, say black versus white, can be said to attend to the "brightness dimension," but this says little about whether this dimension is selected in preference to others. More enlightenment comes from experiments that allow the animal to choose from several alternatives. For example, several studies have shown that performance is better on, for example, a color discrimination (e.g. blue vs green) after the animal has learned another color discrimination (e.g. red vs orange) than it is after training on a different dimension such as an X shape versus and O shape. The reverse effect happens after training on forms. Thus, the earlier learning appears to affect which dimension, color or form, the animal will attend to.

Other experiments have shown that after animals have learned to respond to one aspect of the environment responsiveness to other aspects is suppressed. In "blocking", for example, an animal is conditioned to respond to one stimulus ("A") by pairing that stimulus with reward or punishment. After the animal responds consistently to A, a second stimulus ("B") accompanies A on additional training trials. Later tests with the B stimulus alone elicit little response, suggesting that learning about B has been blocked by prior learning about A. This result supports the hypothesis that stimuli are neglected if they fail to provide new information. Thus, in the experiment just cited, the animal failed to attend to B because B added no information to that supplied by A. If true, this interpretation is an important insight into attentional processing, but this conclusion remains uncertain because blocking and several related phenomena can be explained by models of conditioning that do not invoke attention.

Divided Attention

Attention is a limited resource and is not an all-or-nothing response: the more attention devoted to one aspect of the environment, the less is available for others. A number of experiments have studied this in animals. In one experiment, a tone and a light are presented simultaneously to pigeons. The pigeons gain a reward only by choosing the correct combination of the two stimuli (e.g. a high frequency tone together with a yellow light). The birds perform well at this task, presumably by dividing attention between the two stimuli. When only one of the stimuli varies and the other is presented at its rewarded value, discrimination improves on the variable stimulus but discrimination on the alternative stimulus worsens. These outcomes are consistent with the notion that attention is a limited resource that can be more or less focused among incoming stimuli.

Visual Search and Attentional Priming

The function of attention is to select information that is of special use to the animal. Visual search typically calls for this sort of selection, and search tasks have been used extensively in both humans and animals to determine the characteristics of attentional selection and the factors that control it.

Experimental research on visual search in animals was initially prompted by Tinbergen observed that birds are selective when foraging for insects. For example, he found that birds tended to catch the same type of insect repeatedly even though several types were available. Tinbergen suggested that this prey selection was caused by an attentional bias that improved detection of one type of insect while suppressing detection of others. This "attentional priming" is commonly said to result from a pretrial activation of a mental representation of the attended object, which Tinbergen called a "searching image".

Tinbergen's field observations on priming have been supported by a number of experiments. For example, Pietrewicz and Kamil presented blue jays with pictures of tree trunks upon which rested either a moth of species A, a moth of species B, or no moth at all. The birds were rewarded for pecks at a picture showing a moth. Crucially, the probability with which a particular species of moth was detected was higher after repeated trials with that species (e.g. A, A, A,...) than it was after a mixture of trials (e.g. A, B, B, A, B, A, A...). These results suggest again that sequential encounters with an object can establish an attentional predisposition to see the object.

Another way to produce attentional priming in search is to provide an advance signal that is associated with the target. For example, if a person hears a song sparrow he or she may be predisposed to detect a song sparrow in a shrub, or among other birds. A number of experiments have reproduced this effect in animal subjects.

Still other experiments have explored nature of stimulus factors that affect the speed and accuracy of visual search. For example, the time taken to find a single target increases as the number of items in the visual field increases. This rise in RT is steep if the distracters are similar to the target, less steep if they are dissimilar, and may not occur if the distracters are very different in from the target in form or color.

Concepts and Categories

Fundamental but difficult to define, the concept of "concept" was discussed for hundreds of years by philosophers before it became a focus of psychological study. Concepts enable humans and animals to organize the world into functional groups; the groups may be composed of perceptually similar objects or events, diverse things that have a common function, relationships such as same versus different, or relations among relations such as analogies.

Methods

Most work on animal concepts has been done with visual stimuli, which can easily be constructed and presented in great variety, but auditory and other stimuli have been used as well. Pigeons have been widely used, for they have excellent vision and are readily conditioned to respond to visual targets; other birds and a number of other animals have been studied as well. In a typical experiment, a bird or other animal confronts a computer monitor on which a large number of pictures appear one by one, and the subject gets a reward for pecking or touching a picture of a category item and no reward for non-category items. Alternatively, a subject may be offered a choice between two or more pictures. Many experiments end with the presentation of items never seen before; successful sorting of these items shows that the animal has not simply learned many specific stimulus-response associations. A related method, sometimes used to study relational concepts, is matching-to-sample. In this task an animal sees one stimulus and then chooses between two or more alternatives, one of which is the same as the first; the animal is then rewarded for choosing the matching stimulus.

Perceptual Categories

Perceptual categorization is said to occur when a person or animal responds in a similar way to a range of stimuli that share common features. For example, a squirrel climbs a tree when it sees Rex, Shep, or Trixie, which suggests that it categorizes all three as something to avoid. This sorting of instances into groups is crucial to survival. Among other things, an animal must categorize if it is to apply learning about one object (e.g. Rex bit me) to new instances of that category (dogs may bite).

Natural Categories

Many animals readily classify objects by perceived differences in form or color. For example, bees or pigeons quickly learn to choose any red object and reject any green object if red leads to reward and green does not. Seemingly much more difficult is an animal's ability to categorize natural objects that vary a great deal in color and form even while belonging to the same group. In a classic study, Richard J. Herrnstein trained pigeons to respond to the presence or absence of human beings in photographs. The birds readily learned to peck photos that contained partial or full views of humans and to avoid pecking photos with no human, despite great differences in the form, size, and color of both the humans displayed and in the non-human pictures. In follow-up studies, pigeons categorized other natural objects (e.g. trees) and after training they were able without reward to sort photos they had not seen before. Similar work has been done with natural auditory categories, for example, bird songs. Honeybees (*Apis mellifera*) are able to form concepts of "up" and "down".

Functional or Associative Categories

Perceptually unrelated stimuli may come to be responded to as members of a class if they have a common use or lead to common consequences. Vaughan divided a large set of unrelated pictures into two arbitrary sets, A and B. Pigeons got food for pecking at pictures in set A but not for pecks at pictures in set B. After they had learned this task fairly well, the outcome was reversed: items in set B led to food and items in set A did not. Then the outcome was reversed again, and then again, and so on. Vaughan found that after 20 or more reversals, associating reward with a few pictures in one set caused the birds to respond to the other pictures in that set without further reward, as if they were thinking "if these pictures in set A bring food, the others in set A must also bring food." That is, the birds now categorized the pictures in each set as functionally equivalent. Several other procedures have yielded similar results.

Relational or Abstract Categories

When tested in a simple stimulus matching-to-sample task many animals readily learn specific item combinations, such as "touch red if the sample is red, touch green if the sample is green." But this does not demonstrate that they distinguish between "same" and "different" as general concepts. Better evidence is provided if, after training, an animal successfully makes a choice that matches a novel sample that it has never seen before. Monkeys and chimpanzees do learn to do this, as do pigeons if they are given a great deal of practice with many different stimuli. However, because the sample is presented first, successful matching might mean that the animal is simply choosing the most recently seen "familiar" item rather than the conceptually "same" item. A number of studies have attempted to distinguish these possibilities, with mixed results.

Rule Learning

The use of rules has sometimes been considered an ability restricted to humans, but a number of experiments have shown evidence of simple rule learning in primates and also in other animals. Much of the evidence has come from studies of sequence learning in which the "rule" consists of the order in which a series of events occurs. Rule use is shown if the animal learns to discriminate different orders of events and transfers this discrimination to new events arranged in the same order. For example, Murphy *et al.* trained rats to discriminate between visual sequences. For one group ABA and BAB were rewarded, where A (bright light) and B (dim light). Other stimulus triplets were not rewarded. The rats learned the visual sequence, although both bright and dim lights were equally associated with reward. More importantly, in a second experiment with auditory stimuli, rats responded correctly to sequences of novel stimuli that were arranged in the same order as those previously learned. Similar sequence learning has been demonstrated in birds and other animals as well.

Memory

The categories that have been developed to analyze human memory (short term memory, long term memory, working memory) have been applied to the study of animal memory, and some of the phenomena characteristic of human short term memory (e.g. the serial position effect) have been detected in animals, particularly monkeys. However most progress has been made in the analysis of spatial memory; some of this work has sought to clarify the physiological basis of spatial memory and the role of the hippocampus; other work has explored the spatial memory of scatter-hoarder animals such as Clark's nutcracker, certain jays, tits and certain squirrels, whose ecological niches require them to remember the locations of thousands of caches, often following radical changes in the environment.

Memory has been widely investigated in foraging honeybees, *Apis mellifera*, which use both transient short-term working memory that is non-feeder specific and a feeder specific long-term reference memory. Memory induced in a free-flying honeybee by a single learning trial lasts for days and, by three learning trials, for a lifetime. Slugs, *Limax flavus*, have a short-term memory of approximately 1 min and long-term memory of 1 month.

Methods

As in humans, research with animals distinguishes between "working" or "short-term" memory from "reference" or long-term memory. Tests of working memory evaluate memory for events that happened in the recent past, usually within the last few seconds or minutes. Tests of reference memory evaluate memory for regularities such as "pressing a lever brings food" or "children give me peanuts".

Habituation

This is one of the simplest tests for memory spanning a short time interval. The test compares an animal's response to a stimulus or event on one occasion to its response on a previous occasion. If the second response differs consistently from the first, the animal must have remembered something about the first, unless some other factor such as motivation, sensory sensitivity, or the test stimulus has changed.

Delayed Response

Delayed response tasks are often used to study short-term memory in animals. Introduced by Hunter, a typical delayed response task presents an animal with a stimulus such a colored light, and after a short time interval the animal chooses among alternatives that match the stimulus, or are related to the stimulus in some other way. In Hunter's studies, for example, a light appeared briefly in one of three goal boxes and then later the animal chose among the boxes, finding food behind the one that had been lighted. Most research has been done with some variation of the "delayed matching-to-sample" task. For example, in the initial study with this task, a pigeon was presented with a flickering or steady light. Then, a few seconds later, two pecking keys were illuminated, one with a steady light and one with a flickering light. The bird got food if it pecked the key that matched the original stimulus.

A commonly-used variation of the matching-to-sample task requires the animal to use the initial stimulus to control a later choice between different stimuli. For example, if the initial stimulus is a black circle, the animal learns to choose "red" after the delay; if it is a black square, the correct choice is "green". Ingenious variations of this method have been used to explore many aspects of memory, including forgetting due to interference and memory for multiple items.

Radial Arm Maze

The radial arm maze is used to test memory for spatial location and to determine the mental processes by which location is determined. In a radial maze test, an animal is placed on a small platform from which paths lead in various directions to goal boxes; the animal finds food in one or more goal boxes. Having found food in a box, the animal must return to the central platform. The maze may be used to test both reference and working memory. Suppose, for example, that over a number of sessions the same 4 arms of an 8-arm maze always lead to food. If in a later test session the animal goes to a box that has never been baited, this indicates a failure of reference memory. On the other hand, if the animal goes to a box that it has already emptied during the same test session, this indicates a failure of working memory. Various confounding factors, such as odor cues, are carefully controlled in such experiments.

Water Maze

The water maze is used to test an animal's memory for spatial location and to discover how an animal is able to determine locations. Typically the maze is a circular tank filled with water that has been made milky so that it is opaque. Located somewhere in the maze is a small platform placed just below the surface of the water. When placed in the tank, the animal swims around until it finds and climbs up on the platform. With practice, the animal finds the platform more and more quickly. Reference memory is assessed by removing the platform and observing the relative amount of time the animal spends swimming in the area where the platform had been located. Visual and other cues in and around the tank may be varied to assess the animal's reliance on landmarks and the geometric relations among them.

Spatial Cognition

Whether an animal ranges over a territory measured in square kilometers or square meters, its survival typically depends on its ability to do such things as find a food source and then return to its nest. Sometimes such a task can be performed rather simply, for example by following a chemical trail. Typically, however, the animal must somehow acquire and use information about locations, directions, and distances. The following paragraphs outline some of the ways that animals do this.

- Beacons: Animals often learn what their nest or other goal looks like, and if it is within sight they may simply move toward it; it is said to serve as a "beacon".

- Landmarks: When an animal is unable to see its goal, it may learn the appearance of nearby objects and use these landmarks as guides. Researchers working with birds and bees have demonstrated this by moving prominent objects in the vicinity of nest sites, causing returning foragers to hunt for their nest in a new location.

- Dead reckoning: It is also known as "path integration." It is the process of computing one's position by starting from a known location and keeping track of the distances and directions subsequently traveled. Classic experiments have shown that the desert ant keeps track of its position in this way as it wanders for many meters searching for food. Though it travels in a randomly twisted path, it heads straight home when it finds food. However, if the ant is picked up and released some meters to the east, for example, it heads for a location displaced by the same amount to the east of its home nest.

- Cognitive maps: Some animals appear to construct a cognitive map of their surroundings, meaning that they acquire and use information that enables them to compute how far and in what direction to go to get from one location to another. Such a map-like representation is thought to be used, for example, when an animal goes directly from one food source to another even though its previous experience has involved only travel between each source and home. Research in this area has also explored such topics as the use of geometric properties of the environment by rats and pigeons, and the ability of rats to represent a spatial pattern in either radial arm mazes or water mazes. Spatial cognition is sometimes explored in visual search experiments in which a human or animal searches the environment for a particular object.

- Detour behavior: Some animals appear to have an advanced understanding of their spatial environment and will not take the most direct route if this confers an advantage to them. Some jumping spiders take an indirect route to prey rather than the most direct route, thereby indicating flexibility in behavior and route planning, and possibly insight learning.

Long-distance Navigation: Homing

Many animals travel hundreds or thousands of miles in seasonal migrations or returns to breeding grounds. They may be guided by the sun, the stars, the polarization of light, magnetic cues, olfactory cues, winds, or a combination of these.

It has been hypothesized that animals such as apes and wolves are good at spatial cognition because this skill is necessary for survival. Some researchers argue that this ability may have diminished somewhat in dogs because humans have provided necessities such as food and shelter during some 15,000 years of domestication.

Time of Day: Circadian Rhythms

The behavior of most animals is synchronized with the earth's daily light-dark cycle. Thus, many animals are active during the day, others are active at night, still others near dawn and dusk. Though one might think that these "circadian rhythms" are controlled simply by the presence or absence of light, nearly every animal that has been studied has been shown to have a "biological clock" that yields cycles of activity even when the animal is in constant illumination or darkness.

Interval Timing

Survival often depends on an animal's ability to time intervals. For example, rufous hummingbirds feed on the nectar of flowers, and they often return to the same flower, but only after the flower has had enough time to replenish its supply of nectar. In one experiment hummingbirds fed on artificial flowers that quickly emptied of nectar but were refilled at some fixed time (e.g. twenty minutes) later. The birds learned to come back to the flowers at about the right time, learning the refill rates of up to eight separate flowers and remembering how long ago they had visited each one.

The details of interval timing have been studied in a number of species. One of the most common methods is the "peak procedure". In a typical experiment, a rat in an operant chamber presses a lever for food. A light comes on, a lever-press brings a food pellet at a fixed later time, say 10 seconds, and then the light goes off. Timing is measured during occasional test trials on which no food is presented and the light stays on. On these test trials, the rat presses the lever more and more until about 10 sec and then, when no food comes, gradually stops pressing. The time at which the rat presses most on these test trials is taken to be its estimate of the payoff time.

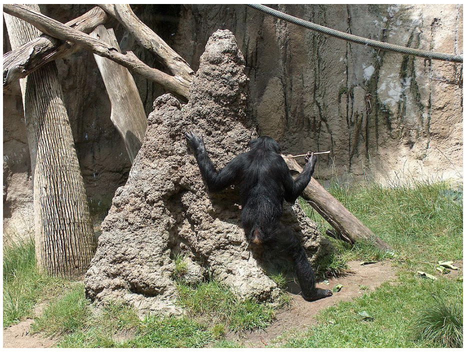
Experiments using the peak procedure and other methods have shown that animals can time short intervals quite exactly, can time more than one event at once, and can integrate time with spatial and other cues. Such tests have also been used for quantitative tests of theories of animal timing, such as Gibbon's Scalar Expectancy Theory ("SET"), Killeen's Behavioral Theory of Timing, and Machado's Learning to Time model. No one theory has yet gained unanimous agreement.

Tool and Weapon Use

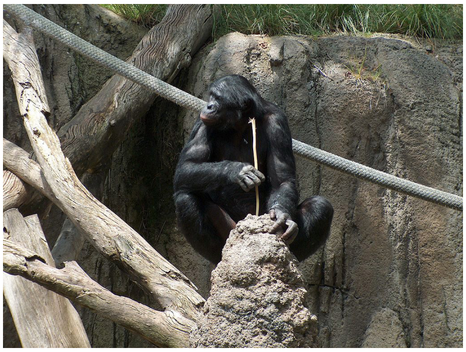
Although tool use was long assumed to be a uniquely human trait, there is now much evidence that many animals use tools, including mammals, birds, fish, cephalopods and insects. Discussions of tool use often involve a debate about what constitutes a “tool”, and they often consider the relation of tool use to the animal’s intelligence and brain size.

Mammals

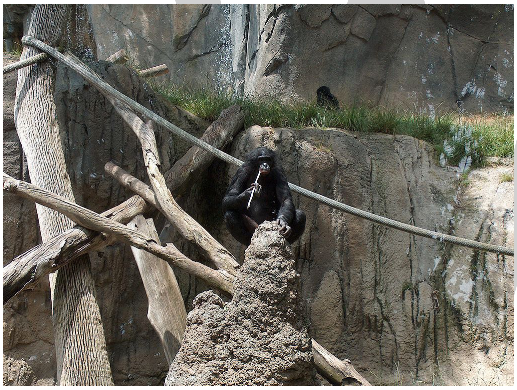
Series of figures below showing a bonobo fishing for termites.



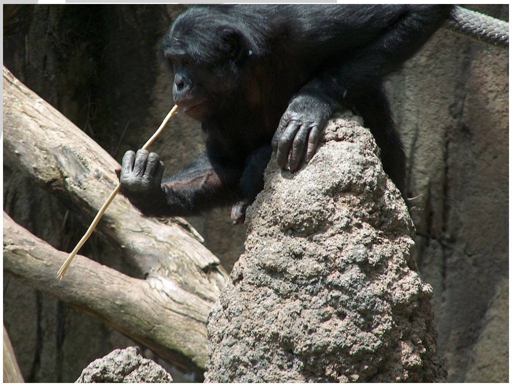
A bonobo inserting a stick into a termite mound.



The bonobo starts “fishing” for the termites.



The bonobo withdraws the stick and begins eating the termites.



The bonobo eats the termites extracted with the tool.

Tool use has been reported many times in both wild and captive primates, particularly the great apes. The use of tools by primates is varied and includes hunting (mammals, invertebrates, fish), collecting honey, processing food (nuts, fruits, vegetables and seeds), collecting water, weapons and shelter. Research in 2007 shows that chimpanzees in the Fongoli savannah sharpen sticks to use as spears when hunting, considered the first evidence of systematic use of weapons in a species other than humans. Other mammals that spontaneously use tools in the wild or in captivity include elephants, bears, cetaceans, sea otters and mongooses.

Birds

Several species of birds have been observed to use tools in the wild, including warblers, parrots, Egyptian vultures, brown-headed nuthatches, gulls and owls. Some species, such as the woodpecker finch of the Galapagos Islands, use particular tools as an essential part of their foraging behavior. However, these behaviors are often quite inflexible and cannot be applied effectively in new situations. A great many species of birds build nests with a wide range of complexities, but although nest-building behavior fulfills the criteria of some definitions of “tool-use”, this is not the case with other definitions.

Several species of corvids have been trained to use tools in controlled experiments. One species examined extensively under laboratory conditions is the New Caledonian crow. One individual called “Betty” spontaneously made a wire tool to solve a novel problem. She was being tested to see whether she would select a wire hook rather than a straight wire to pull a little bucket of meat out of a well. Betty tried poking the straight wire at the meat. After a series of failures with this direct approach, she withdrew the wire and began directing it at the bottom of the well, which was secured to its base with duct tape. The wire soon became stuck, whereupon Betty pulled it sideways, bending it and unsticking it. She then inserted the hook into the well and extracted the meat. In all but one of 10 subsequent trials with only straight wire provided, she also made and used a hook in the same manner, but not before trying the straight wire first.

Fish

Several species of wrasses have been observed using rocks as anvils to crack bivalve (scallops, urchins and clams) shells. This behavior was first filmed in an orange-dotted tuskfish (Choerodon anchorago) in 2009 by Giacomo Bernardi. The fish fans sand to unearth the bivalve, takes it into its mouth, swims several meters to a rock, which it then uses as an anvil by smashing the mollusc apart with sideward thrashes of the head. This behavior has also been recorded in a blackspot tuskfish (Choerodon schoenleinii) on Australia’s Great Barrier Reef, yellowhead wrasse (Halichoeres garnoti) in Florida and a six-bar wrasse (Thalassoma hardwicke) in an aquarium setting. These species are at opposite ends of the phylogenetic tree in this family, so this behavior may be a deep-seated trait in all wrasses.

Invertebrates

Some cephalopods are known to use coconut shells for protection or camouflage.

Ants of the species Conomyrma bicolor pick up stones and other small objects with their mandibles and drop them down the vertical entrances of rival colonies, allowing workers to forage for food without competition.

Reasoning and Problem Solving

It is clear that animals of quite a range of species are capable of solving problems that appear to require abstract reasoning; Wolfgang Köhler’s (1917) work with chimpanzees is a famous early example. He observed that chimpanzees did not use trial and error to solve problems such as retrieving bananas hung out of reach. Instead, they behaved in a manner that was “unwaveringly purposeful,” spontaneously placing boxes so that they could climb to reach the fruit. Modern research has identified similar behavior in animals usually thought of as much less intelligent, if appropriate pre-training is given. Causal reasoning has also been observed in rooks and New Caledonian crows.

It has been shown that Barbados bullfinches (Loxigilla barbadensis) from urbanized areas are better at innovative problem-solving tasks than bullfinches from rural environments, but that they did not differ in colour discrimination learning.

Cognitive Bias

Is the glass half empty or half full?

A cognitive bias refers to a systematic pattern of deviation from norm or rationality in judgment, whereby inferences about other individuals or situations may be drawn in an illogical fashion.

Cognitive bias is sometimes illustrated by using answers to the question "Is the glass half empty or half full?" Choosing "half empty" is supposed to indicate pessimism whereas choosing "half full" indicates optimism. To test this in animals, an individual is trained to anticipate that stimulus A, e.g. a 100 Hz tone, precedes a positive event, e.g. highly desired food is delivered when a lever is pressed by the animal. The same individual is trained to anticipate that stimulus B, e.g. a 900 Hz tone, precedes a negative event, e.g. bland food is delivered when the animal presses a lever. The animal is then tested by being given an intermediate stimulus C, e.g. a 500 Hz tone, and observing whether the animal presses the lever associated with the positive or negative reward. This has been suggested to indicate whether the animal is in a positive or negative mood.

In a study that used this approach, rats that were playfully tickled responded differently than rats that were simply handled. The rats that had been tickled were more optimistic than the handled rats. The authors suggested that they had demonstrated "for the first time a link between the directly measured positive affective state and decision making under uncertainty in an animal model".

There is some evidence for cognitive bias in a number of species, including rats, dogs, rhesus macaques, sheep, chicks, starlings and honeybees.

Language

The modeling of human language in animals is known as animal language research. In addition to the ape-language experiments mentioned above, there have also been more or less successful attempts to teach language or language-like behavior to some non-primate species, including parrots and great spotted woodpeckers. Arguing from his own results with the animal Nim Chimpsky and his analysis of others results, Herbert Terrace criticized the idea that chimps can produce new sentences. Shortly thereafter Louis Herman published research on artificial language comprehension in the bottlenosed dolphin. Though this sort of research has been controversial, especially among cognitive linguists, many researchers agree that many animals can understand the meaning of individual words, and that some may understand simple sentences and syntactic variations, but there is little evidence that any animal can produce new strings of symbols that correspond to new sentences.

Insight

Wolfgang Köhler is usually credited with introducing the concept of insight into experimental psychology. Working with chimpanzees, Köhler came to dispute Edward Thorndike's theory that animals must solve problems gradually, by trial and error. He said that Thorndike's animals could only use trial and error because the situation precluded other forms of problem solving. He provided chimps with a relatively unstructured situation, and he observed sudden "ah-ha!" insightful changes of behavior, as, for example, when a chimp suddenly moved a box into position so that it could retrieve a banana. More recently, Asian elephants (Elephas maximus) were shown to exhibit similar insightful problem solving. A male was observed moving a box to a position where it could be stood upon to reach food that had been deliberately hung out of reach.

Numeracy

A variety of studies indicates that animals are able to use and communicate quantitative information, and that some can count in a rudimentary way. Some examples of this research follow.

In one study, rhesus monkeys viewed visual displays containing, for example, 1, 2, 3, or 4 items of different sorts. They were trained to respond to them in several ways involving numerical ordering, for example touching "1" first, "2" second and so on. When tested with displays containing items they had never seen before, they continued to respond to them in order. The authors conclude that monkeys can represent the numerosities 1 to 9 at least on an ordinal scale.

Ants are able to use quantitative values and transmit this information. For instance, ants of several species are able to estimate quite precisely numbers of encounters with members of other colonies on their feeding territories. Numeracy has been described in the yellow mealworm beetle (*Tenebrio molitor*) and the honeybee.

Western lowland gorillas given the choice between two food trays demonstrated the ability to choose the tray with more food items at a rate higher than chance after training. In a similar task, chimpanzees chose the option with the larger amount of food. Salamanders given a choice between two displays with differing amounts of fruit flies, used as a food reward, reliably choose the display with more flies, as shown in a particular experiment.

Other experiments have been conducted that show animals' abilities to differentiate between non-food quantities. American black bears demonstrated quantity differentiation abilities in a task with a computer screen. The bears were trained to touch a computer monitor with a paw or nose to choose a quantity of dots in one of two boxes on the screen. Each bear was trained with reinforcement to pick a larger or smaller amount. During training, the bears were rewarded with food for a correct response. All bears performed better than what random error predicted on the trials with static, non-moving dots, indicating that they could differentiate between the two quantities. The bears choosing correctly in congruent (number of dots coincided with area of the dots) and incongruent (number of dots did not coincide with area of the dots) trials suggests that they were indeed choosing between quantities that appeared on the screen, not just a larger or smaller retinal image, which would indicate they are only judging size.

Bottlenose dolphins have shown the ability to choose an array with fewer dots compared to one with more dots. Experimenters set up two boards showing various numbers of dots in a pool-side setup. The dolphins were initially trained to choose the board with the fewer number of dots. This was done by rewarding the dolphin when it chose the board with the fewer number of dots. In the experimental trials, two boards were set up, and the dolphin would emerge from the water and point to one board. The dolphins chose the arrays with fewer dots at a rate much larger than chance, indicating they can differentiate between quantities. A particular grey parrot, after training, has shown the ability to differentiate between the numbers zero through six using vocalizations. After number and vocalization training, this was done by asking the parrot how many objects there were in a display. The parrot was able to identify the correct amount at a rate higher than chance. Angelfish, when put in an unfamiliar environment will group together with conspecifics, an action named shoaling. Given the choice between two groups of differing size, the angelfish will choose the larger of the two groups. This can be seen with a discrimination ratio of 2:1 or greater, such that, as long as one group has at least twice the fish as another group, it will join the larger one.

Monitor lizards have been shown to be capable of numeracy, and some species can distinguish among numbers up to six.

Intelligence

As the cognitive ability and intelligence in non-human animals cannot be measured with verbal scales, it has been measured using a variety of methods that involve such things as habit reversal, social learning, and responses to novelty. Principal Component Analysis and factor analytic studies have shown that a single factor of intelligence is responsible for 47% of the individual variance in cognitive ability measures in primates and between 55% and 60% of the variance in mice. These values are similar to the accepted variance in IQ explained by a similar single factor known as the general factor of intelligence in humans (40-50%).

The general factor of intelligence, or *g* factor, is a psychometric construct that summarizes the correlations observed between an individual's scores on various measures of cognitive abilities. It has been suggested that *g* is related to evolutionary life histories and the evolution of intelligence as well as to social learning and cultural intelligence. Non-human models of *g* have been used in genetic and neurological research on intelligence to help understand the mechanisms behind variation in *g*.

Theory of Mind

Theory of mind is the ability to attribute mental states, e.g. intents, desires, pretending, knowledge, to oneself and others and to understand that others have desires, intentions, and perspectives that are different from one's own.

Some research with ravens provides an example of evidence for theory of mind in a non-human species. Ravens are members of the corvidae family, which is widely regarded as having high cognitive abilities. These birds have been observed to hide their food when dominant ravens are visible and audible at the same time. Based on this observation, ravens were tested for their understanding of "seeing" as a mental state. In a first step, the birds protected their cache when dominants were visible but not when they could only be heard from an adjacent room. In the next step, they had access to a small peephole which allowed them to see into the adjacent room. With the peephole open, the ravens guarded their caches against discovery when they could hear dominants in the adjacent room, even when the dominant's sounds were playbacks of recordings.

Consciousness

Mirror test with a baboon.

The sense in which animals can be said to have consciousness or a self-concept has been hotly debated. The best known research technique in this area is the mirror test devised by Gordon G. Gallup, in which an animal's skin is marked in some way while it is asleep or sedated, and it is then allowed to see its reflection in a mirror; if the animal spontaneously directs grooming behavior towards the mark, that is taken as an indication that it is aware of itself. Self-awareness, by this criterion, has been reported for chimpanzees and also for other great apes, the European magpie, some cetaceans and an Asian elephant , but not for monkeys. The mirror test has been criticized by researchers because it is entirely focused on vision, the primary sense in humans, while other species rely more heavily on other senses such as the sense of smell in dogs.

It has been suggested that metacognition in some animals provides some evidence for cognitive self-awareness. The great apes, dolphins, and rhesus monkeys have demonstrated the ability to monitor their own mental states and use an "I don't know" response to avoid answering difficult questions. Unlike the mirror test, which reveals awareness of the condition of one's own body, this uncertainty monitoring is thought to reveal awareness of one's internal mental state.

Some researchers propose that animal calls and other vocal behaviors provide evidence of consciousness. This idea arose from research on children's crib talk by Weir and in investigations of early speech in children by Greenfield and others. Some such research has been done with a macaw.

Biological Constraints

Hedgehogs instinctively roll into a ball when threatened, making them unsuitable for studies on aversion avoidance.

Animals differ widely in many learning and cognitive tasks in ways that reflect their evolutionary history and their instinctual behaviors in natural environments. For example, dogs and rats easily learn to avoid an electric shock from the floor by moving to another part of the experimental chamber when they hear a tone preceding the shock; this is an appropriate response to a dangerous situation. However, hedgehogs fail to learn this avoidance behavior. This might seem to show the hedgehog's inability to learn, but the hedgehog's instinctive reaction to a threat is to curl up into a ball, a response that interferes with possible escape behavior in this situation.

Instinctive drift is another factor that can influence the interpretation of cognitive research. Instinctive drift is the tendency of an animal to revert to instinctive behaviors that can interfere with learned responses. The concept originated with Keller and Marian Breland when they taught a raccoon to put coins into a box. The raccoon drifted to its instinctive behavior of rubbing the coins with its paws, as it would do when foraging for food.

Animal ability to process and respond to stimuli is correlated with brain size. Small-brain animals tend to show simple behaviors that are less dependent on learning than those of large-brained animals. Vertebrates, particularly mammals, have large brains and complex behavior that changes with experience. A formula called the encephalization quotient (EC) expresses a relationship between brain and body size; it was developed by H. J. Jerison in the late 1960s. When the encephalization quotient is plotted as a curve, an animal with an EC above the curve is expected to show more cognitive ability than the average animal of its size, whereas an animal with an EC below the curve is expected to have less. Various formulas been suggested, but the equation $Ew(\text{brain}) = 0.12w(\text{body})^{2/3}$ has been found to fit data from a sample of mammals. The formula is suggestive at best, and should only be applied to non-mammals with extreme caution. For some of the other vertebrate classes, the power of 3/4 rather than 2/3 is sometimes used, and for many groups of invertebrates, the formula may not give meaningful results.

Experimental Evidence against Animal Cognition

Several experiments cannot be readily reconciled with the belief that some animal species are intelligent, insightful, or possess a theory of mind.

Jean-Henri Fabre, setting the stage for all subsequent experiments of this kind, argued that insects "obey their compelling instinct, without realizing what they do." For instance, to understand that she can grab her paralyzed prey by a leg instead of an antenna is utterly beyond the powers of a sand wasp. "Her actions are like a series of echoes each awakening the next in a settled order, which allows none to sound until the previous one has sounded." Fabre's numerous experiments led him, in turn, to the view that scientists often try to "exalt animals" instead of objectively studying them.

C. Lloyd Morgan's observations suggested to him that prima facie intelligent behavior in animals is often the result of either instincts or trial and error. For instance, most visitors watching Morgan's dog smoothly lifting a latch with the back of its head (and thereby opening a garden gate and escaping) were convinced that the dog's actions involved thinking. Morgan, however, carefully observed the dog's prior, random, purposeless actions and argued that they involved "continued trial and failure, until a happy effect is reached," rather than "methodical planning."

E. L. Thorndike placed hungry cats and dogs in enclosures "from which they could escape by some simple act, such as pulling at a loop of cord." Their behavior suggested to him that they did not "possess the power of rationality." Most books about animal behavior, Thorndike wrote, "do not give us a psychology, but rather a eulogy of animals."

Although Wolfgang Köhler experiments are often cited as providing support for the animal cognition hypothesis, his book is replete with counter-examples. For instance, he placed chimpanzees in a situation where they could only get bananas by removing a box. The chimpanzee, Köhler observed, "has special difficulty in solving such problems; he often draws into a situation the strangest and most distant tools, and adopts the most peculiar methods, rather than remove a simple obstacle which could be displaced with perfect ease."

Daniel J Povinelli and Timothy Eddy of the University of Louisiana showed that chimpanzees were just as likely to beg food from a person who could see the begging gesture as from a person who could not, thereby raising the possibility that chimpanzees do not understand that people see.

Moty Nissani of Wayne State University trained Burmese logging elephants to lift a lid in order to retrieve food from a bucket. The lid was then placed on the ground alongside the bucket (where it no longer obstructed access to the food) while the treat was simultaneously placed inside the bucket. All elephants continued to toss the lid before retrieving the reward, thus suggesting that elephants do not grasp simple causal relationships.

Cognitive Faculty by Species

A traditionally common image is the *scala naturae*, the ladder of nature on which animals of different species occupy successively higher rungs, with humans typically at the top. However, there is some disagreement with the use of such a hierarchy, with some critics saying it may be necessary to understand specific cognitive capacities as adaptations to differing ecological niches.

Whether fairly or not, the performance of animals is often compared to that of humans on cognitive tasks. Not surprisingly, our closest biological relatives, the great apes, tend to perform most like humans. Among the birds, corvids and parrots have typically been found to perform well on human-like tasks. Some octopodes have also been shown to exhibit a number of higher-level skills such as tool use, but the amount of research on cephalopod intelligence is still limited.

MOBBING

Crows mobbing a red-tailed hawk.

Mobbing in animals is an antipredator adaptation in which individuals of prey species mob a predator by cooperatively attacking or harassing it, usually to protect their offspring. A simple definition of mobbing is an assemblage of individuals around a potentially dangerous predator. This is most frequently seen in birds, though it is also known to occur in many other animals such as the meerkat, and some bovines. While mobbing has evolved independently in many species, it only tends to be present in those whose young are frequently preyed upon. This behavior may complement cryptic adaptations in the offspring themselves, such as camouflage and hiding. Mobbing calls may be used to summon nearby individuals to cooperate in the attack.

Konrad Lorenz, attributed mobbing among birds and animals to instincts rooted in the Darwinian struggle to survive. In his view, humans are subject to similar innate impulses but capable of bringing them under rational control.

In Birds

A great kiskadee (right) mobbing a hawk.

Birds that breed in colonies such as gulls are widely seen to attack intruders, including encroaching humans. In North America, the birds that most frequently engage in mobbing include mockingbirds, crows and jays, chickadees, terns, and blackbirds. Behavior includes flying about the intruder, dive bombing, loud squawking and defecating on the predator. Mobbing can also be used to obtain food, by driving larger birds and mammals away from a food source, or by harassing a bird with food. One bird might distract while others quickly steal food. Scavenging birds such as gulls frequently use this technique to steal food from humans nearby. A flock of birds might drive a powerful animal away from food. Costs of mobbing behavior include the risk of engaging with predators, as well as energy expended in the process. The black-headed gull is a species which aggressively engages intruding predators, such as carrion crows. Classic experiments on this species by Hans Kruuk involved placing hen eggs at intervals from a nesting colony, and recording the percentage of successful predation events as well as the probability of the crow being subjected to mobbing. The results showed decreasing mobbing with increased distance from the nest, which was correlated with increased predation success. Mobbing may function by reducing the predator's ability to locate nests (as a distraction) since predators cannot focus on locating eggs while they are under attack.


Crows mobbing a perched bald eagle.

Besides the ability to drive the predator away, mobbing also draws attention to the predator, making stealth attacks impossible. Mobbing plays a critical role in the identification of predators and inter-generational learning about predator identification. Reintroduction of species is often unsuccessful, because the established population lacks this cultural knowledge of how to identify local predators. Scientists are exploring ways to train populations to identify and respond to predators before releasing them into the wild.

Adaptationist hypotheses regarding why an organism should engage in such risky behavior have been suggested by Eberhard Curio, including advertising their physical fitness and hence uncatchability (much like stotting behavior in gazelles), distracting predators from finding their offspring, warning their offspring, luring the predator away, allowing offspring to learn to recognize the predator species, directly injuring the predator or attracting a predator of the predator itself. The much lower frequency of attacks between nesting seasons suggests such behavior may have evolved due to its benefit for the mobber's young. Niko Tinbergen argued that the mobbing was a source of confusion to gull chick predators, distracting them from searching for prey. Indeed, an intruding carrion crow can only avoid incoming attacks by facing its attackers, which prevents it from locating its target.

Besides experimental research, the comparative method can also be employed to investigate hypotheses such as those given by Curio above. For example, not all gull species show mobbing behavior. The kittiwake nests on sheer cliffs that are almost completely inaccessible to predators, meaning its young are not at risk of predation like other gull species. This is an example of divergent evolution.

Looking at variation in the behavioral responses of 22 different passerine species to a potential predator, the Eurasian Pygmy Owl, extent of mobbing was positively related with a species prevalence in the owls' diet. Furthermore, the intensity of mobbing was greater in autumn than spring.

Mobbing is thought to carry risks to roosting predators, including potential harm from the mobbing birds, or attracting larger, more dangerous predators. Birds at risk of mobbing such as owls have cryptic plumage and hidden roosts which reduces this danger.

In other Animals

The occurrence of mobbing behavior across widely different taxa, including California ground squirrels, is evidence of convergent evolution.

Another way the comparative method can be used is by comparing gulls with distantly related organisms. This approach relies on the existence of convergent evolution, where distantly related organisms evolve the same trait due to similar selection pressures. Many bird species such as the swallows also mob predators, however more distantly related groups including mammals have been known to engage in this behavior. One example is the California ground squirrel, which distracts predators such as the rattlesnake and gopher snake from locating their nest burrows by kicking sand into their face, which disrupts the snake's sensory organs; for crotaline snakes, this includes the heat-detecting organs in the loreal pits. This social species also uses alarm calls.

Some fish engage in mobbing; for example, bluegills sometimes attack snapping turtles. Bluegills, which form large nesting colonies, were seen to attack both released and naturally occurring turtles, which may advertise their presence, drive the predator from the area, or aid in the transmission of predator recognition. Similarly, humpback whales are known to mob killer whales when the latter are attacking other species, including other cetacean species, seals, sea lions, and fish.

Mobbing Calls

Mobbing calls are signals made by the mobbing species while harassing a predator. These differ from alarm calls, which allow con-specifics to *escape* from the predator. The great tit, a European songbird, uses such a signal to call on nearby birds to harass a perched bird of prey, such as an owl. This call occurs in the 4.5 kHz range, and carries over long distances. However, when prey species are in flight, they employ an alarm signal in the 7–8 kHz range. This call is less effective at traveling great distances, but is much more difficult for both owls and hawks to hear (and detect the direction from which the call came). In the case of the alarm call, it could be disadvantageous to the sender if the predator picks up on the signal, hence selection has favored those birds able to hear and employ calls in this higher frequency range.

The great tit (*P. major*), a passerine bird, employs both mobbing behavior and alarm calls.

Mobbing calls may also be part of an animal's arsenal in harassing the predator. Studies of *Phainopepla* mobbing calls indicate it may serve to enhance the swooping attack on the predators, including scrub jays. In this species, the mobbing call is smoothly upsweeping, and is made when swooping down in an arc beside the predator. This call was also heard during agonistic behavior interactions with conspecifics, and may serve additionally or alternatively as an alarm call to their mate.

Evolution

African buffalo herd confronting a lion.

The evolution of mobbing behavior can be explained using evolutionarily stable strategies, which are in turn based on game theory.

Mobbing involves risks (costs) to the individual and benefits (payoffs) to the individual and others. The individuals themselves are often genetically related, and mobbing is increasingly studied with the gene-centered view of evolution by considering inclusive fitness (the carrying on of one's genes through one's family members), rather than merely benefit to the individual.

By cooperating to successfully drive away predators, all individuals involved increase their chances of survival and reproduction. An individual stands little chance against a larger predator, but when a large group is involved, the risk to each group member is reduced or diluted. This so-called dilution effect proposed by W. D. Hamilton is another way of explaining the benefits of cooperation by selfish individuals. Lanchester's laws also provide an insight into the advantages of attacking in a large group rather than individually.

Another interpretation involves the use of signalling theory, and possibly the handicap principle. Here the idea is that a mobbing bird, by apparently putting itself at risk, displays its status and health so as to be preferred by potential partners.

PRIMATE COGNITION

All animals have to negotiate their environment to allow them to forage for food, avoid predation and find mates. Primates stand out among other taxa for their flexibility in how they deal with the world around them. They inhabit both complex physical and social worlds, which have each been posited as the major selective pressures driving the advancement of primate brain size and, by extension, their cognitive abilities.

Primate Cognition about the Physical World

Cognitive Mapping

Across the world, primates have to master an array of environmental topographies, negotiate weather extremes, and move about their territory safely and efficiently. Within their home range, primates need to understand and recall the features that lie within it, which requires both cognitive mapping skills and a flexible memory. Importantly, cognitive mapping allows primates to remember not just where physical landmarks are but also salient and changing features (when that tree will bear fruit). When navigating their environment, primates do not travel aimlessly, but move about it in a directed manner. Monkeys (e.g. Hylobates lar and Cebus apella) and apes (e.g. Pan troglodytes and Gorilla gorilla) will take the most efficient routes, maximizing the available food that they pass, to reach preferred fruiting trees. Cognitive mapping is essential for increasing fitness, because in dense environments vision is often extremely limited, and fruiting trees (or other valuable resources) may not be easily visible; planning travel paths thus reduces energy expenditure and search costs. Of course, the foci of individual interest may vary, even within species, revealing flexibility in primate decision-making. For instance, chimpanzee females are more likely to plan routes following paths that will lead them to food sources whereas males appear more concerned with monitoring the border of their territory.

Memory and Future Planning

The memory of primates has been studied fairly extensively, revealing, for example, that apes are able to recall locations of items after delays of up to 16 hours and replicate novel actions demonstrated to them over 24 hours previously. Furthermore, like humans, monkeys (Macaca mulatta) and apes (Pan troglodytes) are able to recall serial lists of images. Indeed, the working memory capacities of captive chimpanzees, in some cases, may outdo the performance of humans. Primates' memory also allows for future planning. Chimpanzees, for example, are able to select specific tools and save them to solve particular tasks at a later time and when foraging for fruits in their environment, monkeys (Lophocebus albigena) have been reported to apply knowledge of the past days' temperatures to determine on which trees ripe fruit will now be likely found. This flexibility may require mental representation and both ape (Pan troglodytes) and monkey (Macaca fascicularis, Papio anubis and Saimiri sciureus) species are able to apply Roman numerals to specific quantities in ways comparable with young children, and use such numerals for simple arithmetic.

Tool-use Behavior and Causal Understanding

The sensory-motor cognition of primates is highlighted by their dexterous use of tools. Both ape and monkey species use tools to eat otherwise inaccessible foods. The ability of primates to manufacture tools to specific requirements demonstrates an understanding of causal relations and physical properties (causal understanding). White bearded capuchin monkeys (Cebus libidinosus), for example, select substrates of specific weight and material to use as hammers when cracking nuts. This skill appears to be learnt during the monkey's development, with young brown capuchin monkeys (C. apella) showing indiscriminate and ineffectual preferences for tool material, and their skill increasing with age. This learnt skill highlights the interplay of the material and social world that primates negotiate; individuals learn about the causal relations of their physical environment from both personal interaction and social observation. More formal tests of causal understanding with apes in captivity report that all four apes species show a clear understanding of causal relations, using tools flexibly to negotiate food around obstacles.

Social Cognition

The social world that primates inhabit adds another dimension to their cognitive demands. Tests of self-recognition have led to the hypothesis that some primate species have an understanding of theory of mind, which further enables them to monitor their social world and their relation to it. Research reveals that primates can recognize and distinguish individuals, retain knowledge about social relations, and that chimpanzees, but not capuchin monkeys, recognize what others know. This knowledge of fellow members of their social group enables primates to determine who to associate with, cooperate with, and potentially learn from, and how to manipulate individuals or situations.

Cooperation and Prosocial Behavior

Primates cooperate on tasks as diverse as group hunting, territory defence, and rank acquisition through alliances, and, in some cases, showing quite complex behaviors. In some tasks, at least, non-human primates reach outcomes equivalent to those of humans. Primates are sensitive to task demands, for instance cooperating at a higher rate when rewards cannot easily be dominated by another individual. Intriguingly, species which routinely cooperate with non-kin are also more likely to respond negatively to inequity, indicating that cooperation and an ability to recognise inequity may have co-evolved in some species. Primates also appear to engage in only limited reciprocity; although reciprocity is seen in long-term analyses of wild populations, short-term laboratory experiments have found little evidence for such behavior. This may indicate that most reciprocity is based on longer-term relationships rather than immediate contingency.

While cooperation is common, prosocial behavior is more rare. There is little evidence in apes that individuals change their behavior to bring a partner food, although several monkey species do so, even in cases in which being prosocial actually results in inequity towards the provider. On the other hand, even among chimpanzees, behaviors which help a partner are seen outside of the food context. One hypothesis is that prosocial behaviors are more common among cooperative breeders, due to the unique costs and benefits related to their interactions with each other, leading them to more actively share food with partners.

Machiavellian and social Intelligence

Primates are able to use their skills in social cognition to their advantage by manipulating the behavior of others. In fact, one hypothesis for primates' unusual intelligence is that cognitive skills were strongly selected because of the necessity of outsmarting rivals. This may be most evident in the case of deception. Deception is rarely observed, partially because it is expected to be uncommon to avoid habituation by potential targets. However, a field experiment with capuchin monkeys (Cebus apella) has demonstrated tactical deception. In cases of artificial provisioning, lower-ranking monkeys are more likely to give alarm calls in contested situations in which the departure of the dominant could result in more food for the caller. Thus the absence of an extensive literature on deception may equally be due to an absence of deception, or to the challenges of demonstrating what is by necessity a rare behavior.

Social Learning

The ability of primates to learn socially from one another, taking advantage of the knowledge of others, blurs the distinction between how they learn about their physical and social worlds. The major importance of social learning is that it facilitates the transfer of information between individuals without the need for genetic inheritance and can bypass potentially costly and time-consuming trial-and-error learning. In humans, this has allowed for the emergence of our diverse cultural world. Social learning has been reported for many primate species but do they have cultures like us? Primates do indeed show evidence for socially-learned, behavioral traditions. Although undoubtedly not as rich as human culture, certain wild primate communities sustain multiple site-specific behaviors analogous to our culture with such traditions identified in ape (Pan troglodytes, Pongo pygmaeus) and monkey (Macaca fuscata, Cebus capucinus and Ateles geoffroyi) species in the wild.

There is clearly a marked difference, however, between human culture and the behavioral traditions of primates, and what underlies this contrast is currently a topic of much debate. Cumulative culture has been proposed to describe the underlying mechanism that has allowed for the development of our complex technologies. Without the ability for imitation or teaching, researchers argue, primates may not be capable of cumulative learning because the complex information required for such intricate behaviors cannot be transmitted faithfully. Experimental studies with humans, however, reveal that teaching and imitation are not prerequisite for cumulative culture. Given this, along with the mounting evidence that primates are able to copy even complex tool-use behaviors from observing others, what can explain the relative paucity of the cultural worlds of our closest-living relatives, especially for the chimpanzee? It may well be that the very ability of chimpanzees to copy others leads to their limited ability to build on the knowledge of previous generations. After learning a specific method from observations of others, chimpanzees appear to become entrenched and unable to transition to a new behavior, even if the introduced method is more efficient. Although seemingly a limitation of their learning capacities, such as conformity and conservatism may enable chimpanzees to maintain strong social bonds and potentially avoid risks in the wild. Thus, the key ability here is not just in copying others, but determining when to do so.

References

- Animal-behavior-theory: academia.edu, Retrieved 31 March, 2019
- Tu, h-w; smith, e.; dooling, r. J. (2011). “acoustic and perceptual categories of vocal elements in the warble song of budgerigars (melopsittacus undulates)”. Journal of comparative psychology. 125 (4): 420–430. Doi:10.1037/a0024396. Pmc 4497543. Pmid 22142040
- Types-of-adaptations-in-animals: animalwised.com, Retrieved 14 July, 2019
- King, dennis & green, brian. 1999. Goannas: the biology of varanid lizards. University of new south wales press. Isbn 0-86840-456-x, p. 43
- Primate-cognition, library, knowledge, scitable: nature.com
- Griffin, andrea s.; daniel t. Blumstein; christopher s. Evans (october 2000). “training captive-bred or translocated animals to avoid predators”. Conservation biology. 14 (5): 1317–1326. Doi:10.1046/j.1523-1739.2000.99326.x

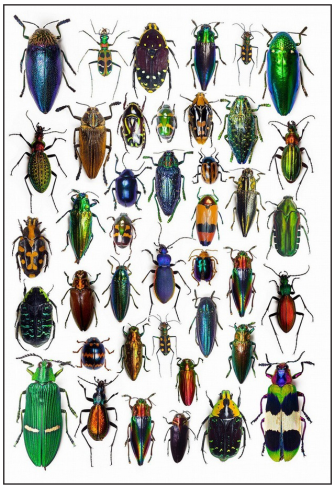
Evolutionary Basis of Animal Behavior

3 CHAPTER

Animal behavior is often considered to be an evolutionarily adaptive trait. Some of the concepts in animal behavior which are studied in the context of evolution are natural selection, behavior mutation and biological altruism. The topics elaborated in this chapter will help in gaining a better perspective about the evolutionary basis of animal behavior.

Mutations are changes in the genetic sequence, and they are a main cause of diversity among organisms. These changes occur at many different levels, and they can have widely differing consequences. In biological systems that are capable of reproduction, we must first focus on whether they are heritable; specifically, some mutations affect only the individual that carries them, while others affect all of the carrier organism's offspring, and further descendants. For mutations to affect an organism's descendants, they must: 1) occur in cells that produce the next generation, and 2) affect the hereditary material. Ultimately, the interplay between inherited mutations and environmental pressures generates diversity among species.

Although various types of molecular changes exist, the word "mutation" typically refers to a change that affects the nucleic acids. In cellular organisms, these nucleic acids are the building blocks of DNA, and in viruses they are the building blocks of either DNA or RNA. One way to think of DNA and RNA is that they are substances that carry the long-term memory of the information required for an organism's reproduction.



The diversity of beetle species. Genetic mutation is the basis of species diversity among beetles, or any other organism.

If mutations occur in non-germline cells, then these changes can be categorized as somatic mutations. Somatic mutations only affect the present organism's body. From an evolutionary perspective, somatic mutations are uninteresting, unless they occur systematically and change some fundamental property of an individual - such as the capacity for survival. For example, cancer is a potent somatic mutation that will affect a single organism's survival. As a different focus, evolutionary theory is mostly interested in DNA changes in the cells that produce the next generation.

Are Mutations Random?

The statement that mutations are random is both profoundly true and profoundly untrue at the same time. The true aspect of this statement stems from the fact that, the consequences of a mutation have no influence whatsoever on the probability that this mutation will or will not occur. In other words, mutations occur randomly with respect to whether their effects are useful. Thus, beneficial DNA changes do not happen more often simply because an organism could benefit from them. Moreover, even if an organism has acquired a beneficial mutation during its lifetime, the corresponding information will not flow back into the DNA in the organism's germline. This is a fundamental insight that Jean-Baptiste Lamarck got wrong and Charles Darwin got right.

However, the idea that mutations are random can be regarded as untrue if one considers the fact that not all types of mutations occur with equal probability. Rather, some occur more frequently than others because they are favored by low-level biochemical reactions. These reactions are also the main reason why mutations are an inescapable property of any system that is capable of reproduction in the real world. Mutation rates are usually very low, and biological systems go to extraordinary lengths to keep them as low as possible, mostly because many mutational effects are harmful. Nonetheless, mutation rates never reach zero, even despite both low-level protective mechanisms, like DNA repair or proofreading during DNA replication, and high-level mechanisms, like melanin deposition in skin cells to reduce radiation damage. Beyond a certain point, avoiding mutation simply becomes too costly to cells. Thus, mutation will always be present as a powerful force in evolution.

Types of Mutations

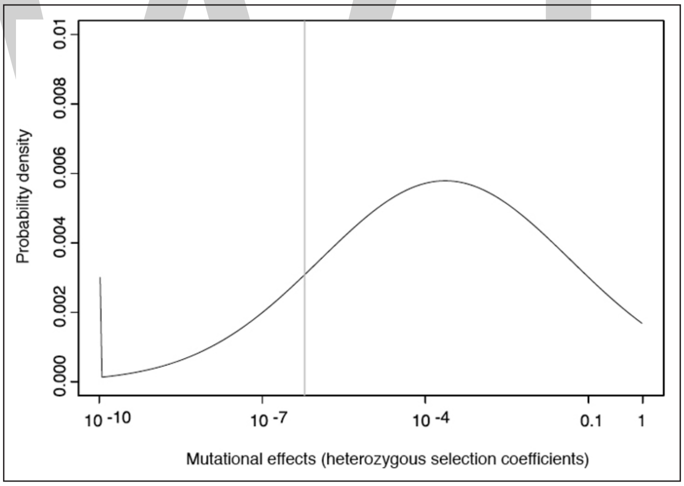
The smallest mutations are point mutations, in which only a single base pair is changed into another base pair. Yet another type of mutation is the nonsynonymous mutation, in which an amino acid sequence is changed. Such mutations lead to either the production of a different protein or the premature termination of a protein.

As opposed to nonsynonymous mutations, synonymous mutations do not change an amino acid sequence, although they occur, by definition, only in sequences that code for amino acids. Synonymous mutations exist because many amino acids are encoded by multiple codons. Base pairs can also have diverse regulating properties if they are located in introns, intergenic regions, or even within the coding sequence of genes. For some historic reasons, all of these groups are often subsumed with synonymous mutations under the label "silent" mutations. Depending on their function, such silent mutations can be anything from truly silent to extraordinarily important, the latter implying that working sequences are kept constant by purifying selection. This is the most likely explanation for the existence of ultraconserved noncoding elements that have survived for more than 100 million years without substantial change, as found by comparing the genomes of several vertebrates.

Mutations may also take the form of insertions or deletions, which are together known as indels. Indels can have a wide variety of lengths. At the short end of the spectrum, indels of one or two base pairs within coding sequences have the greatest effect, because they will inevitably cause a frameshift (only the addition of one or more three-base-pair codons will keep a protein approximately intact). At the intermediate level, indels can affect parts of a gene or whole groups of genes. At the largest level, whole chromosomes or even whole copies of the genome can be affected by insertions or deletions, although such mutations are usually no longer subsumed under the label indel. At this high level, it is also possible to invert or translocate entire sections of a chromosome, and chromosomes can even fuse or break apart. If a large number of genes are lost as a result of one of these processes, then the consequences are usually very harmful. Different genetic systems react differently to such events.

Still other sources of mutations are the many different types of transposable elements, which are small entities of DNA that possess a mechanism that permits them to move around within the genome. Some of these elements copy and paste themselves into new locations, while others use a cut-and-paste method. Such movements can disrupt existing gene functions (by insertion in the middle of another gene), activate dormant gene functions (by perfect excision from a gene that was switched off by an earlier insertion), or occasionally lead to the production of new genes (by pasting material from different genes together).

Effects of Mutations

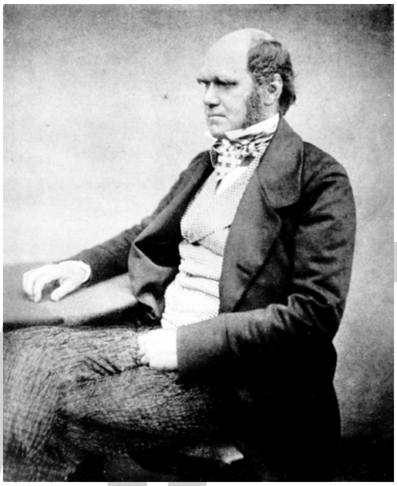


The overwhelming majority of mutations have very small effects.

A single mutation can have a large effect, but in many cases, evolutionary change is based on the accumulation of many mutations with small effects. Mutational effects can be beneficial, harmful, or neutral, depending on their context or location. Most non-neutral mutations are deleterious. In general, the more base pairs that are affected by a mutation, the larger the effect of the mutation, and the larger the mutation's probability of being deleterious.

To better understand the impact of mutations, researchers have started to estimate distributions of mutational effects (DMEs) that quantify how many mutations occur with what effect on a given property of a biological system. In evolutionary studies, the property of interest is fitness, but in molecular systems biology, other emerging properties might also be of interest. It is extraordinarily difficult to obtain reliable information about DMEs, because the corresponding effects span many orders of magnitude, from lethal to neutral to advantageous; in addition, many confounding factors usually complicate these analyses. To make things even more difficult, many mutations also interact with each other to alter their effects; this phenomenon is referred to as epistasis. However, despite all these uncertainties, recent work has repeatedly indicated that the overwhelming majority of mutations have very small effects. Much more work is needed in order to obtain more detailed information about DMEs, which are a fundamental property that governs the evolution of every biological system.

NATURAL SELECTION



Modern biology began in the nineteenth century with Charles Darwin's work on evolution by natural selection.

Natural selection is the differential survival and reproduction of individuals due to differences in phenotype. It is a key mechanism of evolution, the change in the heritable traits characteristic of a population over generations. Charles Darwin popularised the term "natural selection", contrasting it with artificial selection, which in his view is intentional, whereas natural selection is not.

Variation exists within all populations of organisms. This occurs partly because random mutations arise in the genome of an individual organism, and offspring can inherit such mutations. Throughout the lives of the individuals, their genomes interact with their environments to cause variations in traits. The environment of a genome includes the molecular biology in the cell, other cells, other individuals, populations, species, as well as the abiotic environment. Because individuals with certain variants of the trait tend to survive and reproduce more than individuals with other, less successful variants, the population evolves. Other factors affecting reproductive success include sexual selection (now often included in natural selection) and fecundity selection.

Natural selection acts on the phenotype, the characteristics of the organism which actually interact with the environment, but the genetic (heritable) basis of any phenotype that gives that phenotype a reproductive advantage may become more common in a population. Over time, this process can result in populations that specialise for particular ecological niches (microevolution) and may eventually result in speciation (the emergence of new species, macroevolution). In other words, natural selection is a key process in the evolution of a population.

Natural selection is a cornerstone of modern biology. The concept, published by Darwin and Alfred Russel Wallace in a joint presentation in 1858, was elaborated in Darwin's influential 1859 book "On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life". He described natural selection as analogous to artificial selection, a process by which animals and plants with traits considered desirable by human breeders are systematically favoured for reproduction. The concept of natural selection originally developed in the absence of a valid theory of heredity; at the time of Darwin's writing, science had yet to develop modern theories of genetics. The union of traditional Darwinian evolution with subsequent discoveries in classical genetics formed the modern synthesis of the mid-20th century. The addition of molecular genetics has led to evolutionary developmental biology, which explains evolution at the molecular level. While genotypes can slowly change by random genetic drift, natural selection remains the primary explanation for adaptive evolution.

Mechanism

Heritable Variation and Differential Reproduction

During the industrial revolution, pollution killed many lichens, leaving tree trunks dark.

A dark (melanic) morph of the peppered moth largely replaced the formerly usual light morph (both shown here). Since the moths are subject to predation by birds hunting by sight, the colour change offers better camouflage against the changed background, suggesting natural selection at work.

Natural variation occurs among the individuals of any population of organisms. Some differences may improve an individual's chances of surviving and reproducing such that its lifetime reproductive rate is increased, which means that it leaves more offspring. If the traits that give these individuals a reproductive advantage are also heritable, that is, passed from parent to offspring, then there will be differential reproduction, that is, a slightly higher proportion of fast rabbits or efficient algae in the next generation. Even if the reproductive advantage is very slight, over many generations any advantageous heritable trait becomes dominant in the population. In this way the natural environment of an organism "selects for" traits that confer a reproductive advantage, causing evolutionary change, as Darwin described. This gives the appearance of purpose, but in natural selection there is no intentional choice. Artificial selection is purposive where natural selection is not, though biologists often use teleological language to describe it.

The peppered moth exists in both light and dark colours in Great Britain, but during the industrial revolution, many of the trees on which the moths rested became blackened by soot, giving the dark-coloured moths an advantage in hiding from predators. This gave dark-coloured moths a better chance of surviving to produce dark-coloured offspring, and in just fifty years from the first dark moth being caught, nearly all of the moths in industrial Manchester were dark. The balance was reversed by the effect of the Clean Air Act 1956, and the dark moths became rare again, demonstrating the influence of natural selection on peppered moth evolution. A recent study, using image analysis and avian vision models, shows that pale individuals more closely match lichen backgrounds than dark morphs and for the first time quantifies the camouflage of moths to predation risk.

Fitness

The concept of fitness is central to natural selection. In broad terms, individuals that are more "fit" have better potential for survival, as in the well-known phrase "survival of the fittest", but the precise meaning of the term is much more subtle. Modern evolutionary theory defines fitness not by how long an organism lives, but by how successful it is at reproducing. If an organism lives half as long as others of its species, but has twice as many offspring surviving to adulthood, its genes become more common in the adult population of the next generation. Though natural selection acts on individuals, the effects of chance mean that fitness can only really be defined "on average" for the individuals within a population. The fitness of a particular genotype corresponds to the average effect on all individuals with that genotype. A distinction must be made between the concept of "survival of the fittest" and "improvement in fitness". "Survival of the fittest" does not give an "improvement in fitness", it only represents the removal of the less fit variants from a population. A mathematical example of "survival of the fittest" is given by Haldane "The Cost of Natural Selection". Haldane called this process "substitution" or more commonly in biology, this is called "fixation". This is correctly described by the differential survival and reproduction of individuals due to differences in phenotype. On the other hand, "improvement in fitness" is not dependent on the differential survival and reproduction of individuals due to differences in phenotype, it is dependent on the absolute survival of the particular variant. The probability of a beneficial mutation occurring on some member of a population depends on the total number of replications of that variant. The mathematics of "improvement in fitness was described by Kleinman. An empirical example of "improvement in fitness" is given by the Kishony Mega-plate experiment. In this experiment, "improvement in fitness" depends on the number of replications of the particular variant for a new variant to appear that is capable of growing in the next higher drug concentration region. Fixation or substitution is not required for this "improvement in fitness". On the other hand, "improvement in fitness" can occur in an environment where "survival of the fittest" is also acting. The classic Lenski "E. coli long-term evolution experiment" is an example of adaptation in a competitive environment, ("improvement in fitness" during "survival of the fittest"). The probability of a beneficial mutation occurring on some member of the lineage to give improved fitness is slowed by the competition. The variant which is a candidate for a beneficial mutation in this limited carrying capacity environment must first out-compete the "less fit" variants in order to accumulate the requisite number of replications for there to be a reasonable probability of that beneficial mutation occurring.

Competition

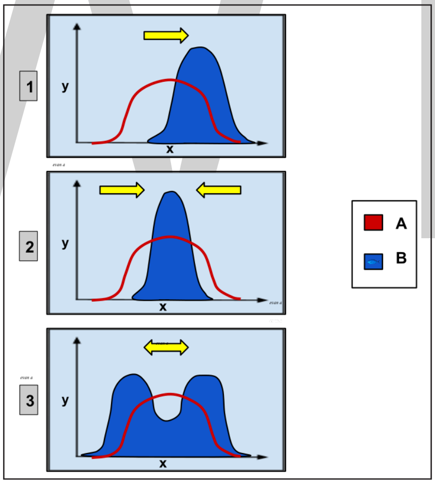
In biology, competition is an interaction between organisms in which the fitness of one is lowered by the presence of another. This may be because both rely on a limited supply of a resource such as food, water, or territory. Competition may be within or between species, and may be direct or indirect. Species less suited to compete should in theory either adapt or die out, since competition plays a powerful role in natural selection, but according to the "room to roam" theory it may be less important than expansion among larger clades.

Competition is modelled by *r/K* selection theory, which is based on Robert MacArthur and E. O. Wilson's work on island biogeography. In this theory, selective pressures drive evolution in one of two stereotyped directions: *r*- or *K*-selection. These terms, *r* and *K*, can be illustrated in a logistic model of population dynamics:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

where *r* is the growth rate of the population (*N*), and *K* is the carrying capacity of its local environmental setting. Typically, *r*-selected species exploit empty niches, and produce many offspring, each with a relatively low probability of surviving to adulthood. In contrast, *K*-selected species are strong competitors in crowded niches, and invest more heavily in much fewer offspring, each with a relatively high probability of surviving to adulthood.

Classification



In figure,

- Directional selection: a single extreme phenotype favoured.
- Stabilizing selection: intermediate favoured over extremes.
- Disruptive selection: extremes favoured over intermediate.
    - X-axis: The phenotypic trait,
    - Y-axis: The number of organisms,
    - Group A: The original population,
    - Group B: After selection.

Natural selection can act on any heritable phenotypic trait, and selective pressure can be produced by any aspect of the environment, including sexual selection and competition with members of the same or other species. However, this does not imply that natural selection is always directional and results in adaptive evolution; natural selection often results in the maintenance of the status quo by eliminating less fit variants.

Selection can be classified in several different ways, such as by its effect on a trait, on genetic diversity, by the life cycle stage where it acts, by the unit of selection, or by the resource being competed for.

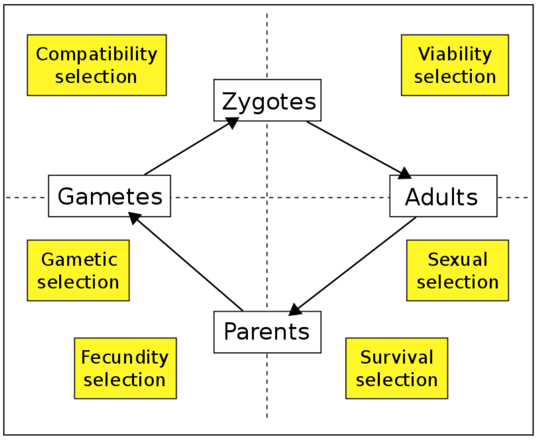
By Effect on a Trait

Selection has different effects on traits. Stabilizing selection acts to hold a trait at a stable optimum, and in the simplest case all deviations from this optimum are selectively disadvantageous. Directional selection favours extreme values of a trait. The uncommon disruptive selection also acts during transition periods when the current mode is sub-optimal, but alters the trait in more than one direction. In particular, if the trait is quantitative and univariate then both higher and lower trait levels are favoured. Disruptive selection can be a precursor to speciation.

By Effect on Genetic Diversity

Alternatively, selection can be divided according to its effect on genetic diversity. Purifying or negative selection acts to remove genetic variation from the population and is opposed by *de novo* mutation, which introduces new variation. In contrast, balancing selection acts to maintain genetic variation in a population, even in the absence of *de novo* mutation, by negative frequency-dependent selection. One mechanism for this is heterozygote advantage, where individuals with two different alleles have a selective advantage over individuals with just one allele. The polymorphism at the human ABO blood group locus has been explained in this way.

By Life Cycle Stage



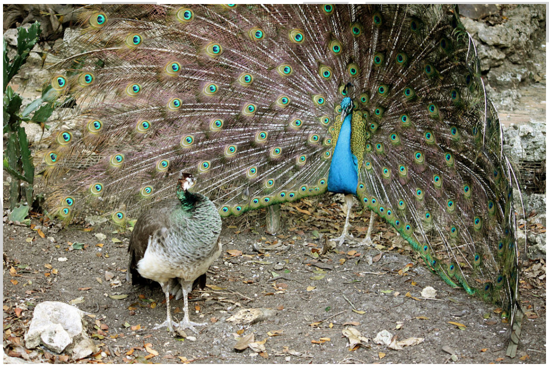
Different types of selection act at each life cycle stage of a sexually reproducing organism.

Another option is to classify selection by the life cycle stage at which it acts. Some biologists recognise just two types: viability (or survival) selection, which acts to increase an organism's probability of survival, and fecundity (or fertility or reproductive) selection, which acts to increase the rate of reproduction, given survival. Others split the life cycle into further components of selection. Thus viability and survival selection may be defined separately and respectively as acting to improve the probability of survival before and after reproductive age is reached, while fecundity selection may be split into additional sub-components including sexual selection, gametic selection, acting on gamete survival, and compatibility selection, acting on zygote formation.

By Unit of Selection

Selection can also be classified by the level or unit of selection. Individual selection acts on the individual, in the sense that adaptations are "for" the benefit of the individual, and result from selection among individuals. Gene selection acts directly at the level of the gene. In kin selection and intragenomic conflict, gene-level selection provides a more apt explanation of the underlying process. Group selection, if it occurs, acts on groups of organisms, on the assumption that groups replicate and mutate in an analogous way to genes and individuals. There is an ongoing debate over the degree to which group selection occurs in nature.

By Resource being Competed for



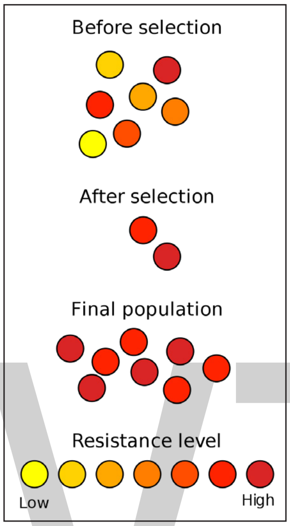
The peacock's elaborate plumage is mentioned by Darwin as an example of sexual selection, and is a classic example of Fisherian runaway, driven to its conspicuous size and coloration through mate choice by females over many generations.

Finally, selection can be classified according to the resource being competed for. Sexual selection results from competition for mates. Sexual selection typically proceeds via fecundity selection, sometimes at the expense of viability. Ecological selection is natural selection via any means other than sexual selection, such as kin selection, competition, and infanticide. Following Darwin, natural selection is sometimes defined as ecological selection, in which case sexual selection is considered a separate mechanism.

Sexual selection as first articulated by Darwin (using the example of the peacock's tail) refers specifically to competition for mates, which can be intrasexual, between individuals of the same sex, that is male–male competition, or intersexual, where one gender chooses mates, most often with males displaying and females choosing. However, in some species, mate choice is primarily by males, as in some fishes of the family Syngnathidae.

Phenotypic traits can be displayed in one sex and desired in the other sex, causing a positive feedback loop called a Fisherian runaway, for example, the extravagant plumage of some male birds such as the peacock. An alternate theory proposed by the same Ronald Fisher in 1930 is the sexy son hypothesis, that mothers want promiscuous sons to give them large numbers of grandchildren and so choose promiscuous fathers for their children. Aggression between members of the same sex is sometimes associated with very distinctive features, such as the antlers of stags, which are used in combat with other stags. More generally, intrasexual selection is often associated with sexual dimorphism, including differences in body size between males and females of a species.

Arms Races



Selection in action: Resistance to antibiotics grows though the survival of individuals less affected by the antibiotic. Their offspring inherit the resistance.

Natural selection is seen in action in the development of antibiotic resistance in microorganisms. Since the discovery of penicillin in 1928, antibiotics have been used to fight bacterial diseases. The widespread misuse of antibiotics has selected for microbial resistance to antibiotics in clinical use, to the point that the methicillin-resistant Staphylococcus aureus (MRSA) has been described as a “superbug” because of the threat it poses to health and its relative invulnerability to existing drugs. Response strategies typically include the use of different, stronger antibiotics; however, new strains of MRSA have recently emerged that are resistant even to these drugs. This is an evolutionary arms race, in which bacteria develop strains less susceptible to antibiotics, while medical researchers attempt to develop new antibiotics that can kill them. A similar situation occurs with pesticide resistance in plants and insects. Arms races are not necessarily induced by man; a well-documented example involves the spread of a gene in the butterfly Hypolimnas bolina suppressing male-killing activity by Wolbachia bacteria parasites on the island of Samoa, where the spread of the gene is known to have occurred over a period of just five years.

Evolution by Means of Natural Selection

A prerequisite for natural selection to result in adaptive evolution, novel traits and speciation is the presence of heritable genetic variation that results in fitness differences. Genetic variation is the result of mutations, genetic recombinations and alterations in the karyotype (the number, shape, size and internal arrangement of the chromosomes). Any of these changes might have an effect that is highly advantageous or highly disadvantageous, but large effects are rare. In the past, most changes in the genetic material were considered neutral or close to neutral because they occurred in noncoding DNA or resulted in a synonymous substitution. However, many mutations in non-coding DNA have deleterious effects. Although both mutation rates and average fitness effects of mutations are dependent on the organism, a majority of mutations in humans are slightly deleterious.

Some mutations occur in "toolkit" or regulatory genes. Changes in these often have large effects on the phenotype of the individual because they regulate the function of many other genes. Most, but not all, mutations in regulatory genes result in non-viable embryos. Some nonlethal regulatory mutations occur in HOX genes in humans, which can result in a cervical rib or polydactyly, an increase in the number of fingers or toes. When such mutations result in a higher fitness, natural selection favours these phenotypes and the novel trait spreads in the population. Established traits are not immutable; traits that have high fitness in one environmental context may be much less fit if environmental conditions change. In the absence of natural selection to preserve such a trait, it becomes more variable and deteriorate over time, possibly resulting in a vestigial manifestation of the trait, also called evolutionary baggage. In many circumstances, the apparently vestigial structure may retain a limited functionality, or may be co-opted for other advantageous traits in a phenomenon known as preadaptation. A famous example of a vestigial structure, the eye of the blind mole-rat, is believed to retain function in photoperiod perception.

Speciation

Speciation requires a degree of reproductive isolation—that is, a reduction in gene flow. However, it is intrinsic to the concept of a species that hybrids are selected against, opposing the evolution of reproductive isolation, a problem that was recognised by Darwin. The problem does not occur in allopatric speciation with geographically separated populations, which can diverge with different sets of mutations. E. B. Poulton realized in 1903 that reproductive isolation could evolve through divergence, if each lineage acquired a different, incompatible allele of the same gene. Selection against the heterozygote would then directly create reproductive isolation, leading to the Bateson–Dobzhansky–Muller model, further elaborated by H. Allen Orr and Sergey Gavrilets. With reinforcement, however, natural selection can favor an increase in pre-zygotic isolation, influencing the process of speciation directly.

Genetic Basis

Genotype and Phenotype

Natural selection acts on an organism's phenotype, or physical characteristics. Phenotype is determined by an organism's genetic make-up (genotype) and the environment in which the organism lives. When different organisms in a population possess different versions of a gene for a certain trait, each of these versions is known as an allele. It is this genetic variation that underlies differences in phenotype. An example is the ABO blood type antigens in humans, where three alleles govern the phenotype.

Some traits are governed by only a single gene, but most traits are influenced by the interactions of many genes. A variation in one of the many genes that contributes to a trait may have only a small effect on the phenotype; together, these genes can produce a continuum of possible phenotypic values.

Directionality of Selection

When some component of a trait is heritable, selection alters the frequencies of the different alleles, or variants of the gene that produces the variants of the trait. Selection can be divided into three classes, on the basis of its effect on allele frequencies: directional, stabilizing, and purifying selection. Directional selection occurs when an allele has a greater fitness than others, so that it increases in frequency, gaining an increasing share in the population. This process can continue until the allele is fixed and the entire population shares the fitter phenotype. Far more common is stabilizing selection, which lowers the frequency of alleles that have a deleterious effect on the phenotype—that is, produce organisms of lower fitness. This process can continue until the allele is eliminated from the population. Purifying selection conserves functional genetic features, such as protein-coding genes or regulatory sequences, over time by selective pressure against deleterious variants.

Some forms of balancing selection do not result in fixation, but maintain an allele at intermediate frequencies in a population. This can occur in diploid species (with pairs of chromosomes) when heterozygous individuals (with just one copy of the allele) have a higher fitness than homozygous individuals (with two copies). This is called heterozygote advantage or over-dominance, of which the best-known example is the resistance to malaria in humans heterozygous for sickle-cell anaemia. Maintenance of allelic variation can also occur through disruptive or diversifying selection, which favours genotypes that depart from the average in either direction (that is, the opposite of over-dominance), and can result in a bimodal distribution of trait values. Finally, balancing selection can occur through frequency-dependent selection, where the fitness of one particular phenotype depends on the distribution of other phenotypes in the population. The principles of game theory have been applied to understand the fitness distributions in these situations, particularly in the study of kin selection and the evolution of reciprocal altruism.

Selection, Genetic Variation and Drift

A portion of all genetic variation is functionally neutral, producing no phenotypic effect or significant difference in fitness. Motoo Kimura's neutral theory of molecular evolution by genetic drift proposes that this variation accounts for a large fraction of observed genetic diversity. Neutral events can radically reduce genetic variation through population bottlenecks which among other things can cause the founder effect in initially small new populations. When genetic variation does not result in differences in fitness, selection cannot directly affect the frequency of such variation. As a result, the genetic variation at those sites is higher than at sites where variation does influence fitness. However, after a period with no new mutations, the genetic variation at these sites is eliminated due to genetic drift. Natural selection reduces genetic variation by eliminating maladapted individuals, and consequently the mutations that caused the maladaptation. At the same time, new mutations occur, resulting in a mutation–selection balance. The exact outcome of the two processes depends both on the rate at which new mutations occur and on the strength of the natural selection, which is a function of how unfavourable the mutation proves to be.

Genetic linkage occurs when the loci of two alleles are in close proximity on a chromosome. During the formation of gametes, recombination reshuffles the alleles. The chance that such a reshuffle occurs between two alleles is inversely related to the distance between them. Selective sweeps occur when an allele becomes more common in a population as a result of positive selection. As the prevalence of one allele increases, closely linked alleles can also become more common by "genetic hitchhiking", whether they are neutral or even slightly deleterious. A strong selective sweep results in a region of the genome where the positively selected haplotype (the allele and its neighbours) are in essence the only ones that exist in the population. Selective sweeps can be detected by measuring linkage disequilibrium, or whether a given haplotype is overrepresented in the population. Since a selective sweep also results in selection of neighbouring alleles, the presence of a block of strong linkage disequilibrium might indicate a 'recent' selective sweep near the centre of the block.

Background selection is the opposite of a selective sweep. If a specific site experiences strong and persistent purifying selection, linked variation tends to be weeded out along with it, producing a region in the genome of low overall variability. Because background selection is a result of deleterious new mutations, which can occur randomly in any haplotype, it does not produce clear blocks of linkage disequilibrium, although with low recombination it can still lead to slightly negative linkage disequilibrium overall.

Impact

Darwin's ideas, along with those of Adam Smith and Karl Marx, had a profound influence on 19th century thought, including his radical claim that "elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner" evolved from the simplest forms of life by a few simple principles. This inspired some of Darwin's most ardent supporters—and provoked the strongest opposition. Natural selection had the power, according to Stephen Jay Gould, to "dethrone some of the deepest and most traditional comforts of Western thought", such as the belief that humans have a special place in the world.

In the words of the philosopher Daniel Dennett, "Darwin's dangerous idea" of evolution by natural selection is a "universal acid," which cannot be kept restricted to any vessel or container, as it soon leaks out, working its way into ever-wider surroundings. Thus, in the last decades, the concept of natural selection has spread from evolutionary biology to other disciplines, including evolutionary computation, quantum Darwinism, evolutionary economics, evolutionary epistemology, evolutionary psychology, and cosmological natural selection. This unlimited applicability has been called universal Darwinism.

Abiogenesis

How life originated from inorganic matter remains an unresolved problem in biology. One prominent hypothesis is that life first appeared in the form of short self-replicating RNA polymers. On this view, life may have come into existence when RNA chains first experienced the basic conditions, as conceived by Charles Darwin, for natural selection to operate. These conditions are: heritability, variation of type, and competition for limited resources. The fitness of an early RNA replicator would likely have been a function of adaptive capacities that were intrinsic (i.e., determined by the nucleotide sequence) and the availability of resources. The three primary adaptive capacities could logically have been: (1) the capacity to replicate with moderate fidelity (giving rise to both heritability and variation of type), (2) the capacity to avoid decay, and (3) the capacity to acquire and process resources. These capacities would have been determined initially by the folded configurations (including those configurations with ribozyme activity) of the RNA replicators that, in turn, would have been encoded in their individual nucleotide sequences.

Cell and Molecular Biology

In 1881, the embryologist Wilhelm Roux published Der Kampf der Theile im Organismus (The Struggle of Parts in the Organism) in which he suggested that the development of an organism results from a Darwinian competition between the parts of the embryo, occurring at all levels, from molecules to organs. In recent years, a modern version of this theory has been proposed by Jean-Jacques Kupiec. According to this cellular Darwinism, random variation at the molecular level generates diversity in cell types whereas cell interactions impose a characteristic order on the developing embryo.

Social and Psychological Theory

The social implications of the theory of evolution by natural selection also became the source of continuing controversy. Friedrich Engels, a German political philosopher and co-originator of the ideology of communism, wrote in 1872 that "Darwin did not know what a bitter satire he wrote on mankind, and especially on his countrymen, when he showed that free competition, the struggle for existence, which the economists celebrate as the highest historical achievement, is the normal state of the animal kingdom." Herbert Spencer and the eugenics advocate Francis Galton's interpretation of natural selection as necessarily progressive, leading to supposed advances in intelligence and civilisation, became a justification for colonialism, eugenics, and social Darwinism. For example, in 1940, Konrad Lorenz, in writings that he subsequently disowned, used the theory as a justification for policies of the Nazi state. He wrote "selection for toughness, heroism, and social utility must be accomplished by some human institution, if mankind, in default of selective factors, is not to be ruined by domestication-induced degeneracy. The racial idea as the basis of our state has already accomplished much in this respect." Others have developed ideas that human societies and culture evolve by mechanisms analogous to those that apply to evolution of species.

More recently, work among anthropologists and psychologists has led to the development of sociobiology and later of evolutionary psychology, a field that attempts to explain features of human psychology in terms of adaptation to the ancestral environment. The most prominent example of evolutionary psychology, notably advanced in the early work of Noam Chomsky and later by Steven Pinker, is the hypothesis that the human brain has adapted to acquire the grammatical rules of natural language. Other aspects of human behavior and social structures, from specific cultural norms such as incest avoidance to broader patterns such as gender roles, have been hypothesised to have similar origins as adaptations to the early environment in which modern humans evolved. By analogy to the action of natural selection on genes, the concept of memes— "units of cultural transmission," or culture's equivalents of genes undergoing selection and recombination—has arisen, first described in this form by Richard Dawkins in 1976 and subsequently expanded upon by philosophers such as Daniel Dennett as explanations for complex cultural activities, including human consciousness.

Information and Systems Theory

In 1922, Alfred J. Lotka proposed that natural selection might be understood as a physical principle that could be described in terms of the use of energy by a system, a concept later developed by Howard T. Odum as the maximum power principle in thermodynamics, whereby evolutionary systems with selective advantage maximise the rate of useful energy transformation.

The principles of natural selection have inspired a variety of computational techniques, such as “soft” artificial life, that simulate selective processes and can be highly efficient in ‘adapting’ entities to an environment defined by a specified fitness function. For example, a class of heuristic optimisation algorithms known as genetic algorithms, pioneered by John Henry Holland in the 1970s and expanded upon by David E. Goldberg, identify optimal solutions by simulated reproduction and mutation of a population of solutions defined by an initial probability distribution. Such algorithms are particularly useful when applied to problems whose energy landscape is very rough or has many local minima.

BEHAVIOR MUTATION

A behavior mutation is a genetic mutation that alters genes that control the way in which an organism behaves, causing their behavioral patterns to change.

A mutation is a change or error in the genomic sequence of a cell. It can occur during meiosis or replication of DNA, as well as due to ionizing or UV radiation, transposons, mutagenic chemicals, viruses and a number of other factors. Mutations usually (but not always) result in a change in an organisms fitness. These changes are largely deleterious, having a negative effect on fitness; however, they can also be neutral and even advantageous.

It is theorized that these mutations, along with genetic recombination, are the raw material upon which natural selection can act to form evolutionary processes. This is due to selection’s tendency to “pick and choose” mutations which are advantageous and pass them on to an organism’s offspring, while discarding deleterious mutations. In asexual lineages, these mutations will always be passed on, causing them to become a crucial factor in whether the lineage will survive or go extinct.

One way that mutations manifest themselves is behavior mutation. Some examples of this could be variations in mating patterns, increasingly aggressive or passive demeanor, how an individual learns and the way an individual interacts and coordinates with others.

Behavior mutations have important implications on the nature of the evolution of animal behavior. They can help us understand how different forms of behavior evolve, especially behavior which can seem strange or out of place. In other cases, they can help us understand how important patterns of behavior were able to arise — on the back of a simple gene mutation. Finally, they can help provide key insight on the nature of speciation events which can occur when a behavior mutation changes the courtship methods and manner of mating in sexually reproducing species.

Notable Experiments

Behavior mutations have been studied in a variety of animals, but most commonly in Drosophila melanogaster due to being able to produce large numbers with short generation time as well as a rich diversity of behaviors. Many tests have been used in drosophila by specifying behavioral mutations to further understand the nervous system. In order to understand how behavior is controlled by the nervous system, it’s key to identify the neuronal substrates important for the specific activity studied, as well as to explain how they are incorporated into a functional circuit. Most tests used allowed researchers to directly observe the mutation, such as altering phototaxis or flight-reduction. It was also shown in some experiments that certain mutations affect experience-based behavior. Behavioral mutation has also been extensively tested in mice.

In one test involving Drosophila, a temperature-sensitive allele of shibire is overexpressed in neuronal subsets using the GAL4/UAS system. The shi gene is used for synaptic vesicle recycling, and a change in the temperature would cause an accelerated and reversible effect on the synaptic transmission of shi expressing neurons. When shi was tested to cholinergic neurons, the flies showed a quick response to the temperature and were paralyzed within two minutes at 30 degrees, which was reversible. When shi was expressed in photoreceptor cell, fly larva showed temporary temperature-dependent blindness. This experiment shows that shi can be expressed in specific neurons to cause temperature-dependent alterations in behaviors.

In more recent studies, the Zebrafish ennui mutation was identified from mutagenesis identification for defects in early behavior. Homozygous ennui embryo swam more slowly than the wild-type but gained normal swimming as it aged. When tested, the motor output of the central nervous system following mechano-sensory stimulation was normal in ennui, which means that the reaction-time and reaction-style was normal to the wild-types and the motoneuron were not affected. The synaptic current at the neuromuscular junction was significantly reduced in ennui which means that the neuromuscular junction was affected. The acetylcholine receptor were significantly reduced in the adult ennui in size as well as localization at the myotome segment borders of fast-twitch muscles. Genetic mosaic analysis revealed that ennui is necessary cell autonomously in muscle fibers for normal synaptic localization of acetylcholine receptors. Also, ennui is very important for agrin function. Ennui is very important in nerve-dependent acetylcholine clustering and the stability of axon growth.

Behavioral Degradation under Spontaneous Mutation Accumulation

In each generation, the genetic variation within a population increases due to accumulation of mutations and decreases in response to natural selection and genetic drift. Mutation accumulation occurs when mutations of small effect accumulate at certain loci, yielding a large phenotypic effect in the aggregate. Multiple genes may simultaneously affect behavioral traits. Spontaneous mutations arise from sources including errors in DNA replication, spontaneous lesions, and transposable genetic elements in the absence of mutagens. Spontaneous mutations play a central role in the maintenance of genetic variation and persistence of natural population of many organisms.

Evolutionary biologists have used mutation accumulation experiments, in which mutations are allowed to drift to fixation in inbred lines, to study the effect of spontaneous mutations on phenotype character. Phenotypic assays significantly determine whether and how quickly population with accumulated deleterious mutational loads can result in degradation of behavioral responses over time.

Based on laboratory experimental evolution with long-term mutation accumulation (MA) lines of the nematode Caenorhabditis elegans, a team of researchers at the University of Oregon investigated that mutation accumulation of behavior is capable of generating significant levels of individual variation in ecologically relevant behavioral traits within populations. This variation will be dependent largely on the genetic structure and demographic characteristics of individuals. As a result, small or isolated populations are at high risk of experiencing behavioral degradation. For instance, the rate of mutation for behavioral traits has more effects for behavioral mutation within captive populations and some endangered species. The study of two closely related behavioral traits of the free-living soil nematode C. elegans, chemotaxis and locomotion, indicates that behavioral degradation is a direct source of competitive fitness loss under genomic mutation accumulation.

Raymond B. Huey and his colleagues used the same MA lines method, suggesting that mutation accumulation in Drosophila melanogaster significantly depresses only some behavioral traits. There are several explanations for this. It is possible that traits are influenced only by few loci so that their mutational target is small. Alternatively, the values of the behavioral traits are not maximized by directional selection, but rather are under the influence of stabilizing selection. Since behavioral traits are highly variable, mutation accumulation does not negatively affect all traits equivalently.

Sex-ratio Behavior

The study of sex allocation has provided some of the most convincing tests of adaptive behavior. Theory predicts that organisms can adjust the allocation of resources to male and female offspring in response to environmental conditions. Sex ratio behavior is the sex ratio response of a female in various conditions. Mutation accumulation is important because it is one evolutionary cause that increases variation between individuals in sex-ratio behavior. For example, female wasps can adjust their offspring sex ratios by choosing whether to fertilize an egg because they are haplodiploid. In particular, female Nasonia vitripennis produce less males when laying eggs alone, and more males when laying eggs on a patch with other females. If female parasitoid wasps produce too few male offspring, then some of the female offspring will remain unmated. On the other hand, if too many sons are produced, then resources are wasted that could have been used to produce more daughters. Females of other strains show no similar conditional sex ratio behaviors. Researchers find that these behaviors are indeed subject to genetic variation. However, genetic variation in natural population is low and it has low heritability as for other fitness-related traits. The observation of this type of behavioral mutation has been argued to pose a problem for sex-ratio theory because the mutations are likely to have decreased fitness.

Mutations Affecting Passive and Aggressive Characteristics

Aggression is a survival trait that can be favoured by Natural Selection in nearly any species. Aggressive individuals can be better able to compete for resources including food, territory and mates, as well as more successful in protecting themselves and their progeny from predators. It can also be energetically costly, and extreme or out of context aggression can be disadvantageous or deleterious, especially in social organisms. Aggression is a complex trait that is regulated by many interacting genes and gene expression is highly variable depending on environment (phenotypic plasticity). Mutations in genes that influence aggressive behaviors can potentially increase aggression or passivity.

Neurotransmitters

Neurotransmitters, dopamine and serotonin in particular, play an important role in the regulation of aggressive behaviors. Many studies are focused on genes that change the way neurotransmitters interact with receptors within the organism. For example, when individuals suffer from a mutation that causes them to have low levels of serotonin, there is an observed increase in impulsivity and depression. With neurotranmitters playing such a central role in the development of aggressive behavior, it isn't surprising that many of the gene mutations that have been implicated with aggressive behaviors are involved in the breakdown and receipt of neurotransmitters.

Alexis Edwards and her team identified 59 mutations in 57 genes that affected aggressive behavior in Drosophila melanogaster. The results of their research showed that 32 of the mutants displayed increased aggression and 27 of the mutants displayed less aggression than the control group. Several of the genes examined were found to affect nervous system development and function. Aggression was assessed in this experiment by depriving mutant Drosophila flies from food and then allowing them to defend a limited food source. The number of contest competitions between flies was recorded and compared to non-mutant flies to assess whether the mutants were more or less aggressive than the wild type. Examples of mutations that increase aggression are mutations in the fruitless or dissatisfaction genes which result in observable increases in male-male aggression.

Amines

Mutations involving amines have been shown to be a prevalent source of changes in behavior. A point mutation in the structural gene for Monoamine Oxidase A, also known as MAO-A, is responsible for the breakdown of neurotransmitters. This mutation is X-linked, affecting only males, and eliminates the production of MAO-A. Males afflicted with this mutation are prone to mild mental retardation as well as violent and antisocial behavior. Another amine affecting aggression is β-alanine which is a bioamine neurotransmitter that has been implicated in Drosophila aggression. A mutation known as the *black* mutation causes reduced levels of β-alanine and results in less reactive flies than the wild type.

Testosterone

In nearly all species, there is an obvious disequilibrium between frequency and severity of aggression in males versus females. Males are almost always the more aggressive sex and there are genetic differences that back up this observation. A common explanation for this phenomenon is the higher testosterone levels in males. Testosterone levels have a direct effect on neurotransmitter functioning contributing to physical aggression. Mutations affecting neurotransmitters, as stated above, are the dominanting cause of changes in aggressive behavior. Another contributors to the unequal male-female aggression ratio are the sex-linked gene mutations that affect only male behavior, such as MAO-A mentioned above. These mutations could be the reason why males are nearly always more aggressive than females, although, testosterone levels are a much more feasible explanation.

Other evolutionary and genetic explanations of violent behavior include: dopamine receptors mutations, DRD2 and DRD4, that, when mutate simultaneously, are hypothesized to cause personality disorders, low serotonin levels increasing irritability and gloom and the effects of testosterone on neurotransmitter functioning to explain the increased occurrence of aggression in males.

Effects of Mutations on Mating

Behavioral mutations play a detrimental part towards the genomes of many species, however they can greatly affect the outcome of mating; affecting the success of fitness, how many offspring will arise and the likelihood that the male will actually procreate. When mutations affect the mating habits of species, different traits that would otherwise benefit the species procreating are compromised.

A couple chemicals that are altered from mutation and have a great impact on mating, are dopamine and serotonin. Each of these chemicals either has a reaction to how the animal acts, or how the species body is formed to benefit their mating success. An example of a mutation in serotonin was found in a species of Nematodes. The serotonin caused their tails to curl during mating, when the mutation occurred the tails did not curl. Without the curling of the tail the nematode was unlikely to find the hermaphrodites sex organs to procreate, and results in less of that nematodes sperm being spread to other offspring. Another example is when the D1 dopamine receptor has a mutation on it; the arousal of a Drosophila melanogaster is increased, which also increases the courtship of the animal.

One example of a study was found in the 'yellow' D. melanogaster, the mating of these males was only beneficial when it was dark outside, or when they were in a dark environment. The mutation is not yet known why it occurs this way, but studies have mentioned that the females of this fly species may be turned off by the certain colour of the mutated fly, and therefore in the dark the female is less likely to tell what colour this fly is.

A beneficial component of a mutation in the behavior of a mating *D. melanogaster*, was when the mutation caused the male to have a longer courtship time period. The flies that had a longer courtship had a tendency to have a higher probability of procreating. This means that the fly that took longer to actually initiate the courtship with the female fly, was more likely to be successful with the female successfully accepting the male.

BIOLOGICAL ALTRUISM

Altruistic behavior is common throughout the animal kingdom, particularly in species with complex social structures. For example, vampire bats regularly regurgitate blood and donate it to other members of their group who have failed to feed that night, ensuring they do not starve. In numerous bird species, a breeding pair receives help in raising its young from other 'helper' birds, who protect the nest from predators and help to feed the fledglings. Vervet monkeys give alarm calls to warn fellow monkeys of the presence of predators, even though in doing so they attract attention to themselves, increasing their personal chance of being attacked. In social insect colonies (ants, wasps, bees and termites), sterile workers devote their whole lives to caring for the queen, constructing and protecting the nest, foraging for food, and tending the larvae. Such behavior is maximally altruistic: sterile workers obviously do not leave any offspring of their own—so have personal fitness of zero—but their actions greatly assist the reproductive efforts of the queen.

From a Darwinian viewpoint, the existence of altruism in nature is at first sight puzzling, as Darwin himself realized. Natural selection leads us to expect animals to behave in ways that increase their own chances of survival and reproduction, not those of others. But by behaving altruistically an animal reduces its own fitness, so should be at a selective disadvantage with regards to one which behaves selfishly. To see this, imagine that some members of a group of Vervet monkeys give alarm calls when they see predators, but others do not. Other things being equal, the latter will have an advantage. By selfishly refusing to give an alarm call, a monkey can reduce the chance that it will itself be attacked, while at the same time benefiting from the alarm calls of others. So we should expect natural selection to favour those monkeys that do not give alarm calls over those that do.

Altruism and the Levels of Selection

The problem of altruism is intimately connected with questions about the level at which natural selection acts. If selection acts exclusively at the individual level, favouring some individual organisms over others, then it seems that altruism cannot evolve, for behaving altruistically is disadvantageous for the individual organism itself. However, it is possible that altruism may be advantageous at the group level. A group containing lots of altruists, each ready to subordinate their own selfish interests for the greater good of the group, may well have a survival advantage over a group composed mainly or exclusively of selfish organisms. A process of between-group selection may thus allow the altruistic behavior to evolve. Within each group, altruists will be at a selective disadvantage relative to their selfish colleagues, but the fitness of the group as a whole will be enhanced by the presence of altruists. Groups composed only or mainly of selfish organisms go extinct, leaving behind groups containing altruists. In the example of the Vervet monkeys, a group containing a high proportion of alarm-calling monkeys will have a survival advantage over a group containing a lower proportion. So conceivably, the alarm-calling behavior may evolve by between-group selection, even though within each group, selection favours monkeys that do not give alarm calls.

The idea that group selection might explain the evolution of altruism was first broached by Darwin himself.

The concept of group selection has a chequered and controversial history in evolutionary biology. The founders of modern neo-Darwinism—R.A. Fisher, J.B.S. Haldane and S. Wright—were all aware that group selection could in principle permit altruistic behaviors to evolve, but they doubted the importance of this evolutionary mechanism. Nonetheless, many mid-twentieth century ecologists and some ethologists, notably Konrad Lorenz, routinely assumed that natural selection would produce outcomes beneficial for the whole group or species, often without even realizing that individual-level selection guarantees no such thing. This uncritical 'good of the species' tradition came to an abrupt halt in the 1960s, due largely to the work of G.C. Williams and J. Maynard Smith. These authors argued that group selection was an inherently weak evolutionary force, hence unlikely to promote interesting altruistic behaviors. This conclusion was supported by a number of mathematical models, which apparently showed that group selection would only have significant effects for a limited range of parameter values. As a result, the notion of group selection fell into widespread disrepute in orthodox evolutionary circles.

The major weakness of group selection as an explanation of altruism, according to the consensus that emerged in the 1960s, was a problem that Dawkins called 'subversion from within'. Even if altruism is advantageous at the group level, within any group altruists are liable to be exploited by selfish 'free-riders' who refrain from behaving altruistically. These free-riders will have an obvious fitness advantage: they benefit from the altruism of others, but do not incur any of the costs. So even if a group is composed exclusively of altruists, all behaving nicely towards each other, it only takes a single selfish mutant to bring an end to this happy idyll. By virtue of its relative fitness advantage within the group, the selfish mutant will out-reproduce the altruists, hence selfishness will eventually swamp altruism. Since the generation time of individual organisms is likely to be much shorter than that of groups, the probability that a selfish mutant will arise and spread is very high, according to this line of argument. 'Subversion from within' is generally regarded as a major stumbling block for group-selectionist theories of the evolution of altruism.

In the 1960s and 1970s a rival theory emerged: kin selection or 'inclusive fitness' theory, due originally to Hamilton. This theory, apparently showed how altruistic behavior could evolve without the need for group-level selection, and quickly gained prominence among biologists interested in the evolution of social behavior; the empirical success of kin selection theory contributed to the demise of the group selection concept. However, the precise relation between kin and group selection is a source of ongoing controversy. Since the 1990s, proponents of 'multi-level selection theory' have resuscitated a form of group-level selection—sometimes called 'new' group selection—and shown that it can permit altruism to evolve. But 'new' group selection turns out to be mathematically equivalent to kin selection in most if not all cases, as a number of authors have emphasized; this point was already appreciated by Hamilton. Since the relation between 'old' and 'new' group selection is itself a point of controversy, this explains why disagreement about the relation between kin and group selection should persist.

Kin Selection and Inclusive Fitness

The basic idea of kin selection is simple. Imagine a gene which causes its bearer to behave altruistically towards other organisms, e.g. by sharing food with them. Organisms without the gene are selfish—they keep all their food for themselves, and sometimes get handouts from the altruists. Clearly the altruists will be at a fitness disadvantage, so we should expect the altruistic gene to be eliminated from the population. However, suppose that altruists are discriminating in who they share food with. They do not share with just anybody, but only with their relatives. This immediately changes things. For relatives are genetically similar—they share genes with one another. So when an organism carrying the altruistic gene shares his food, there is a certain probability that the recipients of the food will also carry copies of that gene. How probable depends on how closely related they are. This means that the altruistic gene can in principle spread by natural selection. The gene causes an organism to behave in a way which reduces its own fitness but boosts the fitness of its relatives—who have a greater than average chance of carrying the gene themselves. So the overall effect of the behavior may be to increase the number of copies of the altruistic gene found in the next generation, and thus the incidence of the altruistic behavior itself.

Though this argument was hinted at by Haldane in the 1930s, and to a lesser extent by Darwin in his discussion of sterile insect castes in "The Origin of Species", it was first made explicit by William Hamilton in a pair of seminal papers. Hamilton demonstrated rigorously that an altruistic gene will be favoured by natural selection when a certain condition, known as Hamilton's rule, is satisfied. In its simplest version, the rule states that $b > c/r$, where c is the cost incurred by the altruist (the donor), b is the benefit received by the recipients of the altruism, and r is the co-efficient of relationship between donor and recipient. The costs and benefits are measured in terms of reproductive fitness. The co-efficient of relationship depends on the genealogical relation between donor and recipient—it is defined as the probability that donor and recipient share genes at a given locus that are 'identical by descent'. Two genes are identical by descent if they are copies of a single gene in a shared ancestor. In a sexually reproducing diploid species, the value of r for full siblings is ½, for parents and offspring ½, for grandparents and grandoffspring ¼, for full cousins 1/8, and so-on. The higher the value of r, the greater the probability that the recipient of the altruistic behavior will also possess the gene for altruism. So what Hamilton's rule tells us is that a gene for altruism can spread by natural selection, so long as the cost incurred by the altruist is offset by a sufficient amount of benefit to sufficiently closed related relatives. The proof of Hamilton's rule relies on certain non-trivial assumptions.

Though Hamilton himself did not use the term, his idea quickly became known as 'kin selection', for obvious reasons. Kin selection theory predicts that animals are more likely to behave altruistically towards their relatives than towards unrelated members of their species. Moreover, it predicts that the degree of altruism will be greater, the closer the relationship. In the years since Hamilton's theory was devised, these predictions have been amply confirmed by empirical work. For example, in various bird species, it has been found that 'helper' birds are much more likely to help relatives raise their young, than they are to help unrelated breeding pairs. Similarly, studies of Japanese macaques have shown that altruistic actions, such as defending others from attack, tend to be preferentially directed towards close kin. In most social insect species, a peculiarity of the genetic system known as 'haplodiploidy' means that females on average share more genes with their sisters than with their own offspring. So a female may well be able to get more genes into the next generation by helping the queen reproduce, hence increasing the number of sisters she will have, rather than by having offspring of her own. Kin selection theory therefore provides a neat explanation of how sterility in the social insects may have evolved by Darwinian means. Note, however, that the precise significance of haplodiploidy for the evolution of worker sterility is a controversial question.

Kin selection theory is often presented as a triumph of the 'gene's-eye view of evolution', which sees organic evolution as the result of competition among genes for increased representation in the gene-pool, and individual organisms as mere 'vehicles' that genes have constructed to aid their propagation. The gene's eye-view is certainly the easiest way of understanding kin selection, and was employed by Hamilton himself in 1964. Altruism seems anomalous from the individual organism's point of view, but from the gene's point of view it makes good sense. A gene wants to maximize the number of copies of itself that are found in the next generation; one way of doing that is to cause its host organism to behave altruistically towards other bearers of the gene, so long as the costs and benefits satisfy the Hamilton inequality. But interestingly, Hamilton showed that kin selection can also be understood from the organism's point of view. Though an altruistic behavior which spreads by kin selection reduces the organism's personal fitness, it increases what Hamilton called the organism's inclusive fitness. An organism's inclusive fitness is defined as its personal fitness, plus the sum of its weighted effects on the fitness of every other organism in the population, the weights determined by the coefficient of relationship r. Given this definition, natural selection will act to maximise the inclusive fitness of individuals in the population. Instead of thinking in terms of selfish genes trying to maximize their future representation in the gene-pool, we can think in terms of organisms trying to maximize their inclusive fitness. Most people find the 'gene's eye' approach to kin selection heuristically simpler than the inclusive fitness approach, but mathematically they are in fact equivalent.

Contrary to what is sometimes thought, kin selection does not require that animals must have the ability to discriminate relatives from non-relatives, less still to calculate coefficients of relationship. Many animals can in fact recognize their kin, often by smell, but kin selection can operate in the absence of such an ability. Hamilton's inequality can be satisfied so long as an animal behaves altruistically towards others animals that are in fact its relatives. The animal might achieve this by having the ability to tell relatives from non-relatives, but this is not the only possibility. An alternative is to use some proximal indicator of kinship. For example, if an animal behaves altruistically towards those in its immediate vicinity, then the recipients of the altruism are likely to be relatives, given that relatives tend to live near each other. No ability to recognize kin is presupposed. Cuckoos exploit precisely this fact, free-riding on the innate tendency of birds to care for the young in their nests.

Another popular misconception is that kin selection theory is committed to 'genetic determinism', the idea that genes rigidly determine or control behavior. Though some sociobiologists have made incautious remarks to this effect, evolutionary theories of behavior, including kin selection, are not committed to it. So long as the behaviors in question have a genetical component, i.e. are influenced to some extent by one or more genetic factor, then the theories can apply. When Hamilton talks about a gene which causes altruism, this is really shorthand for a gene which increases the probability that its bearer will behave altruistically, to some degree. This is much weaker than saying that the behavior is genetically 'determined', and is quite compatible with the existence of strong environmental influences on the behavior's expression. Kin selection theory does not deny the truism that all traits are affected by both genes and environment. Nor does it deny that many interesting animal behaviors are transmitted through non-genetical means, such as imitation and social learning.

The importance of kinship for the evolution of altruism is very widely accepted today, on both theoretical and empirical grounds. However, kinship is really only a way of ensuring that altruists and recipients both carry copies of the altruistic gene, which is the fundamental requirement. If altruism is to evolve, it must be the case that the recipients of altruistic actions have a greater than average probability of being altruists themselves. Kin-directed altruism is the most obvious way of satisfying this condition, but there are other possibilities too. For example, if the gene that causes altruism also causes animals to favour a particular feeding ground (for whatever reason), then the required correlation between donor and recipient may be generated. It is this correlation, however brought about, that is necessary for altruism to evolve.

THE EFFECTS OF MUTATIONS

Since all cells in our body contain DNA, there are lots of places for mutations to occur; however, some mutations cannot be passed on to offspring and do not matter for evolution. Somatic mutations occur in non-reproductive cells and won't be passed onto offspring.

The only mutations that matter to large-scale evolution are those that can be passed on to offspring. These occur in reproductive cells like eggs and sperm and are called germ line mutations.

Effects of Germ Line Mutations

A single germ line mutation can have a range of effects:

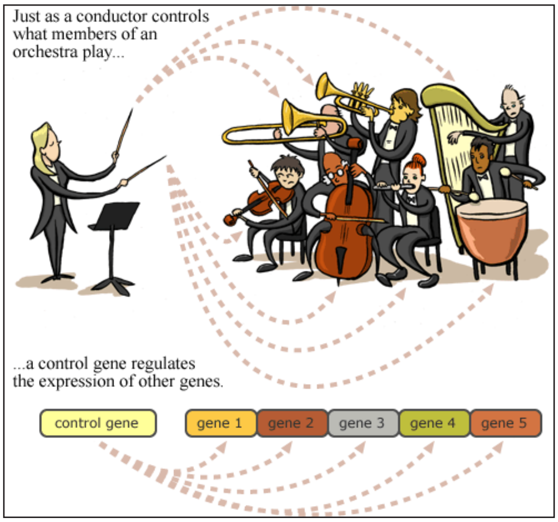
1. No change occurs in phenotype: Some mutations don't have any noticeable effect on the phenotype of an organism. This can happen in many situations: perhaps the mutation occurs in a stretch of DNA with no function, or perhaps the mutation occurs in a protein-coding region, but ends up not affecting the amino acid sequence of the protein.

2. Small change occurs in phenotype: A single mutation caused this cat's ears to curl backwards slightly.
3. Big change occurs in phenotype: Some really important phenotypic changes, like DDT resistance in insects are sometimes caused by single mutations. A single mutation can also have strong negative effects for the organism. Mutations that cause the death of an organism are called lethals and it doesn't get more negative than that.

Little Mutations with Big Effects: Mutations to Control Genes

Mutations are often the victims of bad press — unfairly stereotyped as unimportant or as a cause of genetic disease. While many mutations do indeed have small or negative effects, another sort of mutation gets less airtime. Mutations to control genes can have major (and sometimes positive) effects.

Some regions of DNA control other genes, determining when and where other genes are turned on. Mutations in these parts of the genome can substantially change the way the organism is built. The difference between a mutation to a control gene and a mutation to a less powerful gene is a bit like the difference between whispering an instruction to the trumpet player in an orchestra versus whispering it to the orchestra's conductor. The impact of changing the conductor's behavior is much bigger and more coordinated than changing the behavior of an individual orchestra member. Similarly, a mutation in a gene "conductor" can cause a cascade of effects in the behavior of genes under its control.



Many organisms have powerful control genes that determine how the body is laid out. For example, Hox genes are found in many animals (including flies) and designate where the head goes and which regions of the body grow appendages. Such master control genes help direct the building of body "units," such as segments, limbs, and eyes. So evolving a major change in basic body layout may not be so unlikely; it may simply require a change in a Hox gene and the favor of natural selection.

INFLUENCE OF ENVIRONMENT AND GENETIC MAKEUP ON ANIMAL BEHAVIOR

Both genes and the environment influence behavior. Genes, via their influences on morphology and physiology, create a framework within which the environment acts to shape the behavior of an individual animal. The environment can affect morphological and physiological development; in turn behavior develops as a result of that animal's shape and internal workings. Genes also create the scaffold for learning, memory, and cognition, remarkable mechanisms that allow animals to acquire and store information about their environment for use in shaping their behavior.

Instinct and Behavior

Instinctive, or hard-wired, behavior captured the interest of Charles Darwin, and later, of the ethologists such as Niko Tinbergen. Instinct implies that a behavior is performed without thought and cannot be modified by learning. Examples of instinctive behavior include simple behavioral patterns, displayed in response to a specific stimulus or within a specific context. A cockroach flees to the protection of a dark nook when a light is switched on. A dog may circle on its bedding several times, as if it were trampling vegetation, before settling to sleep. A rattlesnake will strike at a moving, mouse sized, warm object. In none of these cases does the animal engage in learning or thought when shaping its response. Genetic (innate) information best determines behavior when a species' environment varies little from generation to generation, or in communication when unambiguous messages need to be sent and received.

A rattlesnake, ready to strike.

Similarly, many of the signals used in animal communication are innate, produced the same way by all members of a species. The constancy that comes from having the signal and its interpretation genetically encoded makes the message unambiguous. Combinations of facial expressions, hair erection, and tail posture give dogs (to other dogs) a universal set of messages. Other animals use combinations of genetic and learned information in forming their signals. Some birds can produce elements of their songs without ever having heard another bird sing, but require hearing songs during development to reproduce the song of their own species correctly. This last example demonstrates how innate components can be used as building blocks for modifiable behavior, but animal behavior can be innate, reflecting a strong genetic basis.

Imprinting and Development

Imprinting involves the ability to learn a specific essential piece of information at the right stage of development. Openness for learning through imprinting is restricted to a short time span, called a critical period. The most famous example of imprinting comes from Konrad Lorenz and his geese. He found that goslings learn to recognize their mother (and to tell her from other geese) very early in life. By substituting himself for the mother goose at the right developmental stage, he could get the goslings to imprint on him, and faithfully follow him wherever he went. The openness of goslings for learning a leader, even if it does not resemble a goose, is intriguing. Imprinting demonstrates how genes can largely shape a behavior, but that evolution can create a window for learning important information about variation in the environment.

A Canada goose family.

Imprinting provides an opportunity to learn key variable components in an environment while retaining largely innate behavioral patterns. More flexibility may be shown in the development of food preferences, as food availability can vary from habitat to habitat, or from season to season. Insects may imprint on the chemistry of the leaves they eat as caterpillars; when they become adults they then choose to lay their eggs on plants with a chemistry that matches the leaves they ate when young. This insures a suitable diet for the next generation. Young birds and mammals often learn food preferences based on food shared by adults, on observations of feeding preferences of adults, and on sampling possible food items.

Another form of learning involves aversions, which can develop at any point in any animal's life. Birds and mammals develop lifelong aversions to specific foods that contain poisons that cause sickness (such as monarch butterflies). In contrast, some preferences and aversions appear to be innate, or at least to be driven by physiological needs for certain nutrients, such as salt.

Learning about Specific Environments

Many animals learn key information for survival. These abilities are often very specific to a particular context. A species may be very adept at learning facts that are relevant to its survival, but not be able to employ learning across a broad range of situations that did not occur in its evolutionary history. For example, native birds in Guam were completely unequipped to learn how to evade predation by brown tree snakes, which were introduced into Guam about 1950.

An eastern fox squirrel.

Another good example of this comes from animals that store (or cache) food. Caching is an adaptation to cope with food supplies that are abundant during a short season, such as fruits and the nuts from trees. Some animals cache their food at a central location. Honeybees storing honey exemplify this, and centralized caches can require strong defense against thieves, a notable ability of honeybees. Alternatively, cached food can be scattered through the habitat; tree squirrels and gray jays are notable for scatter caching (this is sometimes called scatter hoarding). Scatter caching of food stands out as a particularly challenging context for learning complex information about locations, and birds and mammals that cache food often display impressive abilities to recall cache locations.

Another set of examples comes from animals that leave their nests to forage, and must therefore learn enough about their environment to find their way home. The location of a nest or burrow is highly unlikely to remain constant across many generations; the ability to return home requires the ability to incorporate much environmental information. Some animals, such as the desert ant, Cataglyphis cursor, incorporate learning into navigation by using path integration, which is the ability to remember the distances and directions traveled, to sum them, and then to calculate their return path. Well-developed learning and calculation abilities are required to integrate a navigational path. Other animals use landmarks, like the position of the sun, to learn their outward path, which they then use in reverse to return home. Evolution has provided the innate tools for incorporating learned environmental information in cache retrieval and homing.

Environment, Genetics and Cognitive Development

Cognition allows animals to separate themselves from the immediacy of their environment and to reflect on the past in order to solve future problems. Cognition involves the ability to make novel associations. Cognition was once thought to define humanity, or to separate humans from animals, but scientists now recognize that cognitive abilities are not confined solely to humans. Learning through cognition may be more removed from genetic constraints than other forms of learning, but cognitive problem solving ability can vary substantially among different animals within a species. Variation in ability is inherited, so at its core, there is a genetic element underlying cognitive abilities. Cognition gives animals a high level of flexibility in their social and physical environments, but even cognition is ultimately constrained by genetic limits.

One interesting aspect of cognition is that it can allow an animal to distinguish itself as a distinct identity. If an animal looks at its own image in a mirror and recognizes “self” rather than identifying the image as another animal, then some investigators interpret this as evidence of cognition. A common test is to modify the visual appearance of an animal (e.g., dying a patch of hair) and then observe the reaction of the animal to its mirror image. If it touches the dyed patch this is taken as evidence for the animal having a concept of "self." Apes, some monkey species, elephants and dolphins, all respond positively in mirror tests, supporting the idea that cognition is important in behavioral development across a broad range of animals.

Social cognition, the ability of an animal to forecast how its own actions will affect its future relationships within a social group, exists in chimpanzees and may extend to other species. In social groups without cognition, behavioral interactions are very much "in the moment," driven by factors such as dominance and family membership. Social cognition allows animals to be more calculating and manipulative in their social relationships. Chimpanzees do not appear to be mean to other members of their social group without justification, but they can, and do, exact revenge against group members that exhibit selfish behavior.

References

- Hey, jody; fitch, walter m.; ayala, francisco j., eds. (2005). "drosophila mating behavior". Systematics and the origin of species. Washington, d.c.: national academies press. Pp. 308–31. Isbn 978-0-309-09536-5
- Genetic-mutation, topicpage, scitable: nature.com, Retrieved 17 May, 2019
- Burrus, vincent; waldor, matthew k (2004). "shaping bacterial genomes with integrative and conjugative elements". Research in microbiology. 155 (5): 376–86. Doi:10.1016/j.resmic.2004.01.012. Pmid 15207870
- Altruism-biological, entries: stanford.edu
- Carroll, sean b.; grenier, jennifer; weatherbee, scott (2005). From dna to diversity: molecular genetics and the evolution of animal design (2nd ed.). Oxford: blackwell publishing. Isbn 978-1-4051-1950-4
- Both-environment-and-genetic-makeup-influence-behavior, library, knowledge, scitable: nature.com, Retrieved 19 April, 2019

Animal Migration and Communication

CHAPTER 4

The relatively long distance movement of individual animals is called animal migration. Animal communication refers to the transfer of information from a single animal or a group of animals to one or more animals such that it affects the behavior of the receivers in the present or the future. The diverse aspects of animal migration and communication have been thoroughly discussed in this chapter.

ANIMAL MIGRATION

Animal Migration is the regular, usually seasonal, movement of all or part of an animal population to and from a given area. Familiar migrants include many birds; hoofed animals, especially in East Africa and in the Arctic tundra; bats; whales and porpoises; seals; and fishes, such as salmon.

Migration can be contrasted with emigration, which involves a change in location not necessarily followed by a return journey; invasion or interruption, both of which involve the appearance and subsequent disappearance of great numbers of animals at irregular times and locations; and range expansion, which tends to enlarge the distribution of a species, particularly its breeding area.

The migration cycle is often annual and thus closely linked with the cyclic pattern of the seasons. The migration of most birds and mammals and many of the fishes are on a yearly cycle. In many cases (e.g., salmon and eels), animals with a relatively long life span return to their place of birth in order to reproduce and eventually die. In other cases, as in certain invertebrates, where the animal has a relatively brief life span and reproduces rapidly, migrations may not occur in every generation. The daily movements of certain fishes and invertebrates have also been called migrations because of their regular occurrence.

Sandhill cranes (Grus canadensis) gathering at a marsh during migration.

Most migrations involve horizontal travel. The distance traversed may be a few miles or several thousands of miles. Some migrations take a vertical direction and involve no appreciable horizontal movement. Certain aquatic animals, for example, move from deep water to the surface according to the season. Certain birds, mammals, and insects migrate altitudinally in mountainous areas, going from the upper zones, where they breed, to the foothills or plains during seasons when the weather is severe and unfavourable. Such vertical travels involve essentially the same type of environmental change as horizontal, or latitudinal, migrations over long distances.

Reptiles and Amphibians

The range of seasonal movements of most reptiles and amphibians is probably very limited. Generally incapable of travelling any great distance, they respond to unfavourable conditions by lapsing into a state of lethargy. This type of response makes it possible for them to remain in a particular area for the entire length of the year.

The only migration-like movements of reptiles and amphibians are made during the reproductive period. Frogs and toads then concentrate in particular areas such as ponds and lakes; thousands travel toward these sites from year to year. After reproduction, the animals disperse and again settle over their usual range.

The South American river turtle, or arrau (Podocnemis expansa), migrates along rivers in large masses that may impede the passage of boats. The turtles gather on sandbars of large rivers to lay their eggs. In the Galápagos Islands, giant land tortoises (Testudo elephantopus) stay chiefly in the upper humid zone, where food is abundant, but go down to the dry zone to lay their eggs. Despite their great body weight and slow pace, they travel some 50 kilometres (30 miles) across rough country.

Sea turtles, on the other hand, migrate over long distances, lay their eggs on special beaches, and then disperse over a wide area. Green turtles (Chelonia mydas), which deposit their eggs on the coast of Costa Rica in Central America, disperse through the Gulf of Mexico and the West Indies. Green turtles that have been tagged on Ascension Island, halfway between Africa and South America, have been recovered on the coast of Brazil, 2,300 kilometres (1,400 miles) away.

Birds

Migration is most evident among birds. Most species, because of their high metabolic rate, require a rich, abundant supply of food at frequent intervals. Such a situation does not always prevail throughout the year in any given region. Birds have thus evolved a highly efficient means for travelling swiftly over long distances with great economy of energy.

Snow geese (Chen caerulescens) flying in V-formation.

The characteristics of migratory birds do not differ greatly from those of nonmigratory forms; many intermediate types exist between the two groups. All transitional forms, in fact, may be manifested in a single species or in a single local population, which is then said to undergo partial migration.

In addition to regular migration, nomadic flights may also occur. This phenomenon takes place, for example, among birds of the arid zones of Australia, where ducks, parrakeets, and seedeaters appear in a locality following infrequent and unpredictable rains, breed, and then move to other areas. Nomadism is a response to irregular ecological conditions.

In Europe

The populations of many northern and eastern European species of birds have pronounced migratory tendencies; the populations of western Europe, on the other hand, are more sedentary.

Some birds are nomadic in winter, others spend the colder months in the southwestern part of the continent or in the Mediterranean region. Many migrant populations migrate to Africa south of the Sahara. Geographical conditions determine several main routes. The Alps are an important barrier to migratory birds. About 150 species travel westward and southwestward; others travel southeastward.

Tits (Parus), goldfinches (Carduelis carduelis), and blackbirds (Turdus merula) are usually sedentary in western Europe; they are usually migratory, however, in northern Europe, where their flights resemble a short migration. Starlings (Sturnus vulgaris) are sedentary in western Europe, where large numbers gather from eastern Europe. Large flocks also pass the winter in North Africa.

Insectivorous (insect-eating) species, such as warblers, flycatchers, and wagtails, are highly migratory and spend the winter in the tropics, chiefly in Africa. They migrate to Sierra Leone on the west coast, Tanzania on the east coast, and all the way southward to the tip of the continent. Most of these migrants use different routes to cross the Mediterranean, chiefly in the western portion, although some migrate only southeastward. Golden orioles (Oriolus oriolus) and red-backed shrikes (Lanius collurio) go to East Africa by way of Greece and Egypt. Swallows—particularly barn swallows (Hirundo rustica) and house martins (Delichon urbica)—and swifts (Apus apus) pass the winter in Africa south of 20° N latitude, particularly in South Africa, in the Congo River region, and in some coastal areas of West Africa.

Among nonpasserines—i.e., nonperching birds—one of the best-known migrants is the stork (Ciconia ciconia), which migrates to tropical Africa along two well-defined flyways. The stork population nesting west of a line that follows the Weser River in Germany flies southwestward through France and Spain, past the Strait of Gibraltar, and reaches Africa by way of West Africa; the eastern population, by far more numerous, takes a route over the straits of the Bosporus, through Turkey and Israel, to east Africa. These well-separated routes are probably a result of the stork's aversion to long flights over water.

Ducks, geese, and swans also are migrants. These birds winter partly in western Europe and partly in tropical Africa. In Africa they are likely to spend the winter in lake and river regions from Senegal in western Africa to Sudan in eastern Africa, where thousands of garganeys (Anas querguedula) and pintails (A. acuta) congregate annually. Some ducks leave their breeding grounds to molt (a process by which old feathers are replaced) in areas where they are most secure from predators during the time they are unable to fly; this is known as a molt migration. After molting, the ducks fly to their final winter quarters.

Wading birds (shorebirds) are typical migrants, most of them nesting in tundra of the Arctic region and wintering along the seacoasts from western Europe to South Africa. Scientists have observed that shorebirds, such as the white-rumped sandpiper (Calidris fuscicollis), risk increased mortality from exhaustion and severe weather during the course of their long migrations. They suspect that this cost is balanced by the benefit of reduced nest predation; the Arctic tundra—a preferred shorebird breeding region—supports lower predator population densities than areas farther south, and thus greater numbers of newly hatched young survive to adulthood.

In North America

North American birds must endure the same hazards of winter as European species. The geographical arrangement of the continent determines the main routes of migration, which run from north to south and include the Atlantic oceanic route, the Atlantic Coast route, the Mississippi Flyway, the Central Flyway, the Pacific Flyway, and the Pacific oceanic route. A great many birds pass the winter in the Gulf States, but the principal wintering area extends through Mexico and Central America to Panama, which has the greatest density of winter bird residents in the world.

The ruby-throated hummingbird (Archilochus colubris) nests in southern Canada and winters in Central America as far south as Panama. Some of these birds fly nonstop across the Gulf of Mexico. Because of their food requirements, many American flycatchers (Tyrannidae), which are mainly insectivorous, have the same migratory behavior as the hummingbirds. Others, like the phoebe (Sayornis phoebe), spend the winter in the Gulf States. Birds such as the American robin (Turdus migratorius) and several species of grackles assemble in the Gulf States in enormous flocks. The seasonal flights of the American wood warblers (Parulidae) are among the most spectacular on the North American continent. Some spend the winter in the Gulf States and in the West Indies; others, such as the blackpoll warbler (Dendroica striata), travel to Guiana, Brazil, and Peru by way of the West Indies. The spring migration routes of the Canada goose span the Continent of North America in an east–west direction from Hudson Bay as far south as Chesapeake Bay.

South America is winter quarters for several tanagers, such as the scarlet tanager (Piranga olivacea) and the bobolink (Dolichonyx oryzivorus); these birds migrate through the eastern United States and past Cuba to the swampy regions of Bolivia, southern Brazil, and northern Argentina. This area of South America is also winter quarters for the American golden plover (Pluvialis dominica dominica), which travels in an enormous loop over much of the New World. After nesting in the tundras of Alaska and Canada, the plover assemble in Labrador in easternmost Canada and then fly to Brazil over an oceanic route (the shortest possible route) about 3,900 kilometres (2,400 miles) long. Their return flight traverses South America, Central America, and the Gulf of Mexico, then follows the Mississippi Valley.

In Intertropical Regions

Birds of tropical regions migrate according to the rhythmic succession of wet and dry seasons—a profoundly influential factor on the annual cycle of animals and plants alike.

The migratory behavior of birds has a unique regularity in Africa, where life zones are arranged symmetrically by latitudes away from the Equator. Some migrants never cross the Equator. The standard-wing nightjar (Macrodipteryx longipennis), which nests in a belt extending from Senegal in the west to Kenya in the east along the equatorial forest, migrates northward to avoid the wet season. The plain nightjar (Caprimulgus inornatus), on the other hand, nests in a dry belt from Mali in the west to the Red Sea and Kenya in the east during the rains and then migrates southward to Cameroon and the northern Congo region during the dry season.

Other birds migrate across the Equator to their alternate seasonal grounds. Abdim's stork (Sphenorhynchus abdimii) nests in a belt extending from Senegal to the Red Sea; after the wet season, it winters from Tanzania through most of southern Africa. The pennant-wing nightjar (Cosmetornis vexillarius), in contrast, nests in the Southern Hemisphere south of the Congo forests during the austral, or Southern Hemisphere, summer, then starts north with the onset of the rainy season. It spends its winters in savannas from Nigeria to Uganda.

In Coastal and Pelagic Regions

Among the migrating seabirds, a distinction must be made between the coastal and the pelagic, or open-sea, species. Birds such as guillemots, auks, cormorants, gannets, and gulls—all common to the seashore—stay in the zone of the continental shelf. Except during the breeding season, they are dispersed over a vast area, often preferring specific directions of travel. Gannets (Sula bassana) nesting around the British Isles spread in winter along the Atlantic coast of Europe and Africa to Senegal, the young travelling farther than the adults. Pelagic birds, most of which belong to the order Procellariiformes (petrels and albatrosses), cover much greater distances and, from a few small nesting areas, roam over a large part of the oceans.

Wilson's petrels (Oceanites oceanicus), which nest in the western sector of the Antarctic (South Georgia Island, Shetland Islands, and South Orkney Islands), spread rapidly northward in April along the coasts of North and South America and stay in the North Atlantic during the summer. In September they leave the western Atlantic, travelling east, then southeast, along the coasts of Europe and Africa toward South America and their Antarctic breeding grounds, arriving there in November. These petrels thus travel in a great loop through the whole Atlantic Ocean, in a flight pattern correlated with the direction of prevailing winds. The same pattern is used by other seabirds normally carried by the winds. Albatrosses, such as the wandering albatross (Diomedea exulans) that nests on small Antarctic islands, circle the globe during their migrations. One such bird, banded as a chick at Kerguelen Island in the southern Indian Ocean and recovered at Patache, Chile, travelled in less than 10 months at least 13,000 kilometres (8,100 miles)—perhaps as much as 18,000 kilometres (11,200 miles)—by drifting with the prevailing winds.

In the Pacific, short-tailed shearwaters (Puffinus tenuirostris) nest in enormous colonies along the coasts of southern Australia and in Tasmania, then migrate across the western Pacific to Japan, remaining in the North Pacific and the Arctic Ocean from June to August. On the return migration they go east and southeast along the Pacific coast of North America, then fly diagonally across the Pacific to Australia.

Arctic terns (Sterna paradisaea), whose breeding range includes the northernmost coast of Europe, Asia, and North America, spend the winter in the extreme southern Pacific and Atlantic, chiefly along Antarctic pack ice 17,600 kilometres (11,000 miles) from their breeding range. American populations of the Arctic tern first cross the Atlantic from west to east, then follow the coast of western Europe. Arctic terns thus travel further than any other bird species.

Modes of Migration

The migration flights of birds follow specific routes, sometimes quite well defined over long distances. The majority of bird migrants, however, travel along broad airways. A single population of migrants may be scattered over a vast territory so as to form a broad front hundreds of miles in width. Such routes are determined not only by geographical factors—e.g., river systems, valleys, coasts—and ecological conditions but are also dependent upon meteorological conditions; i.e., birds change their direction of flight in accordance with the direction and force of the wind. Some routes cross oceans. Small passerine (perching) birds migrate across 1,000 kilometres (620 miles) or more of sea in areas such as the Gulf of Mexico, the Mediterranean Sea, and the North Sea. American golden plover, wintering in the Pacific, fly directly from the Aleutian Islands (southwest of Alaska) to Hawaii, the 3,300-kilometre (2,050 miles) flight requiring 35 hours and more than 250,000 wing beats.

The speed of migratory flights depends largely on the species and the type of terrain covered. Birds in migration go faster than otherwise. Rooks (Corvus frugilegus) have been observed migrating at speeds of 51 to 72 kilometres (32 to 45 miles) per hour; starlings (Sturnus vulgaris) at 69 to 78 kilometres (43 to 49 miles) per hour; skylarks (Alauda arvensis) at 35 to 45 kilometres (22 to 28 miles) per hour; and pintails (Anas acuta) at 50 to 82 kilometres (31 to 51 miles) per hour. Although the speeds would permit steadily flying migrants to reach their wintering grounds in a relatively short time, the journeys are interrupted by long stops, during which the birds rest and hunt for food. The redbacked shrike (Lanius collurio) covers an average of 1,000 kilometres (620 miles) in five days as follows: two nights for migration, three nights for rest, five days for feeding.

Most migrations occur at relatively low altitudes. Small passerine birds often fly at less than 60 metres (200 feet). Some birds, however, fly much higher. Migrating passerines, for example, have been observed at altitudes as great as 4,000 metres (14,000 feet). The highest altitude recorded thus far for migrating birds is 9,000 metres (29,500 feet) for geese near Dehra Dun in northwest India.

Pelicans, storks, birds of prey, swifts, swallows, and finches are diurnal (daytime) migrants. Waterbirds, cuckoos, flycatchers, thrushes, warblers, orioles, and buntings are mostly nocturnal (nighttime) migrants. Studies of nocturnal migrants using radar on telescopes focussed on the Moon show that most migratory flights occur between 10 PM and 1 AM, diminishing rapidly to a minimum at 4 AM.

Most birds are gregarious during migration, even those that display a fierce individualism at all other times, such as many birds of prey and insectivorous passerines. Birds with similar habits sometimes travel together, a phenomenon observed among various species of shorebirds. Flocks sometimes show a remarkable cohesion. The most characteristic migratory formation of geese, ducks, pelicans, and cranes is a "V" with the point turned in the direction of flight. In flocks of northern bald ibis (Geronticus eremita), each member of the group takes a turn leading the formation in flight, before dropping back to fly in the wake of another to save energy.

Mammals

Seasonal movements are not widespread among terrestrial species of mammals, because walking speed is relatively slow and energy consumption great. Marine and flying mammals have a much greater tendency to migrate, a tendency that is directly related to their locomotive powers.

Migrating wildebeests and zebras crossing a river in the Maasai Mara National Reserve, Kenya.

Terrestrial Mammals

True migration among mammals occurs mostly among large artiodactyls (even-toed ungulates) living in habitats with wide fluctuations of climatic and biotic conditions.

In North American Arctic regions, herds of caribou (Rangifer tarandus) settle during the summer in the barrens—rather flat wasteland with little vegetation. In July the animals begin to move irregularly southward and spend the winter in the taiga, or northern forests, through which they wander freely with no general directional trend. Each herd seems to move in accordance with local conditions and without a well-defined pattern. The caribou again move northward as early as late February and return to the barrens. These migrations follow the same routes from year to year.

In former times, American bison (Bison bison) migrated regularly through the Great Plains. Herds of as many as 4,000,000 animals moved from north to south in fall and returned when spring rains brought fresh grass to the northern part of their range. Bison travelled over more or less circular routes and spent the winter in areas 320 to 640 kilometres (200 to 400 miles) from the summer range. Other North American mammals, such as elk (Cervus canadensis), mule deer (Odocoileus hemionus), and dall sheep (Ovis dalli), still migrate regularly in areas undisturbed by man.

American bison or plains buffalo (Bison bison).

Large African mammals migrate in accordance with the succession of wet and dry seasons, which can greatly modify the habitat. Some antelope remain in small areas throughout the year, but many species undertake seasonal movements over a large range. In the Serengeti region of Tanzania, plains animals, particularly wildebeests (Connochaetes taurinus) and zebras, travel more than 1,600 kilometres (1,000 miles) in their seasonal migrations. Herds spread outward during the rains and concentrate during the dry season around water holes. Elephants (Loxodonta africana) wander great distances in search of the best food and water supply.

In southern Africa, hundreds of thousands of springbok (Antidorcas marsupialis) once migrated according to the rhythm of rainfall over their vast range. They moved in herds so dense that any animal encountered was either trampled or forced along with the herd. These huge migrations often resulted in enormous losses from starvation, drowning, or disease—natural methods for controlling overpopulation. Such movements, involving lesser numbers, still occur in parts of Namibia and in Botswana.

Flying Mammals: Bats

A few bats native to Europe and Asia make short flights to winter quarters. Others, such as the common pipistrelle (Pipistrellus pipistrellus) and the particoloured bat (Vespertilio murinus), withdraw to hibernating places at some distance from their summer range. In Germany the large mouse-eared bat (Myotis myotis) leaves its winter quarters in Brandenburg in March or April and travels as much as 260 kilometres (160 miles) to its summer habitat in northern Germany. It regularly returns to the same winter locale. Schreiber's long-fingered bat (Miniopterus schreibersii) changes its habitat in winter and moves more than 160 kilometres (100 miles) in a complex pattern. These local movements represent an adjustment to winter conditions and the search for more habitable caves.

Other bats travel even greater distances. In the United States the red bat (Lasiurus borealis), the large hoary bat (L. cinereus), and the silver-haired bat (Lasionycteris noctivagans)—three species that roost primarily in trees and shrubs—are true migrants with strong powers of flight. They summer in the northern United States and in Canada and winter in Georgia, South Carolina, Florida, and probably also in the southwestern states. The southward movement is made from mid-August to November. Migration flights occur at night and, under favourable conditions, during the day. Large numbers follow the coast some distance from land, and all three species are found at sea far from the coast and in Bermuda. Fruit bats and flying foxes (Pteropus) native to the tropical regions of the Old World make regular mass migrations, following the seasons for fruit ripening.

Marine Mammals

Antarctic whales migrate regularly to the tropics, a fact long known to whalers. By systematically marking whales by shooting into them steel tubes engraved with a serial number, man has obtained evidence of actual movements. A young fin whale (Balaenoptera physalus) marked in February in the Antarctic at latitude 65° S was captured two years later, in July, off the coast of South Africa, 3,000 kilometres (1,900 miles) north. During the austral (Southern Hemisphere) winter, whales migrate to areas rich in food, particularly the northwestern coast of Africa, the Gulf of Aden, and the Bay of Bengal. Antarctic whales—particularly humpbacks (Megaptera novaeangliae), a highly migratory species—can be divided into five distinct populations around Antarctica; each population migrates separately, and individuals usually return to their respective zones, though interchange may occur. The Antarctic population does not, however, migrate entirely into warm waters during the winter, and a segment of the population seems to stay behind at about latitude 50° S.

Northern whales have the same migratory habits as Antarctic whales. Northern blue whales (Balaenoptera musculus) migrate northward along the east coast of the United States, then through Davis Strait to Baffin Bay (north of Canada) or Spitsbergen to the waters off northern Scotland or the coast of Norway. They are believed to migrate southward along the same routes. Part of the North Pacific stocks of the northern blue whale winters in the Indian Ocean and in the seas bordering Indonesia.

Smaller cetaceans (porpoises and dolphins) migrate in the same way, as indicated by population fluctuations within a particular area; but little is known about their distribution and migration.

Noteworthy migratory habits occur among the pinnipeds (seals and walrus), some of which disperse over wide areas at times other than the breeding season. The harp seal (Pagophilus groenlandicus) lives in summer in northernmost Arctic waters but reproduces in the White Sea (an arm of the Arctic Ocean extending southward into the Russian landmass), in the eastern North Atlantic, and around Newfoundland, where young are born between January and April. The seal then returns to more northern latitudes. Northern fur seals (Callorhinus ursinus) reproduce only on the Pribilof Islands, off southwestern Alaska, from May to November, and the colonies then disperse into the open seas. The males stay in the Gulf of Alaska and off the Aleutian Islands, while the females go farther south, to southern California, some 4,800 kilometres (3,000 miles) away.

Physiological Stimulus of Migration

Migration, like reproduction and other phases (as molting in birds), is part of the life cycle and depends on a complex internal rhythm that affects the whole organism, particularly the endocrine glands (glands of internal secretion) and the gonads. Migration must thus be viewed in relation to the entire annual cycle.

Each year birds return to particular areas to breed, and remain there until the members of the brood can care for themselves. There is no relation between the reproductive and migratory stimuli, yet the two phenomena, although independent, are nevertheless stimulated by the same factor.

A physiological study of certain migrants has revealed that metabolic patterns usually change prior to migration, and fats accumulate in the body tissues. The whitethroat (Sylvia communis) weighs an average of 12 to 13 grams (about 0.4 ounce) during the breeding season, 16 to 19 grams (about 0.6 ounce) in the autumn, and 20 to 24 grams (about 0.8 ounce) in the winter. Food consumption increases with the autumn molt, reaching a peak at the beginning of the migration season. These fundamental physiological changes, chiefly under the control of the thyroid gland, are correlated with migratory activity. Such fluctuations are not observed in nonmigratory species.

Variations in metabolism and related phenomena are controlled by an endocrine gland, namely the pituitary gland, which is located in the lower part of the brain and acts as a command post, sending out instructions in the form of secretions called hormones. That the pituitary has a cycle independent of environmental factors is demonstrated by the regularity with which phases such as reproduction occur from year to year in the lives of some birds, and by the diverse response of various species and populations to the same environmental factors. That the pituitary is, however, influenced by environmental factors, such as variations in day length and the intensity of the Sun, has been demonstrated experimentally.

Gonadal development and the deposition of fat, for example, are influenced by the pituitary, which responds to increasing day length in springtime by accelerating the rate of gonadal development. The pituitary thus governs the development of gonads and, in addition, affects all metabolic processes, including development of the thyroid gland, so as to prepare the animal physiologically for migration. If only the pituitary and variations in day length were involved, migration would be triggered at definite times, because the pituitary cycle is fixed, and photoperiodism is a highly predictable phenomenon; such a lack of flexibility, however, would inevitably cause migrant populations to suffer catastrophes because ecological conditions are irregular—meteorological events, such as the arrival of spring, and biological phenomena, such as flowering, foliation, hatching of insects, and availability of food, are highly variable from year to year. The pituitary thus serves only to prepare the bird for flight; the proper ecological conditions, on the other hand, are necessary to initiate it. The availability of food is an important factor. Temperature and weather conditions also have an influence—a sudden period of cold weather during autumn may induce the immediate departure of many migrants.

Sensitivity to changes in the weather and other environmental conditions varies markedly among species. Some, such as the woodcock, snipe, lapwing, starling, and lark, rely on surrounding conditions to initiate their spring and autumn migrations, and the patterns of their flight depend on temperature and barometric pressure. Others, such as the swift, cliff swallow, Baltimore oriole, and short-tailed petrel, are less weather dependent, and, since the dates of their arrival and departure are not regulated by the weather, they occur with remarkable regularity each year.

The factors that stimulate migration in animals other than birds are not yet well understood. Ecological conditions play a great part in the migratory activity of mammals, who react to general food shortage by moving to another region. Whale, for example, leave the Antarctic region as winter modifies the oceanographic conditions. Seals disperse when the food supply in the area of their breeding colonies is depleted. Environmental factors are of primary importance in the migration of fishes and marine invertebrates. Annual movements of water masses change physical conditions such as temperature and salinity; biotic conditions are influenced accordingly.

Ecological Significance of Migration

There are many ecological implications of migration. The food resources of some regions would not be adequately exploited without moving populations. The sequence of migratory movement is closely integrated in the annual cycle of ecosystems characterized by productivity fluctuations. Migratory behavior concerns only species located at specific trophic levels (zones of food availability) where maximal fluctuations occur both in breeding areas and in wintering regions. Migrant birds avoid equatorial forests where productivity is constant throughout the year, and food surpluses do not occur. They do congregate, on the other hand, in savannas where productivity varies with the seasons.

Such a coordinated sequence is particularly apparent in the case of birds migrating from the northern Arctic regions to tropical winter regions; both life zones are characterized by broad fluctuations in productivity. In the Arctic, vegetal and animal production is very high during the summer; ducks and waders nest in great numbers, exploiting these resources. As winter comes, food becomes scarce, and water birds migrate to the tropics, where the rainy season has caused food production to increase to optimal levels. Ducks and wading birds concentrate in the most favourable areas, remaining until spring, when productivity is lowest. By then the condition of breeding areas is again favourable for the birds. The life cycles of these birds are closely attuned with the cycles of their various habitats, and the sizes of bird populations are controlled by the capacity of both areas to sustain them.

Migration, then, has considerable ecological significance. It enables fast-moving animals to exploit fluctuating resources and to settle in areas where life would not be tenable for animals incapable of rapid travel. On the other hand, peaks of food production would be unexploited without the periodic presence of migratory populations.

ALTITUDINAL MIGRATION

Bighorn sheep migrate between high mountains, where they are safer from predators, and valleys where there is more food in winter.

Altitudinal migration is a short-distance animal migration from lower altitudes to higher altitudes and back. It is commonly thought to happen in response to climate and food availability changes as well as increasingly due to anthropogenic influence. These migrations can occur both during reproductive and non-reproductive seasons. Altitudinal avian migration is common, and can also be found in other vertebrates, and can be seen in some invertebrates.

Typical characteristics of tropical altitudinal migrants include: a high rate of frugivory or nectarvory; movement between lower elevation areas during non-breeding seasons and higher elevation areas during breeding seasons, or on a consistent annual or seasonal cycle; at least part of the population being migratory with a possible portion of the population residing at breeding sites year-round. This last characteristic can be sex-biased, as it is with juncos, in which the males are less likely to migrate than the females. The white-ruffed manakin provides a good example of an altitudinal migrant by displaying all of these traits. It has a high rate of frugivory, migrates from lower elevations to higher elevations on a predictable breeding-season based cycle, and part of the population is migratory, with a small portion possibly remaining at the breeding sites year-round.

Regions

There are many documented examples of migratory range shifts along an elevation gradient among temperate species. While these migrations are more understood in temperate regions, and far less understood among tropical ecosystems and species, there are documented cases. Altitudinal migration is typically seen among taxa found in montane areas. Generally, as elevation increases, the species richness decreases.

Tropics

The white-ruffed manakin (Corapipo altera) is a well known altitudinal migrant.
Third year male (left) and After Third Year male (right).

In the tropics, altitudinal migrations are most commonly seen among frugivores or nectarvores, such as what is seen among tropical hummingbirds, which migrate altitudinally in response to shifts in food abundance and availability. This migration pattern has been observed in neotropical birds, but has also been seen in other terrestrial, tropical montane species such as Baird's tapir and white-lipped peccary.

Tropical avian species that are altitudinal migrants include the white-ruffed manakin, resplendent quetzal, at least 16 species of raptor, and many species of hummingbird.

Altitudinal migration has also been witnessed in some tropical bat species. As of 2014, there is not much information as to why tropical species migrate altitudinally, other than that it may be for food resources or reproduction, as it is for temperate bat species.

Temperates

While less common in avian species in the temperate regions, altitudinal migration still plays a part in migration patterns in montane zones and is seen in most ungulates in the Rocky Mountains. Avian temperate species that migrate altitudinally include mountain chickadee, and the American dipper.

Ungulates that have been observed to migrate altitudinally include roe deer, bighorn sheep, and mountain goats.

Temperate bat species are also altitudinal migrants. Their migratory patterns are sex-biased altitudinal migrations, with females inhabiting lower elevations during reproductive periods.

Causes

Altitudinal migration, as a short-distance migration pattern, has been easier to trace than long-distance patterns. Still, while the proximate causes and physiological adaptations for migrations are well understood, determining the ultimate causes have been difficult. This difficulty has been linked to limited success of mark and recapture techniques used to track migratory species. There are many hypotheses for why altitudinal migration may occur, including correlations between food abundance and nutrition-the need to migrate in order to meet specific needs associated with varying abundance and nutrition; reproduction-breeding sites being at elevations different than those of non-breeding sites; anthropogenic-species being increasingly driven to higher altitudes due to human actions.

Food Abundance and Nutrition

Migration in response to food abundance has been the most accepted hypothesis for why species migrate altitudinally. This hypothesis states that peaks in food abundance along an elevational gradient, such as the slope of a mountain, drive migration patterns as species exploit available food resources. Peaks in food abundance along this gradient often coincide with the breeding season. Some frugivorous birds, such as white-ruffed manakins (Corapipo altera) migrate to higher elevations to exploit peaks in fruit abundance. Evidence supports the possibility that migrants have a competitive advantage compared to non-migrant (sedentary) species, due to increased foraging ability over a larger area, resulting in greater food and nutrient uptake. The diet differs between non-migratory and migratory species in large-scale analyses and species-pair comparisons of frugivorous tropical birds.

While this hypothesis is supported, and has been the most accepted, it fails to explain why altitudinal migrants return to lower elevations, or if it is done in response to shifting food resources. It has been proposed that weather-related resource availability may trigger the elevational migration of some species, such as the white-ruffed manakin during storms.

Reproduction

A number of species engage in movement that could be defined as altitudinal migration as part of their mating or reproductive behaviors.

For example, in male white-ruffed manakins, migratory behavior has shown to lessen social status and mating success at leks the following breeding season. Most hummingbird species at Monteverde increase altitude during the wet season in order to breed.

Of the 16 species of neotropical raptors (including the Andean condor Vultur gryphus), that are known to be altitudinal migrants, most breed in the high Andes and migrate to lowland areas during non-breeding seasons.

Nest Predation

Studies have shown a decreased risk of nest predation at higher altitudes, which may explain the seasonal (breeding season—non-breeding season) altitudinal migration of some passerine birds. An experiment using 385 nests at varying locations on the Atlantic slope of Costa Rica showed decreased predation at increasing altitudes, with predation highest at intermediate altitudes. This hypothesis proposes that altitudinal migration may have evolved among some species as a response to nest predation, as a way lower the risk. Studies have also shown that elevation of home range influences breeding time.

Anthropogenic

The walia ibex (Capra walie) has increasingly been driven to higher altitudes in Ethiopian mountain ranges. This has occurred because of human activity impacting their native range, including war, expanding human settlement, and cultivation.

Conservation Implications

Climate Change

Climate change could be causing migration patterns to shift into an earlier time frame, coinciding with an earlier start of the growing period. This means that migratory species may leave lower altitudes for higher-altitude breeding sites while those breeding sites still lack the necessary resources. Some species that have shorter migratory paths may be able to return to the lower elevations and wait, but run the risk of running out of the resources in that lower altitude, such as food and cover, that may only be available for a short, set period of time.

Over 30% of birds and other species in montane forests show altitudinal migration patterns. Because of this, changes in climate and seasonality (decrease or increase) would affect a large portion of tropical species and have the potential to cause a trophic cascade on the community-level.

Furthermore, climate change may cause seasonal storms and rainfall patterns to change, shifting the timing and need for altitudinal migration in the future by shifting availability of resources, which is believed to be a driving cause of altitudinal migration.

The upward shift of species caused by climate change also holds the potential to cause both mountaintop extinction and lowland biotic attrition. This is because the lowland tropics lack species that can cope with increasing temperatures. An overall loss of species richness can occur due to there being fewer migratory species to replace lost ones.

This has been seen occurring by looking at the average time of arrival and departure at high altitude areas for the American robin (Turdus migratorius). The average time interval has shifted by as much as two weeks due to the change in seasonal patterns of resource abundance and temperature.

Migrational Corridors

Migrational corridors, connecting lowland and montane habitats are essential for the upkeep and survival of migratory species. Some species can cross cleared lands, suchs as pastures, but many require closed forest areas, such as what is provided by these migrational corridors.

COLLECTIVE ANIMAL NAVIGATION AND MIGRATORY CULTURE

Animal navigation is the ability of many animals to find their way accurately without maps or instruments. Birds such as the Arctic tern, insects such as the monarch butterfly and fish such as the salmon regularly migrate thousands of miles to and from their breeding grounds, and many other species navigate effectively over shorter distances.

Animal movement is a fundamental driver of ecological and evolutionary processes. Movement, and specifically migrations, couple disparate populations and ecosystems by transporting individuals, nutrients, pathogens and genes. For individuals, migrations facilitate access to spatially and temporally varying resources; however, there are significant costs and challenges associated with migration. Perhaps the most serious challenge is navigation—animals must find their way through often complex environments along migration routes that can span tens of thousands of kilometres and take many months (sometimes generations) to traverse. To successfully complete these migrations, animals employ a diverse range of sensory modalities and can respond to an impressive array of cues, including magnetic fields, light polarization, landmarks, odours and celestial bodies. While in some contexts the preferred navigation route is genetically encoded and instinctive, for others this must be discovered or learned from others.

Although the mechanisms of animal navigation have fascinated researchers for decades, focus has primarily been at the level of the individual. However, many migratory species are known to move in large groups and social interactions can alter migratory movement decisions. How individual navigational ability is affected by social interactions, and what unique orientational capacities can emerge at the collective level, has been far less studied, although a growing body of theoretical and empirical results supports the hypothesis that social interactions during collective navigation can lead to improved navigational ability. These outcomes can be beneficial, neutral or detrimental.

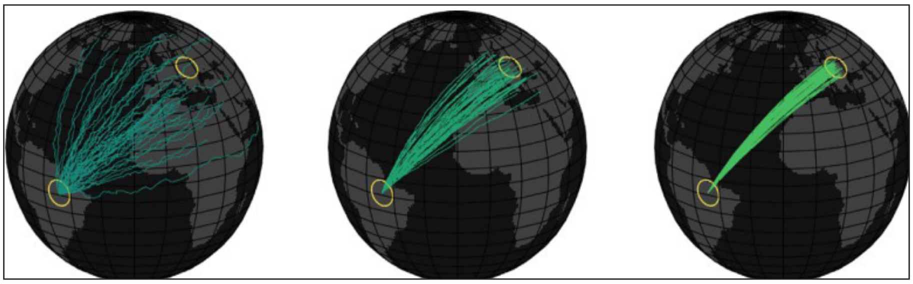


Illustration of the potential benefit of collective navigation. In this hypothetical example, migrants seek to travel from South America to Europe, with each line denoting a particular group of migrants. On average the navigation accuracy improves from left to right, which could be due to an increase in the size of the group, increase in the fraction of leaders in the group, or learning by individuals. for details of collective navigation mechanisms. In reality, the best route may not be the straightest path, as navigational efficiency will be a function of several considerations, including resource distribution, perceived safety and cumulative hydro/aerodynamic efficiency.

Mechanisms Leading to Improved Accuracy during Collective Navigation

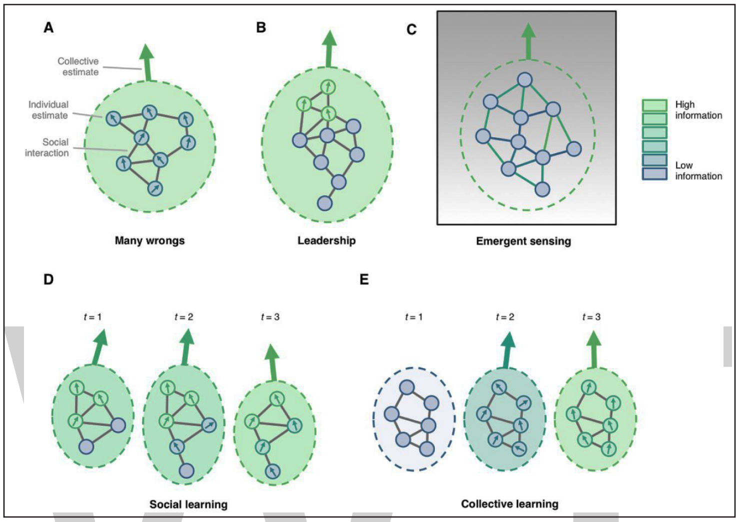
- Many wrongs is the mechanism by which a group of animals, each with a noisy estimate of the ‘correct’ navigation direction, can improve their accuracy by pooling individual estimates. At its core, it is deeply related to the law of large numbers. As long as the errors of individual estimates are not perfectly correlated with each other, and are distributed in an unbiased manner around the true value, then a simple averaging across estimates can increasingly dampen noise and home in on the true value. Known social interaction rules have been shown to effectively average across preferences. This mechanism can operate on either continuous (such as direction of motion) or discrete (such as distinct paths or river branches) variables. In the latter case, majority (or plurality) rule serves an analogous function to simple averaging. For a group composed of individuals with differing accuracies, many wrongs may still improve accuracy, although accuracy would be maximized by a weighted average.

- Leadership results when informed individuals, which may form a small minority of the group, successfully guide naive individuals towards favourable environments. Smaller groups may allow for individuals to recognize leaders and preferentially follow them, while in large groups, leaders are likely to be anonymous. Nonetheless, social influence can lead to successful leadership, with a surprisingly small number of leaders necessary for accurate navigation. Naive individuals can even help ensure democratic decision-making, potentially aiding in a many-wrongs improvement of accuracy. Who is a leader can depend on the specific context, so that over the course of a migration, leadership may be distributed among many members of the group.

- Emergent sensing occurs when a group can navigate collectively even when no individual has the ability to assess the correct direction of motion. If an individual, for example, can make only scalar measurements of an environmental cue and has no memory, then it has no knowledge of the gradient of the cue. But a group can, collectively, measure and follow a gradient if the measurements made by multiple individuals can be compared. The group would then function as a distributed sensor network. Although many animals that navigate together cannot directly communicate and compare measurements with each other, context-dependent behavior (where some aspect of behavior is tied to the value of the measurement) can effectively facilitate such comparisons, even if no individual is aware of them.

- Social learning allows knowledge possessed by informed individuals to percolate through the group and across generations. If naive individuals are led along a particular path by more knowledgeable group members, those individuals may learn about cues associated with that path, therefore becoming part of the informed subset themselves over time. Similarly, individuals with similar ages, or levels of experience, may have differing knowledge of specific routes or cues and this information may be homogenized via learning during group travel. In both contexts, the learning is unidirectional—individuals gain personal information by following others who already have that information. For navigational tasks where there is no genetically encoded preferred direction, social learning can be the primary mechanism by which navigational information persists over generations. Innovations to routes (e.g. novel shortcuts, detours) originate with leaders/demonstrators at the individual level, and can be passed on to followers/observers.

- Collective learning is the emergence and retention of new knowledge resulting from the dynamics of social interactions. It differs from social learning in that route innovations are generated from the interaction of multiple individuals. For example, a group can improve the route that it takes through the many wrongs mechanism, and this new route can then be learned by individuals in the group. Alternatively, naive individuals may inject random noise (stochastic factors such as sensory, or movement, errors) into a travelled route, and improved routes could be haphazardly discovered and subsequently learned—although this may require the group to also have the capacity to filter out ‘bad’ innovations. Both collective and social learning may lead to gradual improvements, or ‘ratcheting’, of the efficiency of the learned route over time.



Mechanisms leading to improved accuracy during collective navigation. (a) Many wrongs: noisy estimates from many individuals are averaged to produce a more accurate collective estimate. (b) Leadership: a subset of informed individuals guides naive individuals. (c) Emergent sensing: comparisons of individual measurements of the environment via social interactions allows a group to detect gradients. Here information is present in the interactions (links) rather than the individuals themselves. (d) Social learning: navigational information passes from informed individuals to naive individuals over time. (e) Collective learning: new navigational information is generated over time through social interactions.

These mechanisms may also apply to many other navigational tasks in addition to migrations. For example, many animals navigate in order to discover new food sources, move up and down the water column, or locate new shelters. Because animals use environmental information to reach specific targets in these and other tasks, collective navigation mechanisms could play a role for group-living animals in improving their performance. Furthermore, while the majority of the direct empirical evidence for collective navigational mechanisms uses birds or fish as study organisms, there are many other taxa, including ungulates, cetaceans and insects, which navigate through their environment while travelling in groups. Where relevant, we allude to some of these less well studied taxa as potential directions for future research.

Theoretical Models and Mechanisms

The idea that the effectiveness of a collective decision-making process covaries with group size dates back several centuries, initially focusing on decision-making in humans. One classic example, from the late eighteenth century, is Condorcet's jury theorem, which posits that when individuals must choose between two discrete options (e.g. the guilt or innocence of a defendant), and each jurist has a greater than 50% chance of choosing the correct option, then the accuracy of decisions will tend to improve as the size of the group increases. Later work, including that of Galton, extended this idea from discrete to continuous estimates, suggesting that the average of many independent estimates will tend to approach the 'true' value with increasing accuracy as group size increases—a phenomenon now known as the 'wisdom of crowds'.

It was only much later that these ideas were adapted to non-human animal groups when, in the 1960s, researchers studying birds and fish independently suggested that these animals could improve their navigational performance by grouping. For example, Larkin & Walton supposed that each fish within a school makes an independent estimate of the best migratory direction, and by travelling together they would tend to move in the average preferred direction of all individuals. In such a scenario, assuming there is no cost to aggregating information, navigational error should decrease as the inverse of the square root of the number of animals in the group, analogous to how the standard error shrinks as the sample size increases in statistical analyses due to the law of large numbers. Similarly, Condorcet's theorem could apply in animal groups when animals must make binary or other discrete choices, such as fish ascending a river network or bees selecting a new nest site, such that decision accuracy improves with group size in these scenarios. Now known as the 'many wrongs principle', the general idea that social interactions dampen individual errors is thought to be a major outcome of collective navigation.

While these relatively simple mathematical arguments provide an intuitive conceptual basis for how individuals in groups could improve their navigational accuracy, they largely ignore the complexity of the behavior of real organisms. In most animal groups, there is no entity to collate 'opinions' and explicitly compute the average of all individual estimates, as each individual can observe only near neighbours. Furthermore, individuals may not be equally informed about the best direction of travel, there may be complex interactions between genetically determined and learned preferences, or group-wide biases in estimates. Because of this, it is not obvious whether navigational accuracy in animal groups would scale as these simple models predict, or whether there are limits to the real-world ability of organisms to benefit from collective navigation. More detailed models are necessary to shed greater light on the mechanisms underlying collective navigation in animals.

Agent-based models, where the motion of each individual is modelled explicitly in space and time, were developed in order to bridge the gap between abstract mathematical models and the behavior of real animal groups. These models can describe how the motion of an individual is determined by its own navigational preferences, physical abilities, sensory information and response to near neighbours. The social interaction rules are often governed by 'zones' of interactions, such that the response to a neighbour depends on the distance between the neighbour and the focal individual. More recently, empirical data have driven the development of alternative models, where, for example, individuals respond to a fixed number of near neighbours irrespective of their distance, where social influence decays continuously as a function of distance or where interactions are modulated by considerations of the animals' sensory capacities and limitations. Agent-based models are particularly useful because 'experiments' can be performed in silico even when the underlying equations are not mathematically tractable. Furthermore, experiments can be performed digitally to address questions that may be difficult or impossible to do with real animals in the laboratory or the field. For example, different parameters of the model (such as sensing ability, social interaction network or the structure of noise) can be varied systematically, and their effect on collective navigation measured. In addition, such models allow an exploration of how collective behavior may change over evolutionary timescales. The results of such virtual experiments can serve as testable predictions regarding which behavioral parameters are likely to be important for real animals, which can lead to more targeted experiments.

The simplest agent-based models of collective navigation assume that all individuals in the group are identical—they follow the same interaction rules and have the same level of navigational information or error, thus approximating the conditions that the many wrongs principle typically assumes. Such simulations have demonstrated that many-wrongs averaging can readily arise from local social interactions if individuals balance their own preference with the direction of motion of their neighbours. Specifically, collective navigational performance is maximized when personal preference is given a low weight, if individuals exhibit some inertia in their movements (which serves to average an individual's noisy compass estimates over time), or if the underlying social structure is evenly distributed, rather than dominated by a few individuals.

For many other contexts, the distribution of directional preferences may be multimodal rather than unimodal. For example, different individuals in a group may have different preferred routes to the same location, and at small spatial scales, individuals can exhibit distinct preferred headings. In other cases, individuals may prefer altogether separate locations, such as when individuals in a breeding population choose from multiple overwintering grounds (i.e. weak migratory connectivity). In such cases, there will be a natural continuum between unimodal and multimodal distributions of preferences depending on the distance individuals are from the final location. Specifically, when locations are very far away, all individuals prefer to move roughly in the same direction (unimodal), but as the group approaches the locations preferences will begin to diverge (become multimodal). In such scenarios, simply taking the average of the preferred directions can be detrimental (there may well be no suitable habitat at the midpoint between preferred locations). Agent-based models that incorporate this diversity of preferences have demonstrated that, despite these challenges, groups are consistently able to reach consensus for one particular location. One robust result of both models and empirical data is that animal groups average when the discrepancy between preferred headings is small, but when the discrepancy is sufficiently large, the group spontaneously selects one of the possible headings, typically the one preferred by the greatest number of individuals or the most strongly opinionated individuals.

Another realistic extension of these agent-based models is to include two classes of individuals, informed and naive, where successful navigation requires leadership by the informed class. In real animal groups, this can occur when the desired navigation direction is not genetically encoded and must be learned: the naive individuals may be juveniles that lack experience of the route, or members of fission–fusion groups that are less knowledgeable about the local geography or other informative cues. One question that arises from these mixed groups is whether, and how, relevant information about which way to go can successfully percolate from a minority of leaders to the entire group. Effective leadership would not be explained by many wrongs, which would predict poor navigational ability in such scenarios, as it describes the averaging of estimates across the entire group. This challenge is compounded if information about who is informed cannot be directly signalled, and leadership must arise despite this anonymity. Models in which a group is composed of an informed subclass and an uninformed subclass show that surprisingly few informed individuals are necessary to effectively lead a group, with a relatively sharp transition from ineffective to effective leadership. Models suggest that leadership can be enhanced if the informed subclass moves more quickly than the naive majority in order to increase their contact rate or to signal information, although this is not a requirement for effective leadership. Further studies have shown that naive individuals can even improve collective navigation, because they contribute error that can actually stabilize consensus decision-making and increase the speed and sensitivity of consensus.

Knowledge heterogeneity may be an outcome of evolution, rather than simply a consequence of age structure or mixing. Evolutionary simulations, in which gathering information is costly (as it necessitates, for example, developing enhanced sensory capabilities or diverting more attention to information gathering) suggest that frequency-dependent selection drives the evolution of leaders (those who predominantly rely on environmental cues) and followers (those who predominantly rely on social cues). This may even occur when individuals are very sparsely distributed in space, and thus rarely interact, demonstrating that individuals can benefit from 'collective' navigation even if they do not appear to be grouping at all.

Differential levels of knowledge also provide opportunities for naive individuals to learn migratory routes and other relevant information socially for use in future journeys. Such unidirectional copying behavior is typically referred to as social learning. Hamilton and others proposed the intuitive idea that young migrants could learn migration routes when travelling with more experienced individuals by being exposed to cues associated with that route. Social learning may also occur between individuals of the same age class. For example, in fission–fusion populations, there may be local heterogeneity in knowledge about the environment due to the mixing of individuals among groups. In such scenarios, animals can gain information about relevant geographical features or landmarks by following better informed, transient, group members. While the role of social learning in collective navigation has received substantial empirical support, there are fewer theoretical models. However, the models that do consider the transmission of information across generations suggest that it could lead to collective memory in a population, allowing for migration routes and destinations to be culturally established and maintained.

In addition to social learning, whereby information is passed from one individual to another (or several others), social interactions can also lead to collective learning, where new information emerges de novo as a result of social interactions. For example, a group can jointly discover an improved route, through many wrongs or randomly by noise injected from social interactions, which can then be learned by the group members. Kao et al. demonstrated theoretically that the collective context within which decisions are made can substantially alter what individuals learn about their environment, enabling them to maximize collective accuracy without the need for special social cognitive abilities.

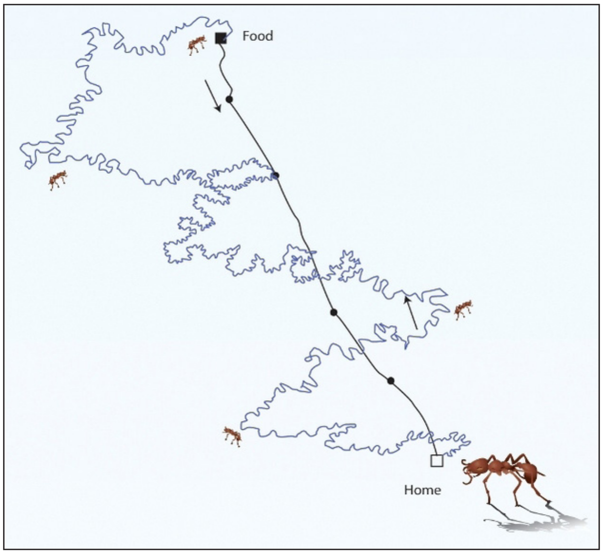
By altering how individuals experience the world, social interactions can affect what aspects of the environment are learned and can contribute to new knowledge within the group that improves navigation. Such learning can lead to the accumulation of increasingly better navigational solutions over time, in a process analogous to cumulative cultural evolution.

While the above models largely presumed a preferred absolute travel direction or target, in many contexts animals navigate by following local cues. Additionally, animals may perform local search to find winds or currents that are favourable for their migration route. In these scenarios, successful navigation can require detecting and climbing environmental gradients, such light, odour, temperature or current. In theory, a group could act as a spatially distributed sensory array spanning weak environmental gradients and amplifying weak signals. In such a scenario, the many wrongs effect could help a group climb a noisy environmental gradient if each individual makes an independent assessment of the direction of the gradient.

However, effective climbing of gradients can also occur collectively even when individuals themselves are unable to detect gradients. Known as emergent sensing, social interactions facilitate comparisons across scalar measurements made by individuals, leading to a collective computation of the environmental gradient. For example, by altering individual-level behavior (e.g. social interactions or swim speed) in response to local scalar values of the environment, movement up a gradient can emerge at the group level. Hein et al. used simulations to demonstrate such group-level traits are an evolutionarily stable outcome, readily arising from selection operating on the behavior of selfish individual agents rather than explicitly on group-level properties. In contrast to the many wrongs effect, which has a known upper bound to accuracy, the limits of emergent group sensing are not well understood. The space of such context-dependent behavioral rules is potentially very large and much remains to be explored, both theoretically and empirically. Because current techniques to infer social interaction rules from data typically average over time and individuals, they potentially miss such context-dependent behaviors that may be highly relevant to navigation.

COGNITIVE CAPACITIES IN NAVIGATION

The physical world poses a number of problems for animals to solve. On a daily basis, animals must find food, avoid predators, and seek shelter. Solving these problems requires cognitive capacities. Cognition involves processing information, from sensing the environment to making decisions based on available information. Such cognitive capacities include, among others, the ability to navigate through space, account for the passage of time, determine quantity, and remember events and locations.



Navigation. Ants use dead reckoning to locate their nests after convoluted foraging trips.

Most animal species move about in their habitat, which requires navigating between locations. Navigation occurs over different spatial scales, from centimetres to thousands of kilometres, and different mechanisms are used at different scales. At small scales, in which animals navigate around their home territory, they can use dead reckoning, landmarks, and cognitive maps to navigate.

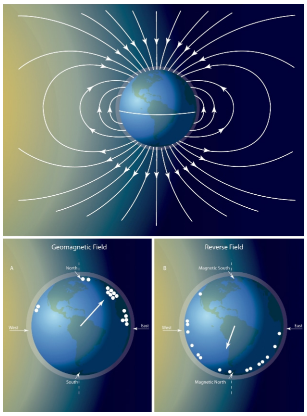
Dead reckoning involves estimating the distance and direction one has traveled. For instance, desert ants (Cataglyphis spp.) track how far away and in what direction they have traveled from home in order to return home after searching for food.

Other species use landmarks to guide their movement. Animals can learn the relationships among landmarks such as rocks, trees, or other large objects to triangulate their position. Landmarks are often the primary cues that animals use to locate their nests. For example, after digger wasps (Philanthus triangulum) leave their nests they circle around the entrance to orient themselves to local landmarks. When the landmarks are moved several centimetres away, the returning wasps land where the nest entrance should be relative to the landmarks and have difficulty finding their nests.

In Tinbergen's experiments, digger wasps were unable to locate their nest entrances after he moved the landmarks surrounding the nests.

Finally, some animals may use a cognitive map to navigate. A cognitive map involves a mental map-like representation of the environment. Though controversial and difficult to demonstrate, honey bees show some evidence of using cognitive maps; when they are physically displaced to a new foraging location, they return home via a direct route. That is, they take a shortcut, suggesting that they possess a cognitive map of their territory.

Many migrating species navigate over long distances. Arctic terns (Sterna paradisaea) travel nearly 80,000 km a year between feeding and mating areas. How do Arctic terns and other migrating species navigate such enormous distances? Many species use something similar to global positioning systems that are based on a sun compass or the earth's magnetic field. A sun compass is the ability to use the sun's position in the sky to determine direction, accounting for both daily and seasonal changes in the sun's position. Honey bees appear to use a sun compass when navigating to their foraging sites. Birds, reptiles, amphibians, and molluscs have also been shown to orient themselves based on the earth's magnetic field. The precise mechanisms enabling such navigation are still under investigation.



Detection of Earth's magnetic field.

(a) Earth's magnetic field generally runs in a north-south direction, providing a cue animals can use to orient their bodies during migration. (b) To test the ability to perceive the magnetic field, animals, such as leatherback sea turtles, are placed in a magnetic coil that reverses the polarity. These turtles reverse their direction of travel in the coils, suggesting that they use magnetic fields to navigate.

Telling Time

Time influences an animal's environment over periods ranging from milliseconds to decades. Annual cycles, in particular, are important for migration, hibernation, caching, mating, and raising young. Though temperature may influence the timing of these activities, photoperiod provides a more accurate cue and plays a large role in initiating or stopping seasonal behaviors. Photoperiod is so important in regulating behavior such as caching that researchers artificially manipulate the photoperiod for animals in captivity to induce this behavior.

The day-night cycle also plays a key role in animal behavior. Some species are active during daylight, others at night, and still others only at dawn or dusk. Activity corresponds to diurnal variation in the availability of food sources, temperature requirements, and the presence or absence of major predators. Even without the cues of light and dark (e.g., in an all-light or all-dark environment), animals maintain a circadian rhythm approximately 24 h long, which suggests the existence of an internal circadian clock used to regulate daily activities.

Conditions also change over finer time scales, requiring another internal clock that works over seconds and minutes. Timing over the short term is particularly important for foraging. To forage efficiently, animals must be able to estimate time periods. This is particularly true for species that consume resources that refresh over time. For example, long-tailed hermit hummingbirds (Phaethornis superciliosus) forage on nectar, and birds must wait for flowers to refill before they return for another meal. Returning too soon would be a waste of time and energy for the hummingbird; waiting too long might mean losing the nectar to a competitor. So the birds learn to return within a few minutes of the time required for the flower to refill. Experiments on timing in rats show that they can estimate short time intervals fairly precisely, but as the interval increases, their accuracy decreases.

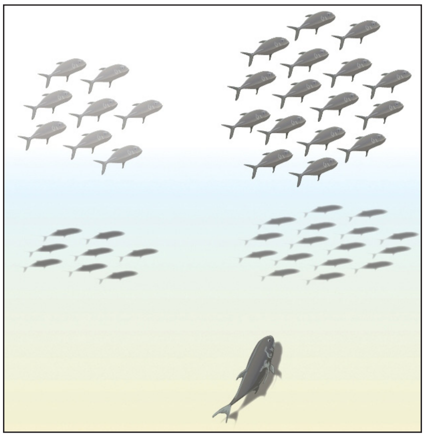
More or Less

Many aspects of an animal's environment vary visibly in size and quantity. Peahens (Pavo spp.), for instance, use the number of eye spots on a male's tail as a cue when selecting a mate. To use this cue, females must have some way to assess the quantity of eye spots. The ability to discriminate numbers is also important for group-living, territorial animals. For example, black howler monkeys (Alouatta pigra), which are highly territorial, can assess relative group size based on the number of males howling in a rival troop. This ability allows the monkeys to avoid potentially injurious encounters with larger troops.

A study was conducted to determine whether animals can precisely distinguish between small numbers. They placed apple slices into each of two boxes in full view of a monkey. They then allowed the monkey to choose a box from which to feed. When the number of slices put into a box was four or less, the monkeys accurately chose the box that contained more slices, but when the number of slices exceeded four for both options, they chose randomly.

Hauser et al. placed apple slices in boxes in full view of rhesus monkeys; the monkeys preferred boxes with more slices, provided the total number of slices in a box was less than four.

When the number of items is larger than three or four, the ability to distinguish precisely between amounts becomes more difficult. Yet in many situations, determining which of two options is "more" is important to an individual's fitness, so animals must use another mechanism to assess quantity. For example, many fish species group together in shoals; a larger shoal should provide greater benefits by decreasing predation risk. Agrillo and colleagues tested mosquitofish (Gambusia holbrooki) and found that the fish could distinguish between shoals that varied by a 1:2 ratio (1:2, 2:4, 4:8, and 8:16), but they were unable to discriminate a ratio of 2:3. Many species show this effect of reduced precision as the ratio increases, and, like timing, animals are less accurate at quantifying as the magnitude increases.



Fish chose larger shoals when one shoal was at least twice as large as the other; at smaller ratios, they were unable to determine which was the larger option

Memory

What is the capital of Germany? With whom did you speak at your last social gathering? How do you ride a bicycle? What was the first question asked here? Each of these questions represents a different type of memory. Storing and retrieving information we have encountered previously can be useful when making predictions about the future. For animals as well, it is often beneficial to remember past information, and some animals seem to have enhanced memory for tasks that they face repeatedly in their natural environments.

Several species of birds cache seeds for the winter. For this to be an effective strategy, they must be able to remember the location of their caches months later, when they need the food. For example, captive black-capped chickadees (Parus atricapillus) are capable of recovering caches up to 28 d after caching. Caching may have strong influences on at least two types of memory. First, caching species may have superior spatial memory. Clark's nutcrackers (Nucifraga columbiana) are corvids that cache up to 30,000 seeds each year. These seeds are an important winter food source for nutcrackers. Compared with non-caching corvid species, nutcrackers excel at remembering the locations of food when these species are tested in spatial memory tasks.

Food caching.

Caching may also impart an advantage to episodic memory. Episodic memory is the memory we use to recall experiences: the who, what, when, and where that we recall from specific episodes in our past. Though difficult to test in animals, there is evidence that some species have "episodic-like memory." Scrub jays (Aphelecoma californica), a relative of nutcrackers, also cache food. In experiments, they were allowed to cache nuts (a stable food source) and waxworms (a decaying food source). After both a 4 h and a 5 d delay, the jays were allowed to recover whichever food they wanted. Because they prefer waxworms, the jays retrieved more waxworms than nuts after the 4 h delay. After 5 d, however, the waxworms had decayed, so the jays retrieved more nuts than waxworms. The jays remembered what they cached, where, and when (either 4 h or 5 d ago) — these are the hallmarks of episodic-like memory.

SWARM BEHAVIOR

Swarm behavior, or swarming, is a collective behavior exhibited by entities, particularly animals, of similar size which aggregate together, perhaps milling about the same spot or perhaps moving en masse or migrating in some direction. It is a highly interdisciplinary topic. As a term, swarming is applied particularly to insects, but can also be applied to any other entity or animal that exhibits swarm behavior. The term flocking or murmuration can refer specifically to swarm behavior in birds, herding to refer to swarm behavior in tetrapods, and shoaling or schooling to refer to swarm behavior in fish. Phytoplankton also gather in huge swarms called blooms, although these organisms are algae and are not self-propelled the way animals are. By extension, the term "swarm" is applied also to inanimate entities which exhibit parallel behaviors, as in a robot swarm, an earthquake swarm, or a swarm of stars.

A flock of auklets exhibit swarm behavior.

From a more abstract point of view, swarm behavior is the collective motion of a large number of self-propelled entities. From the perspective of the mathematical modeller, it is an emergent behavior arising from simple rules that are followed by individuals and does not involve any central coordination. Swarm behavior is also studied by active matter physicists as a phenomenon which is not in thermodynamic equilibrium, and as such requires the development of tools beyond those available from the statistical physics of systems in thermodynamic equilibrium.

Swarm behavior was first simulated on a computer in 1986 with the simulation program boids. This program simulates simple agents (boids) that are allowed to move according to a set of basic rules. The model was originally designed to mimic the flocking behavior of birds, but it can be applied also to schooling fish and other swarming entities.

Models

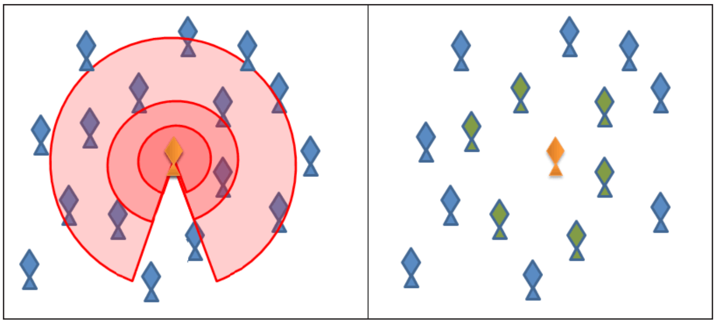
In recent decades, scientists have turned to modeling swarm behavior to gain a deeper understanding of the behavior.

Mathematical Models

Early studies of swarm behavior employed mathematical models to simulate and understand the behavior. The simplest mathematical models of animal swarms generally represent individual animals as following three rules:

- Move in the same direction as their neighbours.
- Remain close to their neighbours.
- Avoid collisions with their neighbours.

The boids computer program, created by Craig Reynolds in 1986, simulates swarm behavior following the above rules. Many subsequent and current models use variations on these rules, often implementing them by means of concentric "zones" around each animal. In the "zone of repulsion", very close to the animal, the focal animal will seek to distance itself from its neighbours to avoid collision. Slightly further away, in the "zone of alignment", the focal animal will seek to align its direction of motion with its neighbours. In the outermost "zone of attraction", which extends as far away from the focal animal as it is able to sense, the focal animal will seek to move towards a neighbour.



In the metric distance model of a fish school (left), the focal fish (yellow) pays attention to all fish within the small zone of repulsion (red), the zone of alignment (lighter red) and the larger zone of attraction (lightest red). In the topological distance model (right), the focal fish only pays attention to the six or seven closest fish (green), regardless of their distance.

The shape of these zones will necessarily be affected by the sensory capabilities of a given animal. For example, the visual field of a bird does not extend behind its body. Fish rely on both vision and on hydrodynamic perceptions relayed through their lateral lines, while Antarctic krill rely both on vision and hydrodynamic signals relayed through antennae.

However recent studies of starling flocks have shown that each bird modifies its position, relative to the six or seven animals directly surrounding it, no matter how close or how far away those animals are. Interactions between flocking starlings are thus based on a topological, rather than a metric, rule. It remains to be seen whether this applies to other animals. Another recent study, based on an analysis of high-speed camera footage of flocks above Rome and assuming minimal behavioral rules, has convincingly simulated a number of aspects of flock behavior.

Evolutionary Models

In order to gain insight into why animals evolve swarming behaviors, scientists have turned to evolutionary models that simulate populations of evolving animals. Typically these studies use a genetic algorithm to simulate evolution over many generations. These studies have investigated a number of hypotheses attempting to explain why animals evolve swarming behaviors, such as the selfish herd theory the predator confusion effect, the dilution effect, and the many eyes theory.

Altruism

Researchers in Switzerland have developed an algorithm based on Hamilton's rule of kin selection. The algorithm shows how altruism in a swarm of entities can, over time, evolve and result in more effective swarm behavior.

Biological Swarming

Bats swarming out of a cave in Thailand

Examples of biological swarming are found in bird flocks, fish schools, insect swarms, bacteria swarms, molds, molecular motors, quadruped herds and people.

Insects

The behavior of insects that live in colonies, such as ants, bees, wasps and termites, has always been a source of fascination for children, naturalists and artists. Individual insects seem to do their own thing without any central control, yet the colony as a whole behaves in a highly coordinated manner. Researchers have found that cooperation at the colony level is largely self-organized. The group coordination that emerges is often just a consequence of the way individuals in the colony interact. These interactions can be remarkably simple, such as one ant merely following the trail left by another ant. Yet put together, the cumulative effect of such behaviors can solve highly complex problems, such as locating the shortest route in a network of possible paths to a food source. The organised behavior that emerges in this way is sometimes called swarm intelligence. The genus Culicoides also known as biting midges have displayed swarming behavior which can cause predatory confusion.

Ants

A swarm of ants which have discovered a food source

Individual ants do not exhibit complex behaviors, yet a colony of ants collectively achieves complex tasks such as constructing nests, taking care of their young, building bridges and foraging for food. A colony of ants can collectively select (i.e. send most workers towards) the best, or closest, food source from several in the vicinity. Such collective decisions are achieved using positive feedback mechanisms. Selection of the best food source is achieved by ants following two simple rules. First, ants which find food return to the nest depositing a pheromone chemical. More pheromone is laid for higher quality food sources. Thus, if two equidistant food sources of different qualities are found simultaneously, the pheromone trail to the better one will be stronger. Ants in the nest follow another simple rule, to favor stronger trails, on average. More ants then follow the stronger trail, so more ants arrive at the high quality food source, and a positive feedback cycle ensures, resulting in a collective decision for the best food source. If there are two paths from the ant nest to a food source, then the colony usually selects the shorter path. This is because the ants that first return to the nest from the food source are more likely to be those that took the shorter path. More ants then retrace the shorter path, reinforcing the pheromone trail.

The successful techniques used by ant colonies have been studied in computer science and robotics to produce distributed and fault-tolerant systems for solving problems. This area of biomimetics has led to studies of ant locomotion, search engines that make use of “foraging trails”, fault-tolerant storage and networking algorithms.

Bees

Bees swarming on a shrub.

When a honey bee swarm emerges from a hive they do not fly far at first. They may gather in a tree or on a branch only a few meters from the hive. In this new location, the bees cluster about the queen and send 20-50 scout bees out to find a suitable new nest locations. The scout bees are the most experienced foragers in the cluster. An individual scout returning to the cluster promotes a location she has found. She uses a dance similar to the waggle dance to indicate direction and distance to others in the cluster. The more excited she is about her findings the more excitedly she dances. If she can convince other scouts to check out the location she found, they may take off, check out the proposed site and promote the site further upon their return. Several different sites may be promoted by different scouts at first. After several hours and sometimes days, slowly a favourite location emerges from this decision making process. When all scouts agree on a final location the whole cluster takes off and flies to it. Sometimes, if no decision is reached, the swarm will separate, some bees going in one direction; others, going in another. This usually results in failure, with both groups dying. A swarm may fly for a kilometre or more to the scouted out location, though some species may establish new colonies within as little as 500 meters from the natal nest, such as Apis dorsata. This collective decision making process is remarkably successful in identifying the most suitable new nest site and keeping the swarm intact. A good nest site has to be large enough to accommodate the swarm (about 15 litres in volume), has to be well protected from the elements, receive a certain amount of warmth from the sun, be some height above the ground, have a small entrance and resist the infestation of ants - hence why trees are often selected.

Cockroaches

Similar to ants, cockroaches leave chemical trails in their faeces as well as emitting airborne pheromones for swarming and mating. Other cockroaches will follow these trails to discover sources of food and water, and also discover where other cockroaches are hiding. Thus, cockroaches can exhibit emergent behavior, in which group or swarm behavior emerges from a simple set of individual interactions.

Cockroaches are mainly nocturnal and will run away when exposed to light. A study tested the hypothesis that cockroaches use just two pieces of information to decide where to go under those conditions: how dark it is and how many other cockroaches there are. The study conducted by José Halloy and colleagues at the Free University of Brussels and other European institutions created a set of tiny robots that appear to the roaches as other roaches and can thus alter the roaches' perception of critical mass. The robots were also specially scented so that they would be accepted by the real roaches.

Locusts

A 19th century depiction of a swarm of desert locusts.

Locusts are the swarming phase of the short-horned grasshoppers of the family Acrididae. Some species can breed rapidly under suitable conditions and subsequently become gregarious and migratory. They form bands as nymphs and swarms as adults—both of which can travel great distances, rapidly stripping fields and greatly damaging crops. The largest swarms can cover hundreds of square miles and contain billions of locusts. A locust can eat its own weight (about 2 grams) in plants every day. That means one million locusts can eat more than one ton of food each day, and the largest swarms can consume over 100,000 tonnes each day.

Swarming in locusts has been found to be associated with increased levels of serotonin which causes the locust to change colour, eat much more, become mutually attracted, and breed much more easily. Researchers propose that swarming behavior is a response to overcrowding and studies have shown that increased tactile stimulation of the hind legs or, in some species, simply encountering other individuals causes an increase in levels of serotonin. The transformation of the locust to the swarming variety can be induced by several contacts per minute over a four-hour period. Notably, an innate predisposition to aggregate has been found in hatchlings of the desert locust, Schistocerca gregaria, independent of their parental phase.

An individual locust's response to a loss of alignment in the group appears to increase the randomness of its motion, until an aligned state is again achieved. This noise-induced alignment appears to be an intrinsic characteristic of collective coherent motion.

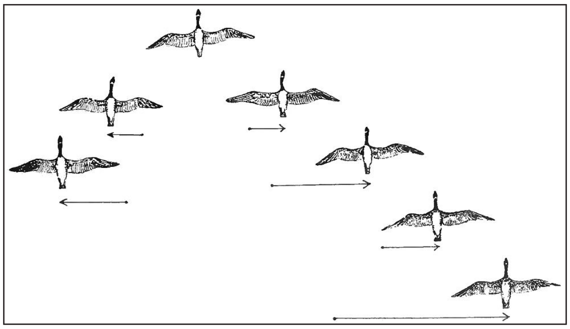
Insect Migration

Cluster of monarch butterflies. Monarch butterflies migrate to Santa Cruz, California where they overwinter.

Insect migration is the seasonal movement of insects, particularly those by species of dragonflies, beetles, butterflies and moths. The distance can vary from species to species, but in most cases these movements involve large numbers of individuals. In some cases the individuals that migrate in one direction may not return and the next generation may instead migrate in the opposite direction. This is a significant difference from bird migration.

Monarch butterflies are especially noted for their lengthy annual migration. In North America they make massive southward migrations starting in August until the first frost. A northward migration takes place in the spring. The monarch is the only butterfly that migrates both north and south as the birds do on a regular basis. But no single individual makes the entire round trip. Female monarchs deposit eggs for the next generation during these migrations. The length of these journeys exceeds the normal lifespan of most monarchs, which is less than two months for butterflies born in early summer. The last generation of the summer enters into a non-reproductive phase known as diapause and may live seven months or more. During diapause, butterflies fly to one of many overwintering sites. The generation that overwinters generally does not reproduce until it leaves the overwintering site sometime in February and March. It is the second, third and fourth generations that return to their northern locations in the United States and Canada in the spring. How the species manages to return to the same overwintering spots over a gap of several generations is still a subject of research; the flight patterns appear to be inherited, based on a combination of the position of the sun in the sky and a time-compensated Sun compass that depends upon a circadian clock that is based in their antennae.

Bird Migration



Large bird typically migrate in V echelon formations. There are significant aerodynamic gains. All birds can see ahead, and towards one side, making a good arrangement for protection.

Approximately 1800 of the world's 10,000 bird species are long-distance migrants. The primary motivation for migration appears to be food; for example, some hummingbirds choose not to migrate if fed through the winter. Also, the longer days of the northern summer provide extended time for breeding birds to feed their young. This helps diurnal birds to produce larger clutches than related non-migratory species that remain in the tropics. As the days shorten in autumn, the birds return to warmer regions where the available food supply varies little with the season. These advantages offset the high stress, physical exertion costs, and other risks of the migration such as predation.

Many birds migrate in flocks. For larger birds, it is assumed that flying in flocks reduces energy costs. The V formation is often supposed to boost the efficiency and range of flying birds, particularly over long migratory routes. All the birds except the first fly in the upwash from one of the wingtip vortices of the bird ahead. The upwash assists each bird in supporting its own weight in flight, in the same way a glider can climb or maintain height indefinitely in rising air. Geese flying in a V formation save energy by flying in the updraft of the wingtip vortex generated by the previous animal in the formation. Thus, the birds flying behind do not need to work as hard to achieve lift. Studies show that birds in a V formation place themselves roughly at the optimum distance predicted by simple aerodynamic theory. Geese in a V-formation may conserve 12–20% of the energy they would need to fly alone. Red knots and dunlins were found in radar studies to fly 5 km per hour faster in flocks than when they were flying alone. The birds flying at the tips and at the front are rotated in a timely cyclical fashion to spread flight fatigue equally among the flock members. The formation also makes communication easier and allows the birds to maintain visual contact with each other.

Other animals may use similar drafting techniques when migrating. Lobsters, for example, migrate in close single-file formation "lobster trains", sometimes for hundreds of miles.

The Mediterranean and other seas present a major obstacle to soaring birds, which must cross at the narrowest points. Massive numbers of large raptors and storks pass through areas such as Gibraltar, Falsterbo, and the Bosphorus at migration times. More common species, such as the European honey buzzard, can be counted in hundreds of thousands in autumn. Other barriers, such as mountain ranges, can also cause funnelling, particularly of large diurnal migrants. This is a notable factor in the Central American migratory bottleneck. This concentration of birds during migration can put species at risk. Some spectacular migrants have already gone extinct, the most notable being the passenger pigeon. During migration the flocks were a mile (1.6 km) wide and 300 miles (500 km) long, taking several days to pass and containing up to a billion birds.

Marine Life

Fish

Schooling predator fish size up schooling anchovies.

The term "shoal" can be used to describe any group of fish, including mixed-species groups, while "school" is used for more closely knit groups of the same species swimming in a highly synchronised and polarised manner.

Fish derive many benefits from shoaling behavior including defence against predators (through better predator detection and by diluting the chance of capture), enhanced foraging success, and higher success in finding a mate. It is also likely that fish benefit from shoal membership through increased hydrodynamic efficiency.

Fish use many traits to choose shoalmates. Generally they prefer larger shoals, shoalmates of their own species, shoalmates similar in size and appearance to themselves, healthy fish, and kin (when recognised). The "oddity effect" posits that any shoal member that stands out in appearance will be preferentially targeted by predators. This may explain why fish prefer to shoal with individuals that resemble them. The oddity effect would thus tend to homogenise shoals.

One puzzling aspect of shoal selection is how a fish can choose to join a shoal of animals similar to themselves, given that it cannot know its own appearance. Experiments with zebrafish have shown that shoal preference is a learned ability, not innate. A zebrafish tends to associate with shoals that resemble shoals in which it was reared, a form of imprinting.

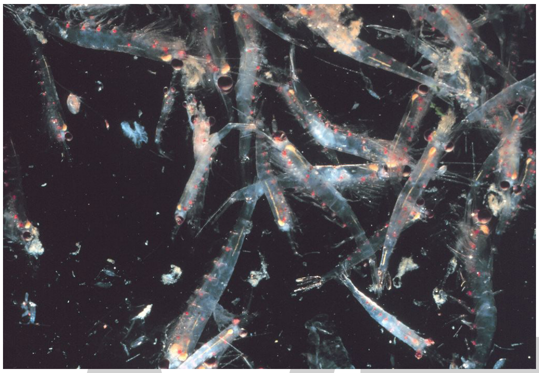
Other open questions of shoaling behavior include identifying which individuals are responsible for the direction of shoal movement. In the case of migratory movement, most members of a shoal seem to know where they are going. In the case of foraging behavior, captive shoals of golden shiner (a kind of minnow) are led by a small number of experienced individuals who knew when and where food was available.

Radakov estimated herring schools in the North Atlantic can occupy up to 4.8 cubic kilometres with fish densities between 0.5 and 1.0 fish/cubic metre. That's several billion fish in one school.

Fish Migration

Between May and July huge numbers of sardines spawn in the cool waters of the Agulhas Bank and then follow a current of cold water northward along the east coast of South Africa. This great migration, called the sardine run, creates spectacular feeding frenzies along the coastline as marine predators, such as dolphins, sharks and gannets attack the schools.

Krill

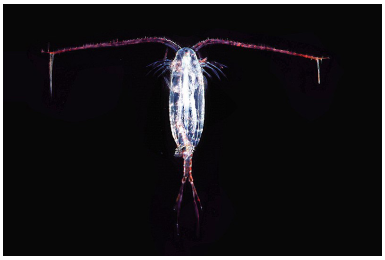


Swarming krill.

Most krill, small shrimp-like crustaceans, form large swarms, sometimes reaching densities of 10,000–60,000 individual animals per cubic metre. Swarming is a defensive mechanism, confusing smaller predators that would like to pick out single individuals. The largest swarms are visible from space and can be tracked by satellite. One swarm was observed to cover an area of 450 square kilometers (175 square miles) of ocean, to a depth of 200 meters (650 feet) and was estimated to contain over 2 million tons of krill. Recent research suggests that krill do not simply drift passively in these currents but actually modify them. Krill typically follow a diurnal vertical migration. By moving vertically through the ocean on a 12-hour cycle, the swarms play a major part in mixing deeper, nutrient-rich water with nutrient-poor water at the surface. Until recently it has been assumed that they spend the day at greater depths and rise during the night toward the surface. It has been found that the deeper they go, the more they reduce their activity, apparently to reduce encounters with predators and to conserve energy.

Later work suggested that swimming activity in krill varied with stomach fullness. Satiated animals that had been feeding at the surface swim less actively and therefor sink below the mixed layer. As they sink they produce faeces which may mean that they have an important role to play in the Antarctic carbon cycle. Krill with empty stomachs were found to swim more actively and thus head towards the surface. This implies that vertical migration may be a bi- or tri-daily occurrence. Some species form surface swarms during the day for feeding and reproductive purposes even though such behavior is dangerous because it makes them extremely vulnerable to predators. Dense swarms may elicit a feeding frenzy among fish, birds and mammal predators, especially near the surface. When disturbed, a swarm scatters, and some individuals have even been observed to moult instantaneously, leaving the exuvia behind as a decoy. In 2012, Gandomi and Alavi presented what appears to be a successful stochastic algorithm for modelling the behavior of krill swarms. The algorithm is based on three main factors: "(i) movement induced by the presence of other individuals; (ii) foraging activity, and (iii) random diffusion."

Copepods

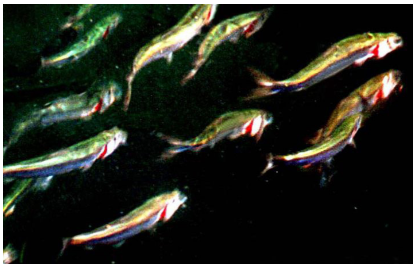


This copepod has its antenna spread. The antenna detects the pressure wave of an approaching fish.

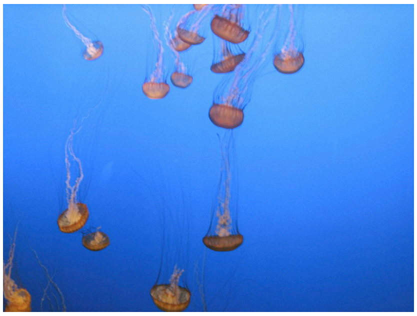
Copepods are a group of tiny crustaceans found in the sea and lakes. Many species are planktonic (drifting in sea waters), and others are benthic (living on the ocean floor). Copepods are typically 1 to 2 millimetres (0.04 to 0.08 in) long, with a teardrop shaped body and large antennae. Although like other crustaceans they have an armoured exoskeleton, they are so small that in most species this thin armour, and the entire body, is almost totally transparent. Copepods have a compound, median single eye, usually bright red, in the centre of the transparent head.

Copepods also swarm. For example, monospecific swarms have been observed regularly around coral reefs and sea grass, and in lakes. Swarms densities were about one million copepods per cubic metre. Typical swarms were one or two metres in diameter, but some exceeded 30 cubic metres. Copepods need visual contact to keep together, and they disperse at night.

Spring produces blooms of swarming phytoplankton which provide food for copepods. Planktonic copepods are usually the dominant members of the zooplankton, and are in turn major food organisms for many other marine animals. In particular, copepods are prey to forage fish and jellyfish, both of which can assemble in vast, million-strong swarms. Some copepods have extremely fast escape responses when a predator is sensed and can jump with high speed over a few millimetres.



School of herrings ram feeding on a swarm of copepods.



Swarms of jellyfish also prey on copepods.

Planktonic copepods are important to the carbon cycle. Some scientists say they form the largest animal biomass on earth. They compete for this title with Antarctic krill. Because of their smaller size and relatively faster growth rates, however, and because they are more evenly distributed throughout more of the world's oceans, copepods almost certainly contribute far more to the secondary productivity of the world's oceans, and to the global ocean carbon sink than krill, and perhaps more than all other groups of organisms together. The surface layers of the oceans are currently believed to be the world's largest carbon sink, absorbing about 2 billion tons of carbon a year, the equivalent to perhaps a third of human carbon emissions, thus reducing their impact. Many planktonic copepods feed near the surface at night, then sink into deeper water during the day to avoid visual predators. Their moulted exoskeletons, faecal pellets and respiration at depth all bring carbon to the deep sea.

Algal Blooms

Many single-celled organisms called phytoplankton live in oceans and lakes. When certain conditions are present, such as high nutrient or light levels, these organisms reproduce explosively. The resulting dense swarm of phytoplankton is called an algal bloom. Blooms can cover hundreds of square kilometres and are easily seen in satellite images. Individual phytoplankton rarely live more than a few days, but blooms can last weeks.

ANIMAL COMMUNICATION

Animal communication is a process by which one animal provides information that other animals can incorporate into their decision making. The vehicle for the provision of this information is called a signal. The signal may be a sound, colour pattern, posture, movement, electrical discharge, touch, release of an odorant, or some combination of these mediums.

Cactus wrens (Campylorhynchus brunneicapillus) sing to communicate with other members of their species.

Animals face daily decisions about how to behave. Choices can be as simple as a sea anemone deciding when to expand its tentacles or as complex as a male lion deciding whether to approach a reluctant mate. The decision, which may be reflexive or conscious, is guided by evolutionary biases based on alternative outcomes of choice, recent experience about likely conditions, and sensory information. An animal with access to complete information can always choose correctly. However, life is rarely so accommodating, and inputs often fail to provide complete information.

Thus, communication is an important source of additional information that is incorporated into the decision-making process.

Signals are actions or anatomical structures whose primary function is the provision of information to another animal. However, not all actions by one animal that provide information to another animal qualify as signals. The noise created by a foraging mouse and used by an owl to locate and kill the mouse is a case in point. Mice have to feed, and the noises they create while feeding (e.g., through movement and chewing) are an inadvertent result of that activity. Thus, these sounds are not a signal. In contrast, the song of a wren is not inadvertent—wrens sing solely to communicate with other birds.

Senders and Receivers

An animal that provides a signal is called a sender. The animal to which the signal is directed is the receiver. The receiver uses the signal information to help make a decision. For example, if a receiver must choose either to fight with or to flee from an opponent, it brings to this decision biases and thresholds passed on to it by successful prior generations. This information helps the receiver avoid harm and find food, shelter, and mates. Prior experience in the receiver's own life may also play a role in shaping its evaluation of the situation. If it has routinely lost fights to larger animals, a useful strategy would be to assess the size of the opponent. This may be done by using vision or other means. For example, in some cases an opponent broadcasts a low-frequency sound signal at the receiver. Because only large animals can produce low-frequency sounds, this signal provides evidence that the opponent is large. The receiver integrates its perception of the sound frequency with its prior experience and inherited avoidance of harmful situations and thus decides to flee.

In this example, the receiver can interpret the signal only if it understands that low-frequency sounds tend to be associated with large body sizes. The association between alternative signals (e.g., sounds of different frequencies) and different alternative circumstances (e.g., relative sizes of opponents) is called a code. Codes can be characterized as probabilities that a sender will emit a given signal in any given circumstance. In a perfect code, only one signal will be used in a given context, and only one context will evoke that signal. Real codes do not need to be perfect, but they do need to be good enough that a receiver attending to signals makes better decisions than if it ignored the signals and relied only on other sources of information.

Animals differ widely in the mechanisms by which they acquire signal codes. Some codes are inherited genetically. For example, the sound-producing structures of many male insects generate a limited range of sound frequencies, and the ears of females are pretuned to be most sensitive to those frequencies. In other species, senders' sounds or body odours are determined by random genetic processes, and receivers must learn which signals go with which individuals. Many songbirds have genetic limits on the range of sounds they can sing, but they can learn one or more local variants within those limits during a short period in their youth. In certain species, such as parrots, both sender and receiver must learn the appropriate vocal coding, and they can continue to learn alternative coding systems throughout life.

Different contexts require different kinds of information and thus different signals. The number of signals in a species' repertoire can range from 5 or 6 in the simplest nonsocial animals to 10–20 in social insects, such as bees and ants, or to 30–40 in social vertebrates, such as wolves and primates. Most animals produce signals to attract mates and then produce additional signals to synchronize mating. Signals for mediating conflicts, including signals of aggressive intention and signals of submission, are also widespread. In addition, territorial species require signals for declaring territory ownership, and in situations in which adults guard or feed their young, both parents and offspring require signals to coordinate parental care. Social animals may use signals to coordinate group movements, to assemble dispersed group members, or to display social affiliations. Some animals have special signals that they use to share food finds, to alert others about predator attacks, and even to alert approaching predators that they have been detected. In addition, bats, oilbirds, porpoises, and electric fish use the differences between their own emitted and subsequently received signals to extract information about the ambient environment. In many of these contexts, the relevant animal signals are designed to provide a receiver with ancillary information about the identity, sex, social affiliation, and location of the sender.

Wolves are social animals, and they thus require a large repertoire of signals to communicate different kinds of information.

Signal Production

The challenge faced by a sender is the creation of a controlled perturbation of the environment that can be detected and recognized by a receiver. Sound production is one mechanism. Sound travels in waves, and thus any sound can be characterized by its component frequencies and the physical size of each wave component (called the wavelength). The wavelength of a sound depends upon its frequency and the speed of sound in the propagating medium. The speed of sound is greatest in solids, intermediate in water, and least in air. Thus, a given frequency of sound in water has a wavelength 4.5 times longer than the same frequency in air, and the same frequency in a solid can be up to 15 times longer than that in air. This is important to animals using sound communication because it is physically difficult for an animal to produce a loud sound with a wavelength much larger than itself. For this reason, small animals tend to communicate with high-frequency sounds, and only large animals use low-frequency sound signals. Aquatic animals require higher-frequency signals than do similarly sized terrestrial animals.

Blue arrow-poison frogs (Dendrobates azureus) can communicate through sound production. Their bright colour also serves as a warning signal to predators.

The lowest frequencies that small insects, frogs, and birds can produce as signals may be many thousands of waves per second. Animal muscles cannot twitch this quickly, which makes sound production challenging. One solution is to use frequency multiplication. For example, hard-bodied animals drag a comblike structure over a sharp edge. A single muscle contraction causes the sharp edge to hit successive teeth in the comb, thereby producing a sequence of sound waves. This is called stridulation. Arthropods all have hard exoskeletons, and by mounting the comb on one external body part and the sharp edge on the other, they can stridulate by rubbing the two hard parts together. For example, lobsters rub an antenna against the head, beetles rub a leg against the body, and crickets and katydids rub one wing over another. There are other techniques for frequency multiplication. Terrestrial vertebrates use muscles to force air into and out of their lungs while breathing. If thin membranes are inserted into this airflow, the membranes will flutter, producing sound waves at much higher frequencies than the airflow cycle. This is how frogs croak, lions roar, and birds sing.

In figure above, katydids use several different forms of communication. One of these forms is called stridulation and is characterized by the rubbing together of the insect's wings to create sound waves. These sound waves convey specific types of information and are detected by members of the same species.

To be able to use different sound signals in different contexts, animals must have some way to control and vary the sounds that they produce. Varying the rhythm of insect stridulation or bird breathing is one way to produce different signals. Air-breathing vertebrates can also change the tension on the vibrating membranes to produce quite complicated frequency modulations. A third mechanism is to produce sounds that initially contain many different frequencies and then selectively filter out some frequencies and amplify others. Animals such as katydids, frogs, bats, and howler monkeys have special resonating structures attached to their sound-producing organs that select the radiated frequencies and couple the sounds to the medium.

Bats have special resonating structures attached to their sound-producing organs that select specific sound frequencies. This enables them to use different sound signals in different contexts.

Light is another modality used for producing signals. Most visual signals rely on the presence of ambient light that is generated by the Sun. Similar to sound, light propagates as waves. When white light—which contains many different light frequencies—strikes an object, some of it is reflected, and it is this reflected light that creates a visual image of the object. If the object absorbs some frequencies of white light and reflects others, the receiver will see the object as coloured. When red light frequencies are absorbed, the object appears green or blue. When the green light frequencies are absorbed, the colour appears purple. Different animal groups tend to have different ranges of light frequencies that they can see. Birds, lizards, and some insects can see light frequencies well into the short-waved ultraviolet.

The challenge for a sender is to produce a visible image that is detectable against the background by a receiver. One way to do this is to move the signal body part in front of a static background or to move it in a different direction relative to a moving background. This simply requires normal muscle movements—no additional structure is needed. However, many senders enlarge or decorate the moved body part to increase the chances that the receiver will notice the signal. The sender may also select a site in which to produce the signal that has a simpler background or that is moving in a very different way.

Another major way to catch a receiver's visual attention is by increasing the contrast between a signal body part and the background. Black-and-white patterns are a common solution. The black is generated by using one of several synthesizable proteins called melanins. White is created by inserting small crystals or bubbles into the organ surface. They are large enough that they scatter all light wavelengths, creating white stimuli. Colours other than black and white are more difficult to produce. Although animals cannot synthesize carotenoid pigments, they can sequester the pigments by eating certain plant parts or by eating other animals that ingest those plants. Carotenoids are relatively stable compounds, generating colours in the yellow-to-red range. There are few natural pigments that are blue or green that animals can utilize for coloration. One exception is the chemical combination of carotenoids and proteins used by arthropods to colour their carapaces (hard outer coverings) dark green or blue. Crabs and lobsters turn red when cooked because the pigment proteins are denatured with heat, releasing the carotenoids. Other animal groups use nonpigment techniques to produce blue or green coloration. One method uses a checkerboard matrix of alternating more-dense and less-dense materials in an external surface layer to selectively scatter certain wavelengths. The colour reflected depends on the size and spacing of the matrix. This mechanism is responsible for producing the blue and green feathers of jays and parrots, the blue skin on the heads of turkeys and male mandrills, and blue eyes in snow leopards. Another technique is to use two thin layers of reflecting material on external surfaces. If the layers have the correct thickness, certain wavelengths are reflected by the two layers out of phase (the crest of one wave coincides with the valley of a second wave), thereby canceling each other out. The remaining light waves are in phase (the crests of the light waves coincide) and are visible as intense colours. Which light waves are canceled depends on the viewing angle of the receiver. Thus, the apparent colour can change as the sender shifts its position relative to the receiver. These are the iridescent colours seen in many hummingbirds and butterflies.

While it is often assumed that ambient light is white, every local environment is actually bathed in its own particular mixture of light frequencies. On a forest floor there may be only small amounts of red and blue light in the ambient mixture because green-reflecting plants absorb both red and blue light strongly. Fine particles in the atmosphere and the dense molecules in water both scatter the shorter blue and ultraviolet light frequencies but transmit the longer red and orange frequencies. The mixture of ambient-light frequencies can be a strong selective force favouring certain colours for signals. Where there is little ambient light, an animal may have to produce its own light (bioluminescence). This ability has evolved in fireflies, ostracod crustaceans (mussel shrimps), deep-sea squid, and marine fish, all of which produce their own light chemically or harbor luminescent symbionts that can produce light for them.

Fireflies such as those of the genus Photinus produce
their own light as a means of communication.

A third major modality used by most animals (with the exception of many birds) is olfactory signaling. Senders deposit or release chemicals called pheromones that receivers later detect by smell or taste. The cost to senders of chemical communication can be minimal, as when feces or urine is used as a signal, or can be substantial, as when complex organic molecules must be synthesized solely for the purpose. Ants are prolific users of chemical communication. Their small bodies contain up to a dozen separate glands, each producing a different chemical compound or mixture of compounds that serves a different social function. Ants use chemical signals to mark their foraging trails, to recruit group members for defense against invaders, to attract mates, to regulate development of different worker castes, to solicit food, and to distinguish colony members from nonmembers. Many mammalian species employ chemical communication for important social functions, such as mate attraction, synchronization of mating, and territory defense. Mammalian glands often produce specialized chemical products, but some species mix various natural body products into a pouch and let bacteria do the work of producing the final pheromone product.

The potential for signal diversity is extremely high in chemical communication, as is the opportunity to create a signal that is very different from background odours. However, this diversity is often constrained by the degree to which chemical signals are appropriately volatile in air or soluble in water, resistant to degradation after release, and detectable by receivers. Animals often limit the volatility or solubility of pheromones by embedding them in an inert carrier compound that releases odorant slowly. This technique is particularly useful for territorial defense. Desert iguanas carry this one step farther by using a carrier that does not release odorant until another lizard flicks the carrier with its wet tongue. The small packets of deposited pheromone absorb ultraviolet light and thus appear as black specks to animals that can see in the ultraviolet spectrum, such as iguanas. Iguanas approach the specks and taste them, thereby releasing the pheromones. Other animals accelerate the dispersal of relatively nonvolatile scents by spreading them over a tuft of fine hairs, actively spraying them into a medium (e.g., air or water), or releasing them into strongly flowing wind or water currents.

Tactile signals involve special patterns of touching, generating persistent eddies in a medium, or the transmission of vibrations through a substrate. Touching during aggressive encounters may provide information about the body size and strength of opponents. The grooming of another individual, called allopreening or allogrooming, has both hygienic and signal functions in many birds and mammals. Courtship signals may include a tactile component for synchronizing mating or gamete release. Roosting with body contact not only preserves heat but also appears to signal pair or group affiliations in mammals and birds. Arthropods make wide use of tactile, eddy, and substrate signals. For example, aquatic male copepods can identify the distinct eddies left by swimming females and track them for mating. The dances of honeybees are usually performed in a dark hive, and attending workers monitor the dancer with their antennae; some signal vibrations may also pass through the honeycomb substrate. Other arthropods attending to substrate-borne vibrations include water striders (using the surface of water), spiders (using their webs), and leafhoppers (using their host-plant stems and leaves).

Electrical discharges can also be used for signals. Two orders of freshwater fish, the Mormyriformes of Africa and the Gymnotiformes of the neotropics, are nocturnal or live in muddy water. These fish create an electric field and use distortions induced by nearby objects to navigate and find food. Not surprisingly, they also use the same electrical discharges to communicate with each other. In both groups, special bioelectric organs have evolved to produce rapid trains of discharges. The waveforms of these discharges vary with species and even with sex, and the rates of discharge can be modulated in complex ways to mediate social interactions. Because of the high resistance of fresh water and the low voltages the fish produce, electrical communication is limited to a distance of about 1 metre (3.3 feet).

Signal Transmission

All animal signals degrade as they propagate between sender and receiver. The farther apart the two parties, the greater this degradation will be and the less a signal will stand out from background noise. Senders can do little to reduce degradation once the signals have left the sender. However, they do have a choice of what kind of signal they produce, and evolution has often favoured choices that minimize degradation.

Elephants communicate by using low-frequency sound waves that can be detected several kilometres away from the animal sending the signal.

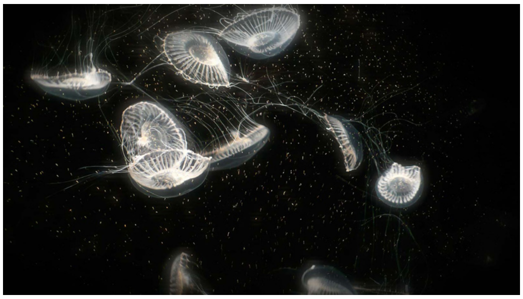
Sound signals transmit efficiently over large distances, around obstacles such as trees and foliage, and in dark environments. Nevertheless, sounds of all frequencies become less intense as they radiate away from a source. Higher frequencies suffer additional attenuation owing to heat losses and scattering of the sounds. Since small animals can produce only high frequencies (short wavelengths), their sound communication is often limited to short distances. Furthermore, ambient sound is often greatest at low and high frequencies, making intermediate frequencies the ones least likely to be obscured by the background.

Propagation of sound is complicated when the sender and receiver are close to a boundary (e.g., the ground for terrestrial animals and the water's surface for aquatic animals). This is because sound can travel to a receiver by two routes: a direct route along the line connecting sender and receiver, and an indirect route in which the sound bounces off the boundary and up to the receiver. If the two replicates of the sound signal arrive at the receiver out of phase, they will cancel each other out. The closer both parties are to the surface, the more acute the cancellation. Low frequencies are most susceptible to these effects. However, for terrestrial animals, very low frequencies can propagate by a third route, called a ground wave, if the surface is sufficiently porous. Intermediate frequencies, however, are still canceled out even when the ground is porous. As a result, intermediately sized animals that cannot produce low-frequency sounds often climb or fly to locations high above the ground before vocalizing. Elephants, which cannot fly or climb, resort to sufficiently low frequencies that they can be detected several kilometres away. Whales also produce low frequencies and move sufficiently far beneath the ocean surface before vocalizing, which enables their signals to be heard hundreds of kilometres away.

In figure above, whales such as humpbacks (Megaptera novaeangliae) communicate by producing low-frequency sound waves. The animals move sufficiently far beneath the ocean surface before vocalizing, which enables their signals to be heard over hundreds of kilometres.

The optimal temporal patterning for sound signals also varies with habitat. Rapid temporal patterns quickly become unrecognizable owing to echoes in heavily forested habitats. In contrast, sounds propagating in open grasslands suffer little from echoes but instead acquire slow artifactual modulations because of air turbulence. Birds, even of the same species, are much more likely to use rapid temporal modulations of their calls, such as trills and buzzes, when they live in grasslands than when they live in forests. Forest birds typically produce long whistlelike notes with slow, if any, modulations.

Light signals also suffer transmission losses. Intervening obstacles such as foliage easily block the straight-line propagation of visual signals, and increasingly distant senders occupy a decreasing part of a receiver's visual field. Light waves are also subject to filtering and scatter that can distort a signal pattern and decrease its contrast with the background. All of these effects make detection and recognition of a visual signal more difficult at a distance. In addition, reflected light signals require some source of ambient light, and visual communication thus becomes more difficult to achieve at night and in very dark environments. Bioluminescence is, one solution to this problem.



Water jelly (Aequorea victoria).

The medusa stage of the bioluminescent water jelly or crystal jelly (Aequorea victoria) in the waters off the west coast of North America. The species is harvested for its luminescent protein called aequorin, which has been used in medical research as a fluorescent marker protein.

Olfactory signaling differs from sound and light communication in significant ways. Pheromones spread from a source by diffusion and medium turbulence. This process is much slower than the propagation of light or sound signals, and its erratic path can make it difficult for a receiver to locate an odorant source. Whereas sound and light largely retain their temporal patterning as they propagate, temporal patterning of pheromone release is quickly lost because of turbulence. The slow speed, the limited ability to be located, and the loss of temporal pattern constrain the uses of olfactory communication to short-range signals and to recurrent functions, such as territory defense and mate attraction.

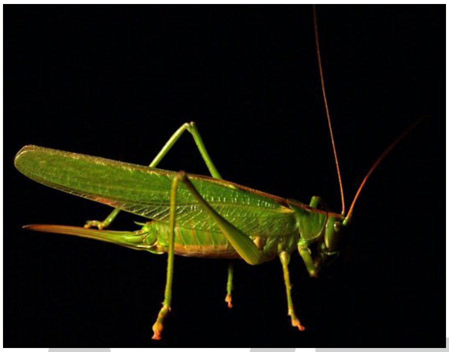
The unpredictable effects of turbulence also limit the range over which an olfactory signal can be detected. Receiver moths get around this constraint by sampling wind direction and flying into the wind to trace the chemical source (a process called anemotaxis). Many nocturnal mammals deposit scent marks at multiple locations within their territories. Although no single scent mark is detectable at a distance, the ensemble ensures that any intruder is aware of the owner’s presence in the territory. Some insects and marine species actively seek out sites where air or water currents can convey olfactory signals over long distances.

Signal degradation during propagation is not always a detriment. Many birds use degradation of songs to estimate the distance to competitors. As long as there is sufficient degradation, a territory owner can conclude that the other singers are too distant to be threatening. Many social insects use olfactory signals to mark feeding trails, to give alarms, or to identify colony mates. To avoid confusion and focus attention on a specific location or individual, it is best if these signals have only limited ranges of detection.

Regardless of the modality used, senders communicating with distant receivers face a number of competing influences. Body size, habitat type, time of day, proximity to a surface, and speed with which a receiver must respond all affect the form of the optimal signal. Because species differ in these factors, optimal signals differ between species even when communicating the same information. The constraints imposed by the physics of signal production and transmission account for an important fraction of the diversity seen in animal signals.

Signal Reception

The receiver's task is to detect signals against the background and to discriminate between different signals. Most animals use the same sense organs (eyes, ears, noses, touch receptors, etc.) for signals that they use to detect other external stimuli. Their brains also process all sensory stimuli, both signals and nonsignals, with similar procedures. However, communication is sufficiently important that most animals show some tuning of their sense organs and some specialization of their brains to improve signal detection and characterization.



Crickets have eardrums on their legs that are connected by tubes to breathing holes on the sides of their bodies. This allows them to obtain multiple samples of a given sound field at each point in time.

Detection of sound is often challenging because the received signals are faint and distorted owing to propagation. Sound traveling in air is largely reflected from solid objects, including animals, with little energy transfer. Sound traveling in water is easily transferred to aquatic animals, but because all parts of the animal vibrate in synchrony, there is no immobile reference allowing the animal to detect the vibrations. As a result, animals have had to acquire some very sophisticated adaptations to hear sounds.

Terrestrial animals often have funnel-shaped structures outside the body to collect and concentrate impinging sounds. The funnel shape also creates a gradual change in the properties of the sound-propagating medium from that of air to that of liquid and solid bodies. This increases the amount of trapped sound energy. At the end of the funnel is a thin membrane (called an eardrum) that is set into vibration by the sounds. Small bones or fibres transfer the eardrum movements to a fluid-filled cavity, within which are sensory cells bearing hairlike cilia. As the fluids move, the cilia sway, thereby stimulating the attached nerve fibres. Ears of orthopteran insects (e.g., crickets and grasshoppers) and vertebrates are designed such that different frequencies of sound stimulate different sets of sensory cells. Thus, the animal is able to decompose a complex sound into its component frequencies. This enables the receiver to separate signal frequencies from those of nonsignal sounds. For each band of useful frequencies, amplitudes and a temporal pattern are encoded in the rates and patterns of nerve impulses sent to the brain. Larger animals usually have two ears and use the time delays or differences in signal amplitude at the two ears to identify the direction of the sender. Small animals cannot use this method because the delays and intensity differences are very small. However, they can achieve some directional information by sampling a sound field at several points simultaneously. For example, crickets have their eardrums on their legs, and fine tubes connect each eardrum internally to breathing holes on the sides of their bodies. This allows them to obtain multiple samples of a given sound field at each point in time. Frogs and birds have a space connecting their eardrums that works in a similar manner.

Some aquatic animals have exterior cilia or hairs that sway as sounds pass over them and stimulate sensory cells. This mechanism is effective only within a few wavelengths of the sound source and tends to be limited to lower frequencies. For sound reception at a greater distance from the source, an aquatic animal must create body parts that are moved in different ways during the passage of sound waves. Some bony fish use swim bladders for this purpose. These are air-filled sacs that provide buoyancy. Because air is much more compressible than water, sound trapped by the swim bladder results in much larger molecular displacements than the same sound energy propagating in the rest of the fish's body. Connecting the swim bladder to the fish's ears makes it possible for the differences in molecular displacement between the swim bladder and the rest of the fish to be used to stimulate the sensory cells of the ear. This allows a fish far from the sender to detect and measure the passing sound waves.

Animal eyes differ markedly in their range of view, their resolution, and their focusing power. The eyes of vertebrates and cephalopods (octopus and squid) have adjustable lenses that extend the range over which images are in focus. They also have an iris that adjusts the amount of light entering the eye. An effective eye must have many receptor cells if it is to preserve the relative positions of the different objects reflecting light to it. To discriminate between different colours, different receptor cells must be sensitive to different light frequencies. In addition, because light intensities are highly variable, eyes may need different receptor cell types to handle both dim and bright light. Vertebrate eyes use cone receptor cells for bright light and colour discrimination and colour-insensitive rod receptors for dim light conditions. All light receptors contain a protein-bound pigment. This pigment, called rhodopsin, occurs in all multicellular animals. These pigment molecules change shape when absorbing light. This triggers a chain of reactions within the receptor cells ending in the production of nerve impulses. Different photopsins and rhodopsins absorb different light frequencies, permitting receptors to differ in colour sensitivity. Arthropod eyes consist of 8–10 receptor cells clustered around each of many facets, or corneal lenses. It is the number of facets, not the number of receptor cells, that determines visual acuity in arthropod eyes.

Unlike the case with auditory signals, the direction of a visual sender is automatically known once a receiver has detected the signal. The relative positions of receptor cells in an eye are preserved in their projections to the brain. This allows the brain to create a map that replicates, to varying degrees, the visual field of the eye. Projections from the visual maps of the two eyes are compared to identify specific objects and their relative distances. The recognition of patterns is a function of the brain and relies on a combination of inherited and learned mechanisms.

Pheromone reception is accomplished by smell (olfactory) or taste (gustatory) organs. These receptors contain sensory cells with fine cilia, or microvilli, that extend into the medium. Pheromone molecules and other stimuli temporarily bind to specific proteins on the cilia or microvilli. The binding triggers a cascade of chemical reactions within the sensory cell that result in the production of nerve impulses flowing to the brain. The more molecules that bind to a cell, the higher the rate of nerve firing. The sensory cells in an olfactory organ can have highly specific or generalized sensitivities. Specific cells tend to respond only to a certain molecule. Animals often use such cells to detect species-specific mating pheromones. Generalized cells respond to several types of molecules. They are used for less-specific functions, such as the recognition of food items. The olfactory organs of different species vary in the mix of specialized versus generalized sensory cells that they host. Olfactory organs can be as simple as a patch in a mammalian breathing passage or as complex as the plumose antennae of male moths. In some mammals the vomeronasal organ (Jacobson's organ), located in the roof of the mouth, is used to mediate a behavioral response known as flehmen, in which an animal raises its head and lifts its upper lip in reaction to specific odours. This response requires special movements of the tongue and lips to admit chemical samples to the sensory cells. The vomeronasal organ is the primary receptor organ for many of the pheromones that dictate interactions in mammalian social life, including pheromones involved in conflict, reproduction, and parental care.

Red imported fire ants (Solenopsis invicta), as well as other ant species, create marker trails using pheromones. A pheromone trail is followed by worker ants traveling between the nest and a food source.

Electroreception appears to have been a widespread sensory ability in primitive fishes, in which it was used to detect muscle and nerve impulses in hidden prey. Modern sharks and rays still use this technique for hunting. Mormyriform and gymnotiform electric fish developed these primitive receptors into sophisticated tuberous organs that are used in social communication. These structures, embedded in the fishes' skin, are encapsulated in ways that make them insensitive to slowly varying electric fields, such as those produced by muscles, but responsive to the rapid discharges of other electric fish. Tuberous receptors are usually tuned to be most responsive to the discharge rate of their own species. The brains of these fish are also highly sensitive to changes in the repetition rates of discharges. This permits sophisticated exchanges between fish during conflicts, courtship, and territorial defense.

CHEMICAL COMMUNICATION IN ANIMALS

Many animals use chemical communication or pheromones to communicate. They may leave their scent to mark territory or attract mates. They often use smell to find prey and identify other animals.

Home, Sweet and Pheromone

Animals often use chemical communication to mark territory. They leave pheromones, or chemical marks behind. Some animals leave scent posts to mark their territory. A scent post is something that is marked by an animal with its scent. Scent posts set the boundaries of an animal's territory.

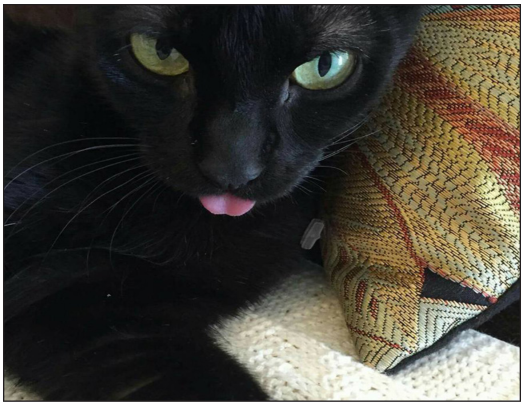
The mountain lion is a solitary animal and it likes to travel alone. A male's territory can be more that 100 square miles. The male mountain lion often kicks up piles of pine needles, dirt or leaves with its hind feet and urinates on the pile to mark its territory.

The Canada lynx also leaves a scent post. It will urinate on trees and tree trunks. It may also leave claw marks on trees. Claw marks are a visual sign, but can also be a chemical one. Many animals have scent glands in their claws! When they scratch a tree, they leave a little of their scent behind.

Something in the Air

Snakes use their forked tongues to taste or collect pheromones of prey animals that are in the air. They have receptors in the roof of their mouths that help them taste and smell the pheromones.

Some animals use scent to identify members of their family! The mule deer has scent glands on its hind legs right above its hooves. Young deer will often identify their mothers by sniffing at the glands. When mule deer are in groups, they often sniff each others hind legs. When male mule deer become aggressive towards each other, the hair around the glands will stand up.



Have you ever seen a house cat rubbing its head up against someone? It is marking its territory! Domestic cats have scent glands near their mouths, on their foreheads and at the base of their tails. They use these glands to mark territory. When other cats smell the scent they know that another cat has marked its territory. Male domestic cats will mark their mating territory by urinating. The next time you see a cat rubbing up against something, you'll know that it is claiming it as its property.

References

- Lovejoy, thomas e.; lee, hannah (2005). Climate change and biodiversity (1 ed.). New haven: yale up. Isbn 978-0300119800
- Mcguire, liam p.; boyle, alice w. (11 march 2013). "altitudinal migration in bats: evidence, patterns, and drivers". Biological reviews. 88 (4): 767–786. Doi:10.1111/brv.12024. Hdl:2097/17273. Pmid 23480862
- Park, chris (2007). A dictionary of environment and conservation. University of florida: oxford university press. Doi:10.1093/acref/9780198609957.001.0001. Isbn 9780198609957
- Boyle, alice w.; guglielmo, christopher g.; hobson, keith a.; norris, d. Ryan (november 2014). "lekking birds in a tropical forest forego sex for migration". Biology letters. 10 (11). Doi:10.1098/rsbl.10.0115 (inactive 2019-08-20). Retrieved december 2, 2014
- R. Piper (2007). Extraordinary animals: an encyclopedia of curious and unusual animals. Greenwood press. Isbn 978-0-313-33922-6
- Animal-cognition, library, knowledge, scitable: nature.com, Retrieved 5 February, 2019
- Bouffanais, roland (2016). Design and control of swarm dynamics. Springerbriefs in complexity (first ed.). Springer. Doi:10.1007/978-981-287-751-2. Isbn 978-981-287-750-5
- Animal-communication, science: britannica.com

Reproductive Behavior in Animals

5 CHAPTER

The reproductive behavior of animals refers to the actions and events which are involved in the process where an organism produces one or more than one replacement of itself. Some of the activities which are displayed by animals as a part of their reproductive behavior are mating calls, courtship display and lordosis behavior. This chapter has been carefully written to provide an easy understanding of these facets of reproductive behavior in animals.

Reproductive behavior is an activity directed toward perpetuation of a species. The enormous range of animal reproductive modes is matched by the variety of reproductive behavior.

Reproductive behavior in animals includes all the events and actions that are directly involved in the process by which an organism generates at least one replacement of itself. In an evolutionary sense, the goal of an individual in reproduction is not to perpetuate the population or the species; rather, relative to the other members of its population, it is to maximize the representation of its own genetic characteristics in the next generation. The dominant form of reproductive behavior for achieving this purpose is sexual rather than asexual, although it is easier mechanically for an organism simply to divide into two or more individuals. Even many of the organisms that do exactly this—and they are not all the so-called primitive forms—every so often intersperse their normal asexual pattern with sexual reproduction.

Basic Concepts and Features

Dominance of Sexual Reproduction

Two explanations have been given for the dominance of sexual reproduction. Both are related to the fact that the environment in which an organism lives changes in location and through time; the evolutionary success of the organism is determined by how well it adapts to such changes. The physiological and morphological aspects of an organism that interact with the environment are governed by the organism's germplasm—the genetic materials that determine hereditary characteristics. Unlike asexual methods, sexual reproduction allows the reshuffling of the genetic material, both within and between individuals of one generation, resulting in the potential for an extraordinary array of offspring, each with a genetic makeup different from that of its parents.

According to proponents of the so-called long-term theory for the dominance of sexual reproduction, sexual reproduction will replace asexual reproduction in the evolutionary development of an organism because it assures greater genetic variability, which is necessary if the species is to keep pace with its changing environment. According to proponents of the short-term theory, however, the above argument implies that natural selection acts on groups of organisms rather than on individuals, which is contrary to the Darwinian concept of natural selection. They prefer to view the advantages of sexual reproduction on a more immediate and individual level: an organism employing sexual reproduction has an advantage over one employing asexual means because the greater variety of offspring produced by the former results in a larger number of genes being transmitted to the next generation. The latter view is probably more nearly correct, especially in violently fluctuating and unpredictable environments. The former theory is probably correct when viewed in terms of its advantage to individuals that are spreading in geographic range, thereby increasing the likelihood of encountering different environments.

Natural Selection and Reproductive Behavior

Natural selection places a premium on the evolution of those physiological, morphological, and behavioral adaptations that will increase the efficiency of the exchange of genetic materials between individuals. Organisms will also evolve mechanisms for sensing whether or not the environment is always permissive for reproduction or if some times are better than others. This involves not only the evolution of environmental sensors but also the concurrent evolution of mechanisms by which this information can be processed and acted upon. Because all seasons are not usually equally conducive, individuals whose genetic backgrounds result in their reproducing at a more favourable rather than less favourable period will eventually dominate succeeding generations. This is the basis for the seasonality of reproduction among most animal species.

Natural selection also results in the evolution of systems for transmitting and receiving information that will increase the efficiency of two individuals' finding each other. These attraction systems are usually, but not always, species specific. Once the proper individuals have found each other, it is clearly important that they are both in a state of reproductive readiness. That their sensory receptors are tuned to the same environmental stimuli is usually sufficient to achieve this synchrony (proper timing) in the lower organisms. Apparently, however, this is not enough in the more complex organisms, in which the fine tuning for reproductive synchrony is accomplished chiefly by a process called courtship. Another evolutionary necessity is a mechanism that will guide the partners into the proper orientation for efficient copulation. Such mechanisms are necessary for both internal and external fertilization, especially the latter, where improper orientation could result in a complete waste of the eggs and sperm.

In most organisms, the period of greatest mortality occurs between birth or hatching and the attainment of maturity. Thus, it is not surprising that some of the most elaborate evolutionary adaptations of an organism are revealed during this period. Natural selection has favoured an enormous variety of behavior in both parents and offspring that serves to ensure the maximum survival of the young to maturity. In some animals this involves not only protecting the young against environmental vicissitudes and providing them with adequate nutrition but also giving them, in a more or less active manner, the information they will need to reproduce in turn.

External and Internal Influences

The external and internal factors that initiate reproductive behavior are:

Environmental Influences

Light, usually in the form of increasing day length, seems to be the major environmental stimulus for most vertebrates and many invertebrates, especially those living in areas away from the

Equator. That this should be such an important factor is quite reasonable in an evolutionary sense: increasing day length signifies the onset of a favourable period for reproduction. In equatorial regions, where changes in day length are usually insignificant throughout the year, other environmental stimuli, such as rain, predominate.

Superimposed on day length are usually several other factors, which, if lacking, often override the stimulating effect of light. Many insects, for example, will not initiate a reproductive cycle if they lack certain protein foods. Many animal groups have an internal cycle of cellular activity that must coincide with the external factors before reproduction can occur; a familiar example is the estrous cycle in most mammals except primates. Females are sexually receptive only during a brief period when they have ovulated (released an egg from the ovary).

Hormonal Influences

Although the exact way by which light affects the reproductive cycle is still disputed, it undoubtedly varies from group to group. In birds, light passes either through the eyes or through the bony tissue of the skull and stimulates the development of certain cells in the forepart of the brain. These cells then secrete a substance that stimulates the anterior pituitary gland, which is located at the base of the brain, to produce an array of regulatory substances (hormones), called gonadotropins, that are carried by the blood to the gonads (ovaries and testes), where they directly stimulate the development of eggs and sperm. The gonads, in turn, produce the sex hormones—estrogen in the female and testosterone in the male—that directly control several overt aspects of reproductive behavior.

Unlike the higher animals, the gonads of insects apparently do not themselves secrete hormones. Instead, stimulation by the corpus allatum, an organ in insects that corresponds in function to the pituitary gland, causes the secretion of liquid substances on the body surface. These substances are transmitted as liquids, or, even more significantly, as gases, to the recipient, in which they are usually detected by olfaction or taste. Such substances, which are called ectohormones, or pheromones, may serve as the major regulation and communication system for reproduction as well as other behavior in insects.

In the absence of all other stimuli, many types of sexual behavior can be induced simply by an injection of the appropriate gonadal hormone. Conversely, removal of the gonads usually inhibits most sexual behavior. The apparent failure of complete hormonal control over reproductive behavior has been a subject of much investigation and dispute. There is much evidence that many types of reproductive behavior are or can be controlled solely by neural mechanisms, bypassing the hormonal system and any effect that it might exert on the nervous system to produce behavior. Several types of reproductive behavior controlled solely or almost solely by neural mechanisms are involved in or triggered by the processes that are initiated by courtship.

Modes of Sexual Attraction

The chief clues by which organisms advertise their readiness to engage in reproductive activity are visual, auditory, and olfactory in nature. Most animals use a combination of two modes; sometimes all three are used.

Visual Clues

The appearance of many higher vertebrates changes with the onset of reproductive activity. The so-called prenuptial molt in many male birds results in the attainment of the nuptial plumage, which often differs radically from that possessed by the bird at other times of the year or from that possessed by a nonreproductive individual. The hindquarters of female baboons become bright red in colour, which indicates, or advertises, the fact that she is in estrus and sexually receptive. Such changes in appearance are less common in the lower animals but do occur in many fishes, crabs, and cephalopods (e.g., squids and octopuses).

Often associated with changes in appearance are changes in behavior, particularly the increase in aggressive behavior between males, often a prime feature in attracting females; such changes have interesting evolutionary implications. In certain grouse, for example, females are most attracted to males that engage in the greatest amount of fighting. No doubt, fighting in some groups of mammals also serves this function as well as others.

In many animals the rise in aggression takes the form of territoriality, in which an individual, usually a male, defends a particular location or territory by excluding from it all other males of his own kind. Occasionally, other species are also excluded when it is to the advantage of the defending individual to do so. Territorial behavior involves many functions, not all of which are directly concerned with reproduction. For purposes of advertising, however, territoriality probably reduces the amount of interference between males and also makes it easier for females to find males at the proper time.

Auditory Clues

The fact that sound signals can travel around barriers, whereas visual signals cannot, accounts for their widespread use in indicating sexual receptiveness, especially in frogs, insects, and birds. Like visual signals, a sound for advertising purposes usually encodes several pieces of information; for example, the signals usually reveal to the receiver the caller's species, its sex, and, in some cases, whether or not it is mated. The vocalizations of one type of frog also reveal the number of other males located nearby. This information, a critical clue for females, is a measure of how good the habitat is for depositing eggs. The sounds produced by the wings of mosquitoes attract females and are species specific. Humans have taken advantage of this signal by using artificial sound generators to eradicate certain mosquitoes. Advertising signals also serve to repel other males; a classical example is the territorial song of many songbirds.

Olfactory Clues

Researchers have now become aware of the enormous amount of information that is passed between animals by chemical means. Well known are the urine, feces, and scent markings employed by most mammals to delimit their breeding territories and to advertise their sexual state. Males of a number of mammals are capable of determining if a female will be sexually receptive simply by smelling her urine markings. A substance in the urine of male mice, on the other hand, actually induces and accelerates the estrous cycle of females. A female gypsy moth is able to attract males thousands of metres downwind of it simply by releasing minute quantities of its sex pheromone each second. It has been calculated that one female silkworm moth carries only about 1.5 micrograms (1.5×10^{-6} gram) of its sex attractant, called bombykol, at any given moment;

theoretically, this is enough to activate more than 1,000,000,000 males. The sex attractant of barnacles, which are otherwise rather sessile (sedentary) organisms, causes individuals to aggregate during the breeding period.

Another possible channel of communication occurs in a few fishes, namely electric discharge. Evidence suggests that weak electric fields and discharges in the Mormyridae of Africa and Gymnotidae of South America represent the major mode of social interaction in these families.

Protective Adaptations

A number of adaptations have evolved to protect the eggs and larvae of species not attended by adults. In one such adaptation, the eggs or larvae are distasteful, inedible, or apparently harmful to potential enemies. The eggs of the jellyfish Bougainvillia, for example, contain stinging cells on the surface that deter predators. Many female butterflies deposit their eggs on plants that contain poisonous compounds, which the larvae incorporate into their bodies, making them distasteful. When disturbed many insect larvae, especially those that are camouflaged, give a so-called startle display; several caterpillars, for example, raise their heads as if to bite or their hindparts, in the manner of a wasp, as if to sting. Others suddenly present striking colour patterns previously hidden. Most of these displays have been shown experimentally to be effective deterrents against predators.

Caring for Offspring

Animals that do not care for their young must provide for the nutritional needs of their offspring. One way of doing so is by producing an egg with a sufficiently large yolk supply that the young, when hatched, are already at an advanced, almost independent state. A peculiar example of this is found in the incubator birds (Megapodiidae), which cover their large eggs with soil and debris to create a mound of considerable depth, effectively providing heat for the developing eggs. After a very long incubation period, the young emerge as fully feathered miniature adults and are capable of flying in 24 hours. Before sealing the nest that they make for their eggs, many insects, such as certain solitary wasps, stock the nest with food. In a more bizarre manner, other solitary wasps place one egg in the body of an insect or spider previously paralyzed by the wasp. Upon hatching, the larva eats the still living host.

Social parasitism, another fascinating aspect of post-fertilization behavior, is found in certain insects and birds. In this case, the true parents do not care for their eggs or offspring; rather, they place them under the foster care of other species, often, but not always, to the detriment of the foster parents' offspring. In certain parasitic species of cuckoos, the females are divided into groups, or gentes, each of which lays eggs with a colour and pattern unlike those of the other groups. The females of each group usually select a particular species as the host, and, more often than not, the eggs of the parasite closely resemble those of the potential foster parent. This mimicry has evolved because many host species throw eggs not resembling their own out of the nest. Some young cuckoos also exhibit a behavior called backing, in which they push out the other nestlings and monopolize the food supply.

Parental Care

Among the organisms that remain with the eggs or offspring, one particular behavior is striking—that of nest construction to keep the eggs and larvae in one spot and to protect them against predators as well as such environmental factors as sun and rain. The placement of a nest usually serves an antipredatory purpose, as in birds that put their nests near those of social wasps or stinging ants. Although they are not normally thought to do so, many mammals, particularly rodents and carnivores, construct special nests, dens, or burrows solely for reproductive purposes.

A number of fishes build nests made of bubbles that not only hold the eggs together but also provide the oxygen necessary for the developing embryos. Other fishes, particularly those that live in oxygen-poor waters, display elaborate fanning behavior to keep the water moving around the eggs. In some fishes, the female incubates the egg in her mouth, thus providing protection against predators as well as constant aeration. The fry (young) of some of these mouthbreeders travel in a school near the parent. When danger approaches, they flee into the parent's mouth and later swim out after the danger passes.

Birds have the problem of keeping the eggs at an optimum temperature for development of the embryo. With the onset of egg laying in many species, the feathers of the lower abdomen are lost, and the skin in that area becomes thickened and highly vascularized (filled with blood vessels), forming the so-called brood patches. Usually the female develops these patches, which serve to transfer more effectively to the eggs the warmth from the adult's body. It has been shown that, like much of parental behavior in the higher vertebrates, brood patches and "broodiness" are controlled by several hormones, combined with visual and tactile stimuli. Chief among these hormones is prolactin, which also controls the production of pigeon milk, a cheeselike substance produced only in the crops of adult doves and pigeons and fed to the nestlings by regurgitation.

Although there are some outstanding exceptions, most young mammals are completely helpless at birth. This helplessness is most striking in the marsupials (e.g., opossums and kangaroos), in which the young are born at a very early stage of development; they crawl through the mother's hair to the brood pouch, where they attach themselves to a nipple and their development continues for many more months.

An early characteristic behavior in mammals following birth is that of the mother licking the newborn. This serves at least two functions—one is general cleanliness to avoid infections or the attraction of parasites; the other would appear to be purely social. If a newborn mammal is removed from its mother and cleaned elsewhere before she can lick it, she usually will not accept it. Thus, licking behavior also serves, in some manner, to establish a unique relationship between the mother and her offspring. Another characteristic mammalian behavior is the suckling response of the newborn. Although this behavior has been claimed to be the perfect instinctive response, it apparently is not so in many species; the trial-and-error period during which the newborn discovers the nipple, however, is quite short.

In birds, especially those that nest on the ground, one of the first adult responses to the hatching of the eggs is to remove the conspicuous eggshells from the area of the nest. It has been shown experimentally that, in gulls at least, this is an important antipredatory measure. When birds hatch, they have the ability to stretch their heads and to gape for food in response to any mechanical disturbance, such as that produced when the parent lands on the nest. Later in development, they stretch and gape only when the parents appear. This is another type of adaptive, antipredatory behavior, as it would be dangerous for the nestlings to gape and vocalize in response to any environmental disturbance.

Group Care

The ability of an animal to identify its own offspring at an early stage is apparently not important in animals that nest or are solitary breeders; offspring in the nest belong to that parent. In colonially breeding species or in those where the offspring of different parents are likely to become mixed, however, natural selection has favoured the evolutionary development of behavior that makes possible the recognition by the parent of its own offspring, thereby avoiding the danger of expending energy on offspring that do not possess the parent's genes.

There is, on the other hand, the situation in which the offspring are cared for by individuals who are not the parents. This phenomenon occurs among the social insects in particular and also among several groups of birds and mammals; future investigations may show it to be even more widespread. In such birds as the anis, the effective breeding group consists of several females and males. One nest is constructed in which all the females deposit their eggs, and all individuals participate in the care of the resulting offspring. In certain jays (Corvidae), the offspring of one generation participate in the care of the offspring of the next or another generation, but the exact family relationships among the participants are not clear.

In the social insects, this type of parental behavior apparently results from the peculiar genetic relationships between the individuals in most social-insect colonies (termites are among the exceptions). The female and, in the termites, both the male and the female can control by chemical means the kinds (called castes in ants and termites) and sexes of the offspring. An outstanding feature of such colonial insects as the honeybee is that the majority of the individuals produced by the queen are sterile; these are the workers, the individuals who care for and feed both the queen and her offspring, the sibs of the workers.

The queen is diploid in genetic makeup; that is to say, half of her genes are derived from her mother and half from her father. The males (drones) are haploid; that is, they have only half the genes possessed by the queen, all of them derived from the mother. A queen produces eggs fertilized by sperm she has retained in her body from the mating flight; thus the individuals produced are diploid, but, unlike the queen, they are sterile. This sterility results indirectly from a chemical secreted by the queen, called the queen substance. It inhibits the workers from building special brood cells that give rise to sexually developed individuals. If the queen fails to secrete this substance because of age or death, the workers immediately construct special brood cells with a substance they secrete; called royal jelly, it is necessary for the development of a larva then destined to be a queen.

How can the evolution of sterility in workers and their care of offspring not their own be accounted for? One possible explanation concerns the coefficient of relationship (the number of genes on the average shared in common) among the individuals of a colony. Because of the peculiar haplo-diploid mode of sex determination, the workers (sisters) share all the genes from their father and on the average, half of those from their mother. Since each worker receives half of its genes from the father and half from the mother, the average genes shared between any two workers (sisters) is three-fourths. But between mother (the queen) and daughter (a worker) this average is only one-half. The offspring (the sterile workers), therefore, may contribute more to their fitness (the maximum representation of their genes in the next generation) by caring for their sisters than by providing an equal amount of care to their "own" offspring, had they been fertile rather than sterile. A drone, on the other hand, has a coefficient of relationship with one of his sterile sisters of only one-fourth, but retains a relationship of one-half with his mother and daughters (future sterile workers). This explains why workers provide more care for their sisters than for their brothers, and why the workers eventually drive off the almost useless drones, which are relatively scarce (having resulted from unfertilized eggs), from the colony. Because sisters share more genes with each other than with their brothers, they maximize the chances of these genes surviving into the next generation by providing more care for their sisters.

This explanation of group care and extreme sociality does not account for all cases. Indeed, termites are perhaps the most extreme among animals in these respects but lack the haplo-diploid sex determination mechanism. In addition, several groups having this mechanism have not evolved extreme brood care and sociality. Other factors have to interact for these systems to evolve, but it is not yet clear what they are.

SEXUAL SELECTION

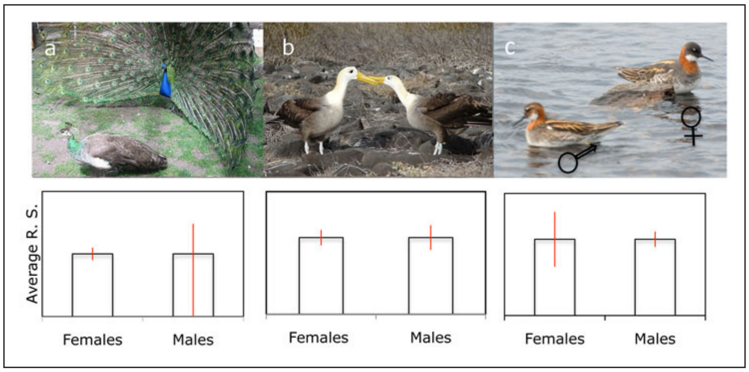
Charles Darwin proposed that all living species were derived from common ancestors. The primary mechanism he proposed to explain this fact was natural selection: that is, that organisms better adapted to their environment would benefit from higher rates of survival than those less well equipped to do so. However he noted that there were many examples of elaborate, and apparently non-adaptive, sexual traits that would clearly not aid in the survival of their bearers. He suggested that such traits might evolve if they are sexually selected, that is if they increase the individual's reproductive success, even at the expense of their survival.

Darwin noted that sexual selection depends on the struggle between males to access females. He recognized two mechanisms of sexual selection: intrasexual selection, or competition between members of the same sex (usually males) for access to mates, and intersexual selection, where members of one sex (usually females) choose members of the opposite sex. The idea of cumbersome traits evolving to aid males in competition during aggressive encounters was readily accepted by scientists shortly after Darwin's publication. However, the idea of female mate choice was received with ridicule, and was not seriously reconsidered until nearly 80 years later. In the 40 years since, there has been much progress in our understanding of how sexual selection operates.

Which Sex is under Stronger Selection?

Sex roles are defined by differences in gametes: females produce relatively few, highly nutritious (usually non-motile) gametes, whereas males produce comparatively abundant, smaller, motile gametes. Because only a single gamete of each type is required to produce an offspring, there will be an excess of male gametes that will not fertilize any eggs. This asymmetry leads to Bateman's principle, whereby female reproduction is primarily limited by their access to resources to nourish and produce these large gametes, whereas male reproduction is mainly limited by access to females. Therefore males typically compete among themselves for access to females, whereas females tend to be choosy and mate only with preferred males.

In sexually reproducing species, every offspring has one father and one mother, so the average reproductive success is equal for both males and females. A successful male can potentially sire many offspring. If a male gains a disproportionate share of reproduction, he will take away reproductive opportunities from other males, leading to a high reproductive variance among males. A successful female, on the other hand, will not take away reproductive opportunities from other females, leading to a smaller variance in reproductive success. The higher the reproductive variance, the stronger the effects of sexual selection. Strong sexual selection typically results in sexually dimorphic traits that are exaggerated, or more elaborate, in the sex with highest reproductive variance.



Variance in reproductive success explains which sex is subject to stronger sexual selection.

Males and females in a population have the same average reproductive success (R. S., black bars) but they may differ in the reproductive variance among members of each sex (shown in red). Differences in the selection gradient will result in sexual dimorphism. (a) When males are subject to stronger sexual selection than females, males will evolve secondary sexual characters that result in marked differences between the sexes. Peacocks do not provide any parental care, and some males are more successful than others who may never reproduce, leading to marked dimorphism. (b) When males contribute to offspring care, the selection gradient is lower and the sexes will be monomorphic. Many seabirds are monogamous and raise offspring together and the sexes are indistinguishable. (c) When males provide all the parental care, the selection gradient can be reversed and females may have to compete for access to males, leading to reverse sexual dimorphism. Red-necked phalaropes compete for access to males who provide all the parental care. Females are larger and more aggressive than males.

Role of Parental Care

Most species provide little or no care to their offspring, but in species where parental care is required, variance in reproductive success will be impacted not only by fertilization success, but also by the contribution of each sex to the care of the offspring. The degree and direction of sexual dimorphism can be explained by the relative selection gradients of each sex. If females provide more parental care than males, the variance in male reproductive success can be expected to be large, since females providing offspring care will not be immediately available for further reproduction and competition for available females will increase among males. The exaggerated tail of the (male) peacock compared to the shorter tail of the (female) peahen, indicates that males are under stronger sexual selection than females. However, in species where biparental care is required to successfully raise offspring, variance in male reproductive success is generally lower, since males that are engaged in providing parental care will not be able to invest as much energy in pursuing additional mating opportunities. This situation often results in the emergence of sexually monomorphic species, in which the male and female look and behave in similar ways.

Finally, in rare situations where only males provide parental care, males can become the limiting resource for females. Under these circumstances, the variance in reproductive success may be high for females who then tend to monopolize access to one or more males to care for their offspring. Males may then become choosy about which females they mate with. This often results in reversed sexual dimorphism, such that females evolve more elaborate secondary sexual characters than males .

How does Sexual Selection Operate?

Sexual selection can operate both intra- and inter-sexually, either sequentially or simultaneously. During intrasexual selection, members of the same sex attempt to outcompete rivals, often during direct encounters. Intrasexual selection is typically responsible for the evolution of male armaments such as deer antlers, beetle horns, and large body size, that provide individuals with an advantage when fighting off potential competitors. Individuals who are better able to exclude competitors, have a greater chance to acquire mates and father offspring. For example, dominant male red deer monopolize a group of females (also known as harem) by constantly fighting off competitors, and they father most of the offspring produced by the females. By contrast, intersexual selection results from interactions between the sexes, typically involving mate choice. The evolution of elaborate behavioral displays and morphological traits can often be explained as the result of intersexual selection. Usually, females tend to be more choosy, evaluating morphological and behavioral traits from potential mates to determine which will maximize their fitness. Males tend to compete with one another to gain the female's attention. An extreme example of intersexual selection can be found in species where males form leks where multiple males gather to display to females.

Table: Some examples of when and how sexual selection operates.

	Pre-copulatory	Post-copulatory
Intrasexual Selection (Competition)	To monopolize a harem: elephant seals. To monopolize a single female: rhinoceros beetles.	Greater relative testies size in species with greater risk of female multiple mating.
Intrasexual Selection (mate choice)	Males displaying at leks in manakins.	Female reproductive morphology that prevents ejaculated sperm from contacting eggs directly.
Sexual Conflict	Intimidation and sexual harassment.	Traumatic insemination in bed bugs.

Sexual selection episodes can occur before mating takes place (pre-copulatory), or during and after mating (post-copulatory), and they can occur within a sex (intrasexual) and between the sexes (intersexual).

Choosing a Mate

Why do females choose between males rather than mate at random, or with the first male they encounter? Females can directly increase their reproductive success by mating with certain, select males and acquiring direct benefits. For example, females can gain increased access to food, protection from harassing males, or help in raising offspring, and avoid being infected with parasites or other diseases by choosing healthy males. However there are instances where females do not appear to gain any direct benefit from males, yet they still discriminate among them. Under these conditions, females likely gain indirect benefits via their offspring. These indirect benefits are usually genetic rather than resource based. By choosing certain males, their offspring will likely inherit genes that tend to increase their fitness. Males often evolve traits and displays that advertise their ability to provide direct and indirect benefits, and females evolve preferences for these traits. Two major mechanisms to account for female mate choice have been proposed: good genes, and Fisherian arbitrary processes.

Good Genes

Under the 'good genes' scenario, differences among males provide females with information about the genetic qualities of the different males that can be inherited by the offspring. Under the 'good genes,' just as in the 'direct benefits' models, there is correspondence between the putative roles of natural versus sexual selection, since preferring certain males can result in a female gaining higher viability, fecundity, and reproductive success, for her offspring. Good genes can be those that allow males to carry a 'handicap,' yet survive despite having a cumbersome trait, genes that signal resistance to disease, or genes that are more compatible with those of the female. Evidence of female choice for good genes remains scarce despite decades of studies of female mate choice in many taxa. This apparent lack of success continues to create debate as to the importance of the good genes model in the field.

Fisherian Arbitrary Choice

Named after R. A. Fisher, who originally proposed it, this model suggests that female preference can evolve for arbitrary traits that do not provide information about the male's quality, and that therefore do no reinforce the effects of natural selection. If females evolve a preference for a particular trait, males bearing that trait will be selected as mates. This assortative mating will establish a genetic correlation between the preference and the trait. The fitness advantage of the arbitrary trait exists only as a result of its covariance with the preference. By choosing a male with a particular trait value, the females gain the indirect benefit of producing offspring that will be more sexually attractive to females that carry the preference. This type of process can result in a runaway positive feedback loop, whereby the trait becomes more exaggerated as selection on the preference increases, but other models have shown that such a feedback loop is only one of many possible evolutionary outcomes of the Fisherian process.

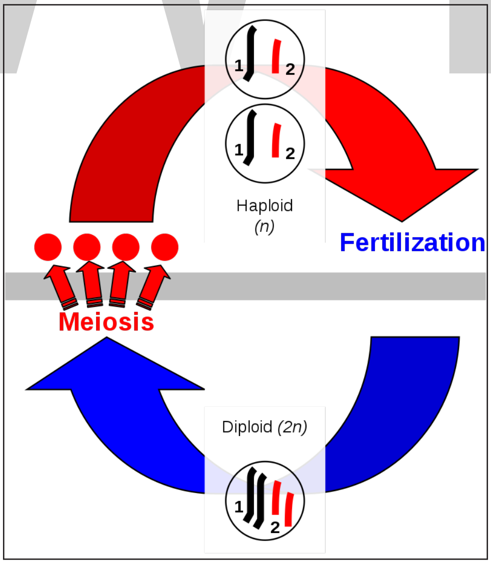
When does Sexual Selection Act?

Sexual selection can affect reproductive success at multiple reproductive stages. First, it acts during all the processes that lead to acquiring mating opportunities (i.e., excluding competitors, attracting, selecting and/or retaining mates). Darwin referred exclusively to pre-copulatory sexual selection in his discussions, erroneously assuming that mating would inevitably result in reproductive success. In recent years, evidence that copulatory and post-copulatory events play an important role in determining the outcome of fertilization and reproduction has been increasing. Post-copulatory selection refers to the events that occur during and after mating. Post-copulatory male-male competition is known as sperm competition a term coined by Parker who recognized that when females mate with multiple males, their ejaculates compete inside the female reproductive tract for access to eggs. Sperm competition has resulted in the evolution of morphologically modified sperm that increase the likelihood of fertilization in many taxa. Post-copulatory female choice refers to the ability of females to affect the likelihood that sperm from a particular male fertilizes their eggs, and their decision to invest in offspring based on the identity of the male with whom they mate. Females exert this choice via morphological, chemical and behavioral adaptations. This type of selection is called cryptic choice because it occurs inside the female reproductive tract and cannot be detected from behavioral studies alone.

Conflict between the Sexes

Although both sexes are seeking to optimize their reproductive success, their genetic interests are not aligned, resulting in sexual conflict. Traits that allow a male to increase his reproductive success at the expense of the female will be positively selected if the female mates with multiple males. These traits will be genetically transmitted and spread in the population, despite their negative effects on female reproductive success, if the reproductive success of these males is higher than that of males lacking such traits. Sexual conflict can often result in an evolutionary arms race, whereby the evolution of a trait that imposes harm on one sex will result in evolution of a counter-trait to mitigate the harm on the affected sex, with subsequent escalation in both. Examples of sexual conflict include traumatic insemination in bed bugs, copulatory grasping and anti-grasping structures in waterstriders, and genital coevolution in waterfowl.

SEXUAL REPRODUCTION



In the first stage of sexual reproduction, "meiosis", the number of chromosomes is reduced from a diploid number (2n) to a haploid number (n). During "fertilization", haploi gametes come together to form a diploid zygote and the original number of chromosomes is restored.

Sexual reproduction is a type of life cycle where generations alternate between cells with a single set of chromosomes (haploid) and cells with a double set of chromosomes (diploid). Sexual reproduction is by far the most common life cycle in eukaryotes, for example animals and plants.

Diploid cells divide into haploid cells in a process called meiosis. Two haploid cells combine into one diploid cell in a process called fertilisation. Between fertilisation and meiosis there can be multiple cell divisions without change of the number of chromosomes.

Fertilisation creates a single-celled zygote which includes genetic material from both gametes. In a process called genetic recombination, genetic material (DNA) joins up so that homologous chromosome sequences are aligned with each other, and this is followed by exchange of genetic information. Two rounds of cell division then produce four daughter cells with half the number of chromosomes from each original parent cell, and the same number of chromosomes as both parents.

Cell division mitosis then initiates the development of a new individual organism in multicellular organisms, including animals and plants, for the vast majority of whom this is the primary method of reproduction.

The evolution of sexual reproduction is a major puzzle because asexual reproduction should be able to outperform it as every young organism created can bear its own young. This implies that an asexual population has an intrinsic capacity to grow more rapidly with each generation. This 50% cost is a fitness disadvantage of sexual reproduction. The two-fold cost of sex includes this cost and the fact that any organism can only pass on 50% of its own genes to its offspring. One definite advantage of sexual reproduction is that it impedes the accumulation of genetic mutations.

Sexual selection is a mode of natural selection in which some individuals out-reproduce others of a population because they are better at securing mates for sexual reproduction. It has been described as “a powerful evolutionary force that does not exist in asexual populations.”

Prokaryotes, whose initial cell has additional or transformed genetic material, reproduce through asexual reproduction but may, in lateral gene transfer, display processes such as bacterial conjugation, transformation and transduction, which are similar to sexual reproduction although they do not lead to reproduction.

Evolution

The first fossilized evidence of sexual reproduction in eukaryotes is from the Stenian period, about 1 to 1.2 billion years ago.

Biologists studying evolution propose several explanations for why sexual reproduction developed and why it is maintained. These reasons include reducing the likelihood of the accumulation of deleterious mutations, increasing rate of adaptation to changing environments, dealing with competition, DNA repair and masking deleterious mutations. All of these ideas about why sexual reproduction has been maintained are generally supported, but ultimately the size of the population determines if sexual reproduction is entirely beneficial. Larger populations appear to respond more quickly to some of the benefits obtained through sexual reproduction than do smaller population sizes.

Maintenance of sexual reproduction has been explained by theories that work at several levels of selection, though some of these models remain controversial. However, newer models presented in recent years suggest a basic advantage for sexual reproduction in slowly reproducing complex organisms.

Sexual reproduction allows these species to exhibit characteristics that depend on the specific environment that they inhabit, and the particular survival strategies that they employ.

Sexual Selection

In order to sexually reproduce, both males and females need to find a mate. Generally in animals mate choice is made by females while males compete to be chosen. This can lead organisms to extreme efforts in order to reproduce, such as combat and display, or produce extreme features caused by a positive feedback known as a Fisherian runaway. Thus sexual reproduction, as a form of natural selection, has an effect on evolution. Sexual dimorphism is where the basic phenotypic traits vary between males and females of the same species. Dimorphism is found in both sex organs and in secondary sex characteristics, body size, physical strength and morphology, biological ornamentation, behavior and other bodily traits. However, sexual selection is only implied over an extended period of time leading to sexual dimorphism.

Sex Ratio

Apart from some eusocial wasps, organisms which reproduce sexually have a 1:1 sex ratio of male and female births. The English statistician and biologist Ronald Fisher outlined why this is so in what has come to be known as Fisher's principle. This essentially says the following:

1. Suppose male births are less common than female.
2. A newborn male then has better mating prospects than a newborn female, and therefore can expect to have more offspring.
3. Therefore parents genetically disposed to produce males tend to have more than average numbers of grandchildren born to them.
4. Therefore the genes for male-producing tendencies spread, and male births become more common.
5. As the 1:1 sex ratio is approached, the advantage associated with producing males dies away.
6. The same reasoning holds if females are substituted for males throughout. Therefore 1:1 is the equilibrium ratio.

Animals

Insects

Insect species make up more than two-thirds of all extant animal species. Most insect species reproduce sexually, though some species are facultatively parthenogenetic. Many insects species have sexual dimorphism, while in others the sexes look nearly identical. Typically they have two sexes with males producing spermatozoa and females ova. The ova develop into eggs that have a covering called the chorion, which forms before internal fertilization. Insects have very diverse mating and reproductive strategies most often resulting in the male depositing spermatophore within the female, which she stores until she is ready for egg fertilization. After fertilization, and the formation of a zygote, and varying degrees of development, in many species the eggs are deposited outside the female; while in others, they develop further within the female and are born live.

Australian emperor laying egg, guarded by the male.

Mammals

There are three extant kinds of mammals: monotremes, placentals and marsupials, all with internal fertilization. In placental mammals, offspring are born as juveniles: complete animals with the sex organs present although not reproductively functional. After several months or years, depending on the species, the sex organs develop further to maturity and the animal becomes sexually mature. Most female mammals are only fertile during certain periods during their estrous cycle, at which point they are ready to mate. Individual male and female mammals meet and carry out copulation. For most mammals, males and females exchange sexual partners throughout their adult lives.

Fish

The vast majority of fish species lay eggs that are then fertilized by the male, some species lay their eggs on a substrate like a rock or on plants, while others scatter their eggs and the eggs are fertilized as they drift or sink in the water column.

Some fish species use internal fertilization and then disperse the developing eggs or give birth to live offspring. Fish that have live-bearing offspring include the guppy and mollies or Poecilia. Fishes that give birth to live young can be ovoviviparous, where the eggs are fertilized within the female and the eggs simply hatch within the female body, or in seahorses, the male carries the developing young within a pouch, and gives birth to live young. Fishes can also be viviparous, where the female supplies nourishment to the internally growing offspring. Some fish are hermaphrodites, where a single fish is both male and female and can produce eggs and sperm. In hermaphroditic fish, some are male and female at the same time while in other fish they are serially hermaphroditic; starting as one sex and changing to the other. In at least one hermaphroditic species, self-fertilization occurs when the eggs and sperm are released together. Internal self-fertilization may occur in some other species. One fish species does not reproduce by sexual reproduction but uses sex to produce offspring; Poecilia formosa is a unisex species that uses a form of parthenogenesis called gynogenesis, where unfertilized eggs develop into embryos that produce female offspring. Poecilia formosa mate with males of other fish species that use internal fertilization, the sperm does not fertilize the eggs but stimulates the growth of the eggs which develops into embryos.

COURTSHIP DISPLAY

Male blackbuck, *Antilope cervicapra*, courting a female.

A courtship display is a set of display behaviors in which an animal attempts to attract a mate and exhibit their desire to copulate. These behaviors often include ritualized movement (dances), vocalizations, mechanical sound production, or displays of beauty, strength, or agonistic ability.

Male Display

Male peacock spider, *Maratus volans, courtship display*.

In some species, males will perform ritualized movements to attract females. The male Six-plumed bird-of-paradise, Parotia lawesii, exemplifies male courtship display with its ritualized "ballerina dance" and unique occipital and breast feathers that serve to stimulate the female visual system. This stimulation, along with many other factors, results in subsequent copulation or rejection.

In other species, males may exhibit courtship displays that serve as both visual and auditory stimulation. For example, the male Anna's hummingbird (*Calypte anna*) and Calliope hummingbird (Stellula calliope) perform two types of courtship displays involving a combination of visual and vocal display – a stationary shuttle display and dive display. When engaging in the stationary shuttle display, the male displays a flared gorget and hovers in front of the female, moving from side to side while rotating his body and tail. The rhythmic movements of the male's wings produce a distinctive buzzing sound. When conducting a dive display, the male typically ascends approximately 20–35 m (66–115 ft) in the air then abruptly turns and descends in a dive-like fashion. As the male flies over the female, he rotates his body and spreads his tail feathers, which flutter and collide to produce a short, buzzing sound.

A male satin bowerbird makes and uses a bower to attract potential mates.

In addition, some animals attempt to attract females through the construction and decoration of unique structures. This technique can be seen in Australia's satin bowerbirds (*Ptilonorhynchus violaceus*), in which males build and decorate nest-like structures called "bowers". Bowers are decorated with bright and colourful objects (typically blue in colour) to attract and stimulate visiting females. Typically, males who acquire the largest number of decorations tend to have greater success in mating.

In some species, males initiate courtship rituals only after mounting the female. Courtship may even continue after copulation has been completed. In this system, the ability of the female to choose her mate is limited. This process, known as copulatory courtship, is prevalent in many insect species.

In most species, the male sex initiates courtship displays in pre-copulatory sexual selection. Performing a display allows the male to present his traits or abilities to a female. Mate choice, in this context, is driven by females. Direct or indirect benefits to the female often determine which males reproduce and which do not.

Direct benefits may accrue to the female during male courtship behavior. Females can raise their own fitness if they respond to courtship behavior that signals benefits to the female rather than the fitness of the male. For example, choosing to mate with males that produce local signals would require less energy for a female as she searches for a mate. Males may compete by imposing lower mating costs on the female or even providing material or offspring contributions to the female.

Indirect benefits are benefits that may not directly affect the parents' fitness but instead increase the fitness of the offspring. Since the offspring of a female will inherit half of the genetic information from the male counterpart, those traits she saw as attractive will be passed on, producing fit offspring. In this case, males may compete during courtship by displaying desirable traits to pass on to offspring.

Female Display

Female courtship display is less common in nature as a female would have to invest a lot of energy into both exaggerated traits and in their energetically expensive gametes. However, situations in which males are the sexually selective sex in a species do occur in nature. Male choice in reproduction can arise if males are the sex in a species that are in short supply, for example, if there is a female bias in the operational sex ratio. This could arise in mating systems where reproducing comes at an energy cost to males. Such energy costs can include the effort associated in obtaining nuptial gifts for the female or performing long courtship or copulatory behaviors. An added cost from these time and energy investments may come in the form of increased male mortality rates, putting further strain on males attempting to reproduce.

In pipefish (*Syngnathus typhle*), females use a temporary ornament, a striped pattern, to both attract males and intimidate rival females. In this case, the female of a species developed a sexually selected signal which serves a dual function of being both attractive to mates and deterring rivals.

Multi-modal Signal Processing

Bosc's fringe-toed lizard *Acanthodactylus boskianus* love bite.

Many species of animals engage in some type of courtship display to attract a mate, such as dancing, the creation of sounds, and physical displays. However, many species are not limited to only one of these behaviors. It has been shown that the males of a multitude of species ranging across many taxa create complex multi-component signals that have an effect on more than one sensory modality, also known as multi-modal signals. There are two leading hypotheses about the adaptive significance of multi-modal signal processing. The multiple message hypothesis states that each signal that a male exhibits will contribute to a possible mate's perception of the male. The redundant signal hypothesis states that the male exhibits multiple signals that portray the same "message" to the female, with each extra signal acting as a fall-back plan for the male should there be a signaling error. The choosy sex may only evaluate one, or a couple, of traits at a given time when interpreting complex signals from the opposite sex. Alternatively, the choosy sex may attempt to process all of the signals at once to facilitate evaluation of the opposite sex.

The process of multi-modal signaling is believed to help facilitate the courtship process in many species. One such species in which multi-modal signaling is seen to improve mating success is the green tree frog (Hyla cinerea). Many anuran amphibians, such as the green tree frog, may use visual cues as well as auditory signals to increase their chances of impressing a mate. When the calls of the tree frogs were held equal, it was determined that females tended to overlook an auditory-only stimulus in favor of males who combined auditory/visual multi-modal signals. It was seen that female green tree frogs preferred when males coupled the visual display with the auditory communication, concluding that male green tree frogs that are visually accessible can increase their probability of mating success.

Peacock spiders (Maratus volans) are exceptionally sexually dimorphic in appearance and signaling behavior. During courtship, male peacock spiders compete using both visual displays and vibratory signals for intersexual communication. Because of the intense sexual selection on male peacock spiders, the reproductive success of an individual relies heavily on a male spider's ability to combine visual and vibratory displays during courtship. The combination of these displays in courtship offers support both to the redundant signal and multiple messages hypotheses for the evolution of multi-modal signaling in species.

Multi-modal signaling is not limited to males. Females in certain species have more than one trait or characteristic that they use in a courtship display to attract mates. In dance flies (Rhamphomyia longicauda), females have two ornaments — inflatable abdominal sacs and pinnate tibial scales — that they use as courtship displays in mating swarms. Intermediate variations of such female-specific ornaments are sexually selected for by male dance flies in wild populations. These ornaments may also be a signal of high fecundity in females.

Mutual Display

Male and female long-billed curlew, Numenius americanus, mutual courtship display.

Often, males and females will perform synchronized or responsive courtship displays in a mutual fashion. With many socially monogamous species such as birds, their duet facilitates pre-copulatory reassurance of pair bonding and strengthens post-copulatory dedication to the development of offspring (e.g., great crested grebe, *Podiceps cristatus*). For example, male and female crested auklets, *Aethia cristatella,* will cackle at one another as a vocal form of mutual display that serves to strengthen a bond between the two. In some cases, males may pair up to perform mutual, cooperative displays in order to increase courtship success and attract females. This phenomenon can be seen with long-tailed manakins, Chiroxiphia linearis.

Wild turkeys (*Meleagris gallopavo)* also engage in co-operative displays in which small groups of males (typically brothers) work together to attract females and deter other competitive males. In many cases, only one male within the group will mate, typically the dominant male. To explain this behavior, Hamilton's theory of kin selection suggests that subordinate males receive indirect benefits by helping related males copulate successfully.

Sexual Ornaments

Sexual ornaments can serve to increase attractiveness and indicate good genes and higher levels of fitness. When exposed to exaggerated male traits, some females may respond by increasing maternal investments. For example, female canaries have been shown to produce larger and denser eggs in response to male supranormal song production.

Sexual Conflict

Sexual conflict is the phenomenon in which the interests of males and females in reproduction are not the same, they are often quite different:

- Males: Their interest is to mate with a large number of completely faithful females, thus spreading their genes widely throughout a population.
- Females: Their interest is to mate with a large number of fit males, thus producing a large quantity of fit and varied offspring.

This has many consequences. Courtship displays allow the mate performing the selection to have a means on which to base the copulatory decision. If a female chooses more than one male, then sperm competition comes into play. This is competition between sperm to fertilize an egg, which is very competitive as only a single sperm will achieve union. In some insects, the male injects a cocktail of chemicals in seminal fluid together with sperm. The chemicals kill off older sperm from any previous mates, up-regulates the female's egg-laying rate, and reduces her desire to re-mate with another male. The cocktail also shortens the female's lifespan, also reducing her likelihood of mating with other males. Also, some females can get rid of the previous male's sperm.

After mating has taken place, males perform various actions to prevent females from mating again. What action is performed depends on the animal. In some species, the male plugs the female copulatory duct after insemination. In some hymenoptera, the male provides a huge quantity of sperm, enough to last the female's entire life. In some birds and mammals, the male may participate in agonistic behaviors with other candidate males.

Agonistic Behavior and Courtship

Although rare, agonistic behavior between males and females during courtship displays is seen in nature. Intraspecific agonistic behavior that results in the death of a combatant is rare because of the associated risk of death or injury. However, agonistic behavior that turns dangerous does occur.

In some species, physical traits that are sexually selected for in male courtship displays may also be used in agonistic behavior between two males for a mate. In fiddler crabs (Genus Uca), males have been sexually selected to have one enlarged claw, which can take up anywhere from a third to a half of their total body mass, and one regular claw. Although the enlarged claw is believed to have developed for use in combat for territorial defense, it is not uncommon for males to employ this claw in battle for a mate. Even though this claw developed as a weapon, it is also closely linked with the crabs' courtship display: it is waved in a certain pattern to attract females for mating.

Agonistic behavior in courtship displays is not limited to male-male interactions. In many primate species, males direct agonistic behavior toward females prior to courtship behaviors. Such behavior can include aggressive vocalizations, displays, and physical aggression. In the western gorilla *(Gorilla gorilla*), dominant males exhibit agonistic behavior toward female gorillas at very high rates, with the majority of those interactions being courtship-related. Most documented cases of male gorilla aggression toward females is courtship-related, and is used primarily as a strategy to prevent females from migrating to another male.

In many cases, male courtship displays will cause forms of contest competition to develop. This is often seen within lek mating systems. For example, males will seek to obtain a certain spot or position to perform their courtship display. The best spots are regions of high contention as many males want them for themselves. Because of this direct conflict, agonistic encounters between males are fairly common.

Extended Courtship Period

Mating is preceded by a courtship/pairing period in many animal mating systems. It is during this period that sexually mature animals select their partners for reproduction. This courtship period, which involves displays to attract a mate by a member of a species, is usually short, lasting anywhere from 15 minutes to a few days. However, certain animals may undergo an extended courtship period, lasting as long as two months.

One such exception is the emperor penguin *(Aptenodytes forsteri)*. Emperor penguins engage in an extended courtship period that can last up to two months, the longest of any Arctic seabird. Their courtship period accounts for 16% of the total time they spend breeding, whereas in their closest relatives, the king penguin *(Aptenodytes patagonicus)*, the courtship period takes up just three percent of their breeding cycle.

Energetic Costs of Courtship Display

Courtship displays typically involve some sort of metabolic cost to the animal performing it. The energy expended to perform courtship behavior can vary among species. Some animals engage in displays that expend little energy, as seen in the salamander (*Desmognathus ochrophaeus)*. Under laboratory settings, courtship behaviors in this species, although complex and involving the release of pheromones, represent as little as approximately one percent of its daily calorie intake.

In contrast, species that engage in prolonged or elaborate displays expend considerable amounts of energy and run the risk of developing fatigue. To prepare and prevent such a risk, some animals may gain weight before a courtship period, only to lose the weight afterward. An example of this can be seen in the Greater Sage-Grouse *(Centrocercus urophasianus)*. During the peak of their breeding season, which lasts up to three months during spring, leks are frequently visited by groups of up to 70 females. In response to such a large presence of females, males engage in a strutting display up to six to ten times per minute for approximately three to four hours per day. This frequent and repetitive behavior can result in energy expenditures of up to 2524 kJ/day compared to the inactive males that typically expend 1218 kJ/day.

Greater sage-grouse lek males perform a courtship “strutting” display for visiting females.

Environmental Factors

Various environmental factors, such as temperature, photoperiod, resource and light availability, have an effect on the timing and effectiveness of courtship displays in certain species of animals.

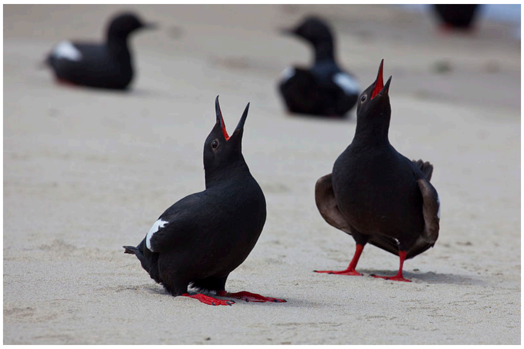
In guppies (Poecilia reticulata), variation in the light environment plays a huge role in their ability to attract mates. Guppy males alter both their 'courtship mode', whether they perform a full courtship display or try to 'engage' in sneak copulations, and distance from females as light intensity changes. Courtship mode also varies with light spectrum and relates to predation risk. On average, male guppies seek out and spend more time in the environment in which their color pattern is the most visible. Males, in the light environment that made them most visible, copulated with the most females.

In emperor penguins (Aptenodytes forsteri), resource availability determines when male emperor penguins will be able to return to their breeding grounds to initiate their courtship rituals. The greater the concentration of resources in their feeding ground, the quicker they will be able to restore their body reserves for winter, and the sooner they will be able to return to their breeding grounds. An early return to their breeding grounds comes with an increased likelihood of finding a mate.

Evolutionary Significance

There are multiple hypotheses about how courtship displays may have evolved in animals, including the Fisherian runaway modell and the good genes hypothesis.

As explained by the Fisherian runaway model, sexually dimorphic males with exaggerated ornamentation may have been sexually selected for in species with female choice. Fitness of these males would increase, resulting in the proliferation of males with such ornamentation over time. This means that a gene or set of genes will be favoured by female choice over time. This would explain why and how such elaborate traits develop within certain species. However, as time goes on and generations pass, the survival advantage associated with one trait may dissipate due to extreme exaggeration to the point that it decreases fitness.



Male and female Pigeon Guillemot, Cepphus columba, mutual courtship display.

The "good genes" hypothesis proposes that female selection of a mate is dependent on whether or not the male has genes that would increase the quality of the offspring of the female. In some cases, exaggerated male ornamentation may be indicative to a choosing female that a male who is able to place such a large investment in trait somewhat counterintuitive to survival would carry good genes. For example, the costs associated with bright and complex plumage can be high. Only males with good genes are able to support a large investment into the development of such traits, which, in turn displays their high fitness.

MATING CALL

A mating call is the auditory signal used by animals to attract mates. It can occur in males or females, but literature is abundantly favored toward researching mating calls in males. In addition, mating calls are often the subject of mate choice, in which the preferences of one gender for a certain type of mating call can drive sexual selection in a species. This can result in sympatric speciation of some animals, where two species diverge from each other while living in the same environment.

There are many different mechanisms to produce mating calls, which can be broadly categorized into vocalizations and mechanical calls. Vocalizations are considered as sounds produced by the larynx and are often seen in species of birds, mammals, amphibians, and insects. Mechanical calls refer to any other type of sound that the animal produces using unique body parts and tools for communication with potential mates. Examples include crickets that vibrate their wings, birds that flap their feathers, and frogs that use an air sac instead of lungs.

Vocalizations

Birds

The use of vocalizations is widespread in avian species and are often used to attract mates. Different aspects and features of bird song such as structure, amplitude and frequency have evolved as a result of sexual selection.

Song sparrow.

Large song repertoires are preferred by females of many avian species. One hypothesis for this is that song repertoire is positively correlated with the size of the brain's song control nucleus (HVC). A large HVC would indicate developmental success. In song sparrows, males with large repertoires had larger HVCs, better body condition and lower heterophil-to-lymphocyte ratios indicating better immune health. This supports the idea that song sparrows with large song repertoires have better lifetime fitness and that song repertoires are honest indicators of the male's "quality". Possible explanations for this adaptation include direct benefits to the female, such as superior parental care or territory defense, and indirect benefits, such as good genes for their offspring.

Japanese bush warbler songs from island populations have an acoustically simple structure when compared to mainland populations. Song complexity is correlated with higher levels of sexual selection in mainland populations, showing that a more complex song structure is advantageous in an environment with high levels of sexual selection. Another example is in purple-crowned fairy-wrens; larger males of this species sing advertising songs at a lower frequency than smaller rival males. Since body size is a characteristic of good health, lower frequency calls are a form of honest signaling. Negative correlation between body size and call frequency is supported across multiple species within the taxa. In the rock sparrow, song frequency is positively associated with reproductive success. Slower song rate is associated with age and is preferred by females. Reproductive status of the individual is communicated through higher maximum frequency. There was also positive correlation between age and extra-pair copulation frequency.

Red deer stag during rut.

Bird calls are also known to continue after pair formation in several socially monogamous bird species. In one experimental population of zebra finches, there was increased singing activity by the male after breeding. This increase is positively correlated with the partner's reproductive investment. The female finches were bred in cages with two subsequent males that differed with varying amounts of song output. Females produced larger eggs with more orange yolks when paired with a male with a high song output. This suggests that the relative amount of song production in paired zebra finch males might function to stimulate the partner rather than to attract extra-pair females.

Mammals

During the breeding season, mammals will call out to the opposite sex. Male koalas that are bigger will let out a different sound than smaller koalas. The bigger males which are routinely sought out for are called sires. Females choose sires because of indirect benefits that their offspring could inherit, like larger bodies. Non-sires and females do not vary in their body mass and can reject a male by screaming or hitting him. Male-male competition is rarely exhibited in koalas. Acoustic signaling is a type of call that can be used from a significant distance encoding an organism's location, condition and identity. Sac-winged bats display acoustic signaling, which is often interpreted as songs. When females hear these songs, named a 'whistle', they call onto the males to breed with a screech of their own. This action is termed 'calling of the sexes'. Red deer and spotted hyenas along with other mammals also perform acoustic signaling.

Amphibians

Most frogs use an air sac located under their mouth to produce mating calls. Air from the lungs channels to the air sac to inflate it, and the air sac resonates to produce a mating call. The larynx is larger and more developed in males, which causes their call to be louder and stronger.

Tungara frog.

In the tungara frog, males use a whining call followed by up to seven clucks. Males who have a whine-cluck call are more successful in attracting females than males whose call is a whine alone. The ability to produce clucks is due to a specialized fibrous mass attached to the frog's vocal folds, creating an unusual vocalization similar to the two-voiced songs found in some birds.

In the common toad, sexual competition is driven in large part by fighting—successful males often physically displaced other males from the backs of a female in order to gain access to mating with that female. Larger males were more successful in such takeovers, and had higher reproductive success as a result. However, the vocalizations of these toads provide a reliable signal of body size and thus fighting ability, allowing contests for possession of females to be settled without risk of injury.

Insects

While mating calls in insects are usually associated with mechanical mating calls, such as in crickets, several species of insects use vocalizations to attract mates. In the Asian corn borer, males emit clicking sounds that mimic the echolocation of bats which prey on the moths. They then take advantage of the female's "freezing" response to mate with the female.

In the Japanese lichen moth, however, the female is able to distinguish between the sounds made by males and those made by bats and other predators. As a result, the males use ultrasonic clicking as a more conventional mating signal, compared to the "deceptive" courtship song used in the Asian Corn Bearer.

Mechanical Calls

Mating calls also take form through mechanical processes. Animals that are unable to vocalize their call may use their body to attract mates.

Crickets

In the field cricket, Gryllus integer, males rub their wings together to create a rapid trill that produces sound. Males individually vary in the durations of their trilling or what is more sophisticatedly called, bout length. The bout length of each male is heritable and passed on to his future offspring. Also, females prefer to mate with males that have longer bout lengths. The end result is that males with longer bout lengths produce more offspring than males with shorter bout lengths.

Other factors that influence the formation of these bout lengths include temperature and predation. In field crickets, males prefer warmer sites for mating as shown by an increase in the frequency of their mating calls when they were living in warmer climates. Predation also affects the mating calls of field crickets. When in a potentially dangerous environment, males cease calling for longer periods of time when interrupted by a predator cue. This suggests that there is an interplay between intensity of mating call and risk of predation.

Sonation

In Sonation, "the term sonate is described as the deliberate production of sounds, not from the throat, but rather from structures such as the bill, wings, tail, feet and body feathers, or by the use of tools". In several amphibian and fish species, other special structures are used to produce different sounds to attract mates. Birds are common users of sonation, although several amphibian and fish species have been shown to use sonation as a form of mating call as well. In general, sonation is one factor that plays into how a female may choose a mate. There are other features of mating such as territory defense or mate defense, which contribute to the cause of finding suitable mates.

Each species uses a distinct method to produce a non-vocal mating call in order to be most successful in attracting mates. The examples below represent the most common examples found in the literature, although many more examples may exist in nature that are still currently unknown.

Feather of male *Pavo cristatus* (Indian peafowl). These feathers are used in sonation to create infrasound with intent of mating.

Birds

The feathers, the beak, the feet, and different tools are all used by different bird species to produce mating calls to attract mates. For example, the snipe uses its feathers to produce a "drumming" sound to attract mates during a special mating dance. Snipes used specialized tail feathers to create a sound described as a "rattle" or "throbbing" noise. Palm cockatoos use sticks to drum on hollow trees, creating a loud noise to attract the attention of mates. Bustards are large, highly terrestrial birds that stamp their feet during mating displays to attract mates. *Mirafra apiata*, commonly known as the Clapper lark, engages in a complex display flight that is characterized by the rattling of the wings.

Many species of birds, such as manakins and hummingbirds, use sonation for mating calls. However, peacocks exhibit a feature of sonation that reveals intrasexual and intersexual properties of this type of mating call. Males move their feathers to produce a low-frequency sonation (infrasound) and sonate more frequently in response to a sonation by other males. This is attributable to a male's desire to advertise its presence above other males looking for mates, suggesting that sonation carries an intrasexual function. In addition, females show increased alertness when hearing the infrasound signals produced by males' wing-shaking, which highlights how the two sexes use sonation to interact with each other.

Fish

While most bird species use their feathers, tools, or feet to produce sounds and attract mates, many fish species use specialized internal organs to sonate. In Gadoid fish, special muscles attached to the swimbladder assist in the production of knocking or grunting sounds to attract mates.

Lepidoptera

In many lepidoptera species including the adzuki bean borer (Ostrinia scapulalis), ultrasonic mating calls are used to attract females and keep them motionless during copulation. These pulses have an average frequency of 40 kHz.

Speciation due to Mating Call Differences

Differences in mating calls can lead to the separation of different populations within a species. These differences can be due to several factors, including body size, temperature, and other ecological factors. These can arise in the form of tonal, temporal, or behavioral variations in mating calls that subsequently lead to the separation of populations. The separation of these populations due to differences in mating call and mating call preferences can lead to the evolution and creation of new, unique species.

This type of speciation is most often sympatric speciation: where two or more species are created from an existing parent species that all live in the same geographic location. Although there is an absence of research on mammals and birds, this phenomenon has been heavily researched in several frog species around the world.

Microhyla Olivacea and Microhyla Carolinensis

Two *Microhyla olivacea* in a mating position.

These two species of narrow-mouthed frog live in the southern United States and have overlapping ranges in Texas and Oklahoma. Researchers have discovered that these two different species alter the frequencies of their call in the overlap zone of their ranges. For example, the *Microhyla olivacea* mating call has a significantly lower midpoint frequency in the overlap zone than the mating call outside this zone. This leads researchers to suggest that the differences in mating call in the overlap zone of *M. olivacea and M. carolinensis* act as an isolating mechanism between the two species. They also hypothesize that the evolution of these differences in mating call led to the separation of these two different frog species from one common species.

Engystomops Petersi

Female preferences for specific male mating calls can lead to sexual selection in mating calls. Females may prefer a specific type of call that certain males possess, in which only those males will be able to mate with females and pass on their genes and specific mating call. As a result, this female preference may lead to divergence of two species.

Engystomops petersi.

In Amazonian frogs, sexual selection for different calls has led to the behavioral isolation and speciation of the túngara frog (Engystomops petersi). From genetic and mating call analysis and, researchers were able to identify that two populations of the túngara frog were almost completely reproductively isolated. From their research, scientists believe that differences in female preferences for mating call type have led to the evolution of this speciation process. Specifically, the Yasuní population females prefer the male mating call that includes a whine, while the other population does not prefer this whine. Subsequently, the Yasuní males include the whine in their call, while the other males do not. For this reason, the differences in call have led to the mechanical separation of this species.

Pseudacris Triseriata

A Chorus Frog making a mating call.

Several studies have shown that the species *Pseudacris triseriata* (Chorus Frog) can be divided into two subspecies, *P. t. maculata* and *P. t. triseriata,* due to speciation events from mating call differences. The Chorus Frog has a very large home range, from New Mexico to Southern Canada. These two subspecies have an overlapping range from South Dakota to Oklahoma. In this overlapping range, both the call duration and the calls per second for each species is much different than outside of this range. This means that calls of these two subspecies are more similar outside of this range, and starkly different within the range. For this reason, scientists suggest that these subspecies evolved from differences in mating call type. Additionally, these subspecies are rarely recorded to have hybrid offspring, which further suggests that there is complete speciation due to mating call differences. The differences in mating calls also help to reinforce the speciation process.

REPRODUCTIVE ISOLATION

Reproductive isolation can be either prezygotic (barriers that prevent fertilization) or postzygotic (barriers that occur after zygote formation such as organisms that die as embryos or those that are born sterile).

Some species may be prevented from mating with each other by the incompatibility of their anatomical mating structures, or a resulting offspring may be prevented by the incompatibility of their gametes.

Postzygotic barriers include the creation of hybrid individuals that do not survive past the embryonic stages (hybrid inviability) or the creation of a hybrid that is sterile and unable to produce offspring (hybrid sterility).

Temporal isolation can result in species that are physically similar and may even live in the same habitat, but if their breeding schedules do not overlap then interbreeding will never occur.

Behavioral isolation, in which the behaviors involved in mating are so unique as to prevent mating, is a prezygotic barrier that can cause two otherwise-compatible species to be uninterested in mating with each other.

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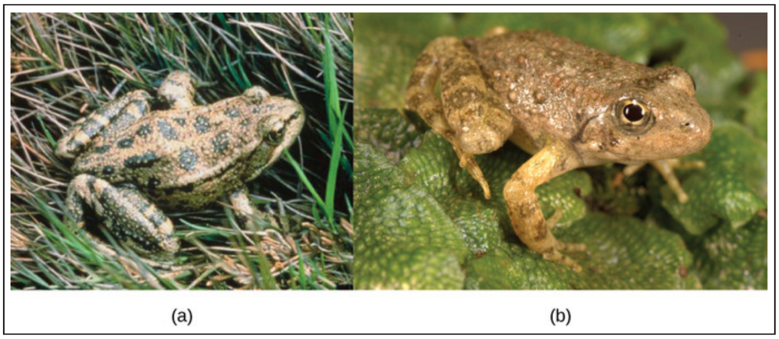
Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction: if individuals of the two populations were to be brought together, mating would be improbable, but if mating did occur, offspring would be non-viable or infertile. Many types of diverging characters may affect reproductive isolation, the ability to interbreed, of the two populations. Reproductive isolation is a collection of mechanisms, behaviors, and physiological processes that prevent the members of two different species that cross or mate from producing offspring, or which ensure that any offspring that may be produced is not fertile.

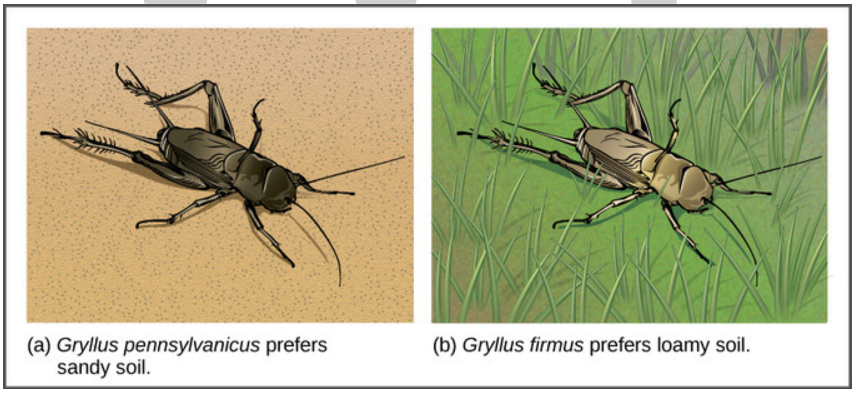
Scientists classify reproductive isolation in two groups: prezygotic barriers and postzygotic barriers. Recall that a zygote is a fertilized egg: the first cell of the development of an organism that reproduces sexually. Therefore, a prezygotic barrier is a mechanism that blocks reproduction from taking place; this includes barriers that prevent fertilization when organisms attempt reproduction. A postzygotic barrier occurs after zygote formation; this includes organisms that don't survive the embryonic stage and those that are born sterile.

Some types of prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually. Differences in breeding schedules, called temporal isolation, can act as a form of reproductive isolation. For example, two species of frogs inhabit the same area, but one reproduces from January to March, whereas the other reproduces from March to May.



Temporal isolation: These two related frog species exhibit temporal reproductive isolation. (a) Rana aurora breeds earlier in the year than (b) Rana boylii.

In some cases, populations of a species move to a new habitat and take up residence in a place that no longer overlaps with other populations of the same species; this is called habitat isolation. Reproduction with the parent species ceases and a new group exists that is now reproductively and genetically independent. For example, a cricket population that was divided after a flood could no longer interact with each other. Over time, the forces of natural selection, mutation, and genetic drift will likely result in the divergence of the two groups.

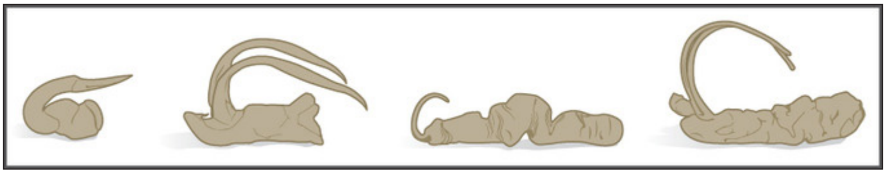

(a) *Gryllus pennsylvanicus* prefers sandy soil.

(b) *Gryllus firmus* prefers loamy soil.

Habitat isolation: Speciation can occur when two populations occupy different habitats. The habitats need not be far apart. The cricket (a) Gryllus pennsylvanicus prefers sandy soil, while the cricket (b) Gryllus firmus prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated.

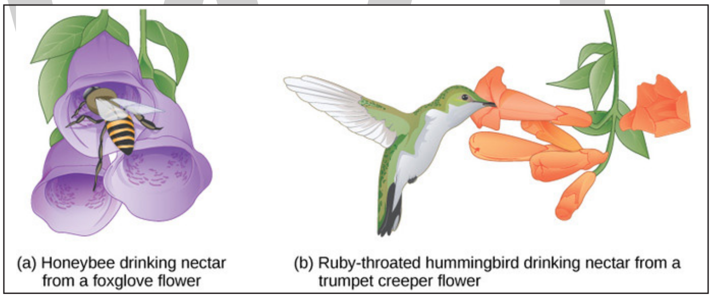
Behavioral isolation occurs when the presence or absence of a specific behavior prevents reproduction from taking place. For example, male fireflies use specific light patterns to attract females. Various species display their lights differently; if a male of one species tried to attract the female of another, she would not recognize the light pattern and would not mate with the male.

Other prezygotic barriers work when differences in their gamete cells prevent fertilization from taking place; this is called a gametic barrier. Similarly, in some cases, closely-related organisms try to mate, but their reproductive structures simply do not fit together. For example, damselfly males of different species have differently-shaped reproductive organs. If one species tries to mate with the female of another, their body parts simply do not fit together.



Differences in reproductive structures in male damselflies: The shape of the male reproductive organ varies among male damselfly species and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated.

In plants, certain structures aimed to attract one type of pollinator simultaneously prevent a different pollinator from accessing the pollen. The tunnel through which an animal must access nectar can vary in length and diameter, which prevents the plant from being cross-pollinated with a different species.



(a) Honeybee drinking nectar from a foxglove flower

(b) Ruby-throated hummingbird drinking nectar from a trumpet creeper flower

Reproductive isolation in plants: Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by humming birds.

When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction. Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages; this is called hybrid inviability. In another postzygotic situation, reproduction leads to the birth and growth of a hybrid that is sterile and unable to reproduce offspring of their own; this is called hybrid sterility.

SEXUAL CONFLICT

Sexually reproducing organisms are under evolutionary selection pressure to maximise their Darwinian fitness, but adaptations that function to increase fitness in one sex can reduce or constrain fitness in the other. Sexual conflict is the conflict that exists as a result of the divergent evolutionary interests of males and females.

Sexual conflict is inevitable and ubiquitous because the evolutionary interests of males and females never exactly coincide. This has identifiable consequences at genomic and whole organism levels. At an intra-locus level, genes may be expressed in both males and females that may be beneficial only to one sex. Ultimately, this favours sex-limited gene expression, but because this may take time to evolve, the adaptive evolution of each sex can, at least in the short term, be impeded by counter-selection in the other sex.

Other conflicts are mediated by genes at different loci that can evolve independently in the two sexes. These 'inter-locus' conflicts arise over diverse aspects of reproduction, from mating decisions (how often and with whom mating should occur), to levels of parental investment (how much each parent expends on offspring production). For example, males can typically achieve high fitness by mating with many females, but females are generally unwilling to mate indiscriminately as such behavior is not in their best interests. Similarly, where both parents care for their offspring, each could potentially achieve higher fitness if their partner were to provide more care, providing the other parent with opportunities to divert 'saved' investment into additional reproductive attempts. In each case, individuals could potentially achieve higher fitness if their prospective or actual mating partners were to 'agree' with their strategy for doing so, but the divergent evolutionary interests of the sexes means that their optimal strategies for maximising fitness rarely coincide.

Theory suggests several broad scenarios: male win, female win, compromise or endless evolutionary chases. Predicting outcomes can be complicated, however, and in optimality models they depend on relative power and benefits of winning. Power in these models is the relative cost of a unit of escalation: if it is relatively cheaper for a female to overcome a male adaptation than it is for a male to counter-adapt, then females have an evolutionary advantage in the conflict, and this may frequently be the case.

The benefits of winning are perhaps even more difficult to assess, but one may expect that this part of the equation is weighted more heavily in favour of males, as for them the issue will frequently be whether or not they reproduce at all, while for females it may only be an issue of who they mate with. Individuals of either sex may also attempt to shift the balance of conflict in their favour by coercion or manipulation.

An interesting example of this phenomenon is found among poeciliid fish, where males have evolved a sneak-mating strategy that completely circumvents active female mate choice. Rather than actively court females to gain female consent to copulate, males sneak up on females, insert their modified anal fin that acts as an intromittent organ, and transfer sperm. This tactic is the means by which almost all insemination occurs in the mosquito fish.

Where adaptations in one sex generate counter-adaptations in the other sex, such as increased resistance to manipulation, sexual conflict may result in prolonged or continuous evolutionary chases. Such evolutionary chases or sexual arms races can have important evolutionary consequences, and have been the subject of much recent investigation. However, theory predicts that unresolvable sexual arms races may be infrequent, and that it is more usual for one sex or the other to gain an evolutionary advantage, halting antagonistic co-evolution, even though the underlying conflict may not be resolved, or that a balance in 'arms levels' results. Exceptions may be common at the molecular level — for example, involving seminal proteins and receptors — where costs of escalation are probably relatively low.

Sexual conflict has been implicated as the driving force behind many important biological phenomena, including the rapid molecular evolution of reproductive genes and proteins, genome evolution and genomic imprinting. Conflict over reproductive investment may even explain the evolution of the sexes: proto-males may have parasitized the larger gametes of proto-females. Recently, sexual conflict has been implicated in speciation. In any evolutionary arms race between the sexes, there are potentially many different ways individuals of either sex could evolve to enhance their fitness. Any adaptation then counter-selects on the opposite sex, which again has many ways it could counter-adapt, and so on.

In any sexual arms race, it is genes involved in reproduction that are the focus of conflict, and molecular evidence suggests that many reproductive genes evolve extremely rapidly. As a result, populations can, in principle, evolve differences in almost any reproductive trait extremely rapidly through sexual conflict, and it is largely this feature that has prompted the promotion of sexual conflict as a speciation agent. It is important to note, however, that more traditional mechanisms of sexual selection can also generate rapid evolution of reproductive characters, and that distinguishing between the different selection pressures that can potentially lead to reproductive isolation is likely to be difficult.

The two concepts are intimately related. Sexual selection, selection in exclusive relation to securing matings (more strictly fertilizations), inherently generates sexual conflict because, for example, females will mate with some males, but not with others. Additionally, sexual conflict can be thought of as a sexual selection mechanism, as adaptation to win sexual conflicts can increase variance in reproductive success. Traditionally, sexual selection via female choice was seen to be generated by either direct or indirect benefits to females.

References

- Schilthuizen, menno. 2001. Frogs, flies and dandelions: the making of species. Oxford university press p. 92 isbn 0-19-850392-x
- Sexual-selection, library, knowledge, scitable: nature.com, Retrieved 26 July, 2019
- Vogt, yngve (january 29, 2014). “large testicles are linked to infidelity”. Phys.org. Retrieved january 31, 2014.
- Agrawal, a. F. (2001). “sexual selection and the maintenance of sexual reproduction”. Nature. 411 (6838): 692–5. Doi:10.1038/35079590. Pmid 11395771
- M. Cavendish (2001). Endangered wildlife and plants of the world. Marshall cavendish. P. 1252. Isbn 978-0-7614-7194-3. Retrieved 2013-11-03
- Hamao, shoji (2012). “acoustic structure of songs in island populations of the japanese bush warbler, cettia diphone, in relation to sexual selection”. Journal of ethology. 31 (1): 9–15. Doi:10.1007/s10164-012-0341-1
- Muller, m. N. (2009). Sexual coercion in primates and humans. Harvard university press. Pp. 3–22. Isbn 9780674033245

Feeding Behavior in Animals

6 CHAPTER

The actions of an animal for procurement of nutrition are termed as feeding behavior. Some of the commonly observed behavior in animals related to feeding are hoarding, predation and cannibalism. This chapter closely examines these feeding behaviors in animals to provide an extensive understanding of the subject.

Feeding behavior of an animal is an action hat is directed toward the procurement of nutrients. The variety of means of procuring food reflects the diversity of foods used and the myriad of animal types.

The living cell depends on a virtually uninterrupted supply of materials for its metabolism. In multicellular animals the body fluids surrounding each cell are the immediate source of nutrients. The contents of these fluids are kept at a relatively constant level in spite of tolls taken by the cells, primarily by mobilization of nutrients stored in the body; in vertebrates, for example, glucose is stored in the liver, fats in the fat tissues, calcium in the bones. These stores, however, will become exhausted unless the animal takes up nutrients from outside. Movements performed for this purpose are termed feeding behavior.

Nutritional Requirements of Higher Animals

Cells use nutrients as fuel for energy production (catabolism) and as material for processes of maintenance and growth (anabolism). Multicellular animals derive energy solely from the breakdown of complex organic molecules, mainly carbohydrates and fats. Because the fuel for the maintenance of animal life comes only from other living organisms or their remains, animals are known as heterotrophic organisms. All animal life depends ultimately on the existence of organisms (largely green plants) that can use inorganic sources of energy, of which solar radiation is by far the most important; some microorganisms, however, obtain energy from oxidation of simple inorganic compounds.

For anabolic purposes, food must provide adequate amounts of all chemical elements needed by the cells. Of the approximately 35 elements now known to occur in animal cells, four (oxygen, carbon, hydrogen, and nitrogen) make up about 95 percent of the cell weight; another nine (calcium, phosphorus, chlorine, sulfur, potassium, sodium, magnesium, iodine, and iron) contribute about 4 percent. All of these elements have indispensable functions. The remaining 20-odd, together constituting less than 1 percent of cell weight, are called trace elements, because they occur in minute quantities. Although some of them may become incorporated into cells by accident, many fulfill vital functions.

It is important to note that animal cells cannot synthesize from simple compounds certain necessary complex molecules. Instead, certain large organic molecules must serve as building blocks;

such so-called essential dietary components include the vitamins, some amino acids, and certain fatty substances. In general, higher animals appear to have more restricted synthetic powers than lower ones and to require a correspondingly greater number of essential foodstuffs. Microorganisms in the intestines of vertebrates may synthesize materials essential for the host, so that the food of the latter need not contain these substances.

Types of Food Procurement

Because much of animal evolution involves adaptation for the procurement of food, the extent of the meaning of the term feeding behavior is not clear. Migratory habits of birds, for instance, no doubt evolved in part as a result of seasonal food shortages; individual birds now, however, start migration before food becomes scarce.

“many animals make use of a variety of feeding mechanisms, conjointly, or separately as occasion demands”:

I. Mechanisms for dealing with small particles.

  A. Pseudopodial (e.g., many protozoans): Pseudopods consist of fingerlike projections of the cell membrane and its contents (cytoplasm) that surround and engulf food.

  B. Ciliary (e.g., sponges, bivalve mollusks): Cilia are minute hairlike projections of cell membranes that, by concerted beating in wave rhythm, set up water currents or physically move food particles.

  C. Tentacular (e.g., certain sea cucumbers): Tentacles are slender, flexible organs on the head. They may function in sensory perception and in actually securing food.

  D. Mucoid (e.g., many snails, such as Vermetus): In this case, the food particles become attached to a sticky mucous sheet secreted by special cells.

  E. Muscular (e.g., certain coelenterates): In the jellyfish Rhizostoma, pulsations of the bell-shaped body draw water and food in through perforations in the arms, then expel the water after the food is removed.

  F. Setous (e.g., many small crustaceans, such as copepods): Setae are bristlelike projections of the cuticle and are found on the appendages of many invertebrates.

II. Mechanisms for dealing with large particles or masses.

  A. For swallowing inactive food, such as bottom deposits (e.g., many polychaete worms, some fishes).

  B. For scraping and boring (e.g., some gastropod and bivalve mollusks).

  C. For seizing prey.

    - For seizing and swallowing only (e.g., Hydra, many polychaete worms, many lower vertebrates).
    - For seizing and masticating (e.g., Crustacea, mammals).

- For seizing followed by external digestion (e.g., some starfishes, spiders). (In such cases, the secretory and absorptive surfaces of the digestive system may be applied to the food by everting [i.e., turning inside out] the stomach, a method employed by starfish. Alternatively, digestive enzymes may be injected into the prey, liquefying the tissues, which may then be ingested by the predator. This mechanism is found in spiders.)

III. Mechanisms for taking in fluid or soft tissues.

A. For piercing and sucking (e.g., leeches, mosquitoes).

B. For sucking only (e.g., many flies, butterflies).

C. For absorption through surface of body (e.g., various invertebrates feeding on decaying organic matter, internal parasites such as tapeworms, which lack a digestive tract).

A different classification, often used, rests on the nature of the behavior for procuring food:

A. Filter feeders strain food from the surrounding medium more or less indiscriminately.

B. Selective feeders analyze the environment with their sense organs before aiming feeding responses at chosen items.

Some feeding patterns, however, cannot be easily fitted into either of these classes alone; spiders, for example, sieve prey from the air with webs but perform directed responses to the insects trapped. Class I of the Yonge–Nicol system comprises mainly filter feeders; most members of classes II, IIIA, and IIIB are selective feeders. Selective feeding requires good sensory and nervous equipment and, in most cases, considerable mobility. It is therefore found mainly among higher animals. Yet the primitive sea anemones are selective feeders in that, capable of paralyzing relatively large prey with their stinging cells, they do not discharge them until informed by chemical and tactile senses that prey is present. At the other extreme, whalebone whales are filter feeders, even though they are highly evolved mammals. Swimming at the surface with mouth open, they filter off large plankton (krill) using several hundred horny plates with hairlike fringes hanging down from the roof of the mouth; availability of a rich food source has caused the evolution of their feeding patterns to diverge widely from that of most other mammals.

In all cases, the feeding patterns adopted by species are the result of evolutionary interplay between structural properties inherent in their phylogenetic line and the ecological situations to which they have been exposed. These interactions are too complex to make generalizations profitable. The best approach is to study each species as a separate case in the light of its entire biology.

Filter feeders occur among sponges, coelenterates, polychaete worms, echinoderms, brachiopods, mollusks, arthropods, protochordates, fish, birds, and several other groups. As might be expected, filtering devices are diverse.

In the oyster, constantly lashing cilia drive a water current—up to 34 litres (about 36 quarts) per hour—through the openings of perforated gill plates. Particles only two microns (0.002 millimetre) in size are wrapped in mucus and transported by other cilia to special food grooves, along which they pass to the mouth by the action of yet further cilia; particles that are too large, too heavy, or capable of producing irritation are sorted out and rejected by various mechanical means.

The polychaete worm Chaetopterus uses a bag of mucus, secreted by special body appendages, to strain the water it pumps through its burrow. The mesh openings of the bag, about 40 angstroms (40×10^{-7} millimetre) wide, can even trap single molecules of large proteins. Every 20 minutes, the food-laden bag is taken to the mouth, consumed, and replaced by a new one.

The sessile marine snail Vermetus gigas secretes mucus strings up to 30 centimetres (12 inches) long that extend away from the shell and entangle fine plankton. At intervals, the strings are drawn back toward the mouth and swallowed.

Selective feeders, found among major animal groups, including coelenterates, annelids, echinoderms, mollusks, arthropods, and vertebrates, show even greater diversity of feeding patterns than do filter feeders. One striking point is that different groups deal in different ways with the same food in accordance with special capacities. Animals feeding on bivalve mollusks provide one example. The starfish Asterias forces the valves apart by the relentless pull of its sucker tube feet and then everts its stomach through its mouth to digest the soft tissues inside the shell. The snail Sycotypus attacks an oyster by stealth: waiting until the valves open, it thrusts its shell between the valves and pushes its tubular feeding organ, or proboscis, into the soft parts. Another snail, Natica, supports the scraping action of a filelike structure called a radula with chemical dissolution by sulfuric acid, which is secreted by a gland on the proboscis, and drills a neat hole in a clam. Another snail, Fulgur, cracks a clam shell against its own shell by contracting its columellar muscle. Among birds, the oyster catcher (Haematopus ostralegus) adroitly cuts the closing muscles of a cockle with its chisel-shaped bill; herring gulls (Larus argentatus) break a shell by dropping it onto a rock. A sea otter (Enhydra lutris) cracks a clam on its chest, while floating on its back, by pounding it on a stone held between the forepaws.

The sluggish praying mantis (orthopteran insects of the family Mantidae) stalk insect prey until within reach, then carefully orient themselves and accurately and rapidly extend forelegs adapted for grasping. For detecting prey in murky habitats, bats use an ultrasonic echolocation system; some fish use electric pulses in a somewhat comparable manner. Anglerfish dangle a baitlike appendage of the first dorsal spine (luminous in deep-sea species) to lure the fish on which they feed toward their enormous mouths. Certain labroid fishes, which eat parasites off the bodies of other fish, induce their hosts to submit to treatment by a dancing approach; certain blennies treacherously mimic this behavior and then rapidly bite the fin of the unsuspecting victim. Shrikes perform special wiping movements to remove the sting from certain prey, even without previous experience of stinging insects. The peregrine falcon (Falco peregrinus) dives at birds at speeds above 160 kilometres (100 miles) per hour; and the cheetah, or hunting leopard (Acinonyx jubatus), pursues antelope at more than 95 kilometres (60 miles) per hour. More than a thousand cormorants may join in a single fish drive. Instead of hunting, some species rob food collected by members of other species; among these robbers are the marauding skuas and jaegers (Stercorariidae) and man-of-war birds (Fregata), which force weaker cousins to disgorge already swallowed prey, and various tropical flies that take up positions along the line of march of army ants and rob the passing workers.

The driving force for the evolution of each of these adaptations is the survival value to the species of selecting the food sources for which it can successfully compete. For the same reason, closely related species living in the same area may exploit separate parts of the environment; e.g., woodland titmice (Parus) forage in different parts of the trees, and the larvae of different species of the moth genus Eupithecia prefer different food plants. The result of such evolution may be that a species becomes specialized to one kind of food, as have many internal parasites and phytophagous (plant-eating) insects. Such food may be exotic, as that of the larva of a moth (Galleria) that feeds on beeswax. In other species, such as the herring gull, each individual exploits a broad range of foods, thereby lessening the risk of starvation, as it is unlikely that all types of food will become exhausted at the same time.

Selection of Food Items

Most natural habitats offer a diversity of food objects, and most selective feeders are more or less euryphagic—i.e., they ingest a variety of different foods; strict monophagy is less common. On the other hand, no euryphagic species includes in its diet all potential food objects present in the habitat, nor are those that it does eat taken in proportion to the amounts in which they are available. On what grounds, then, are diets selected?

Vertebrates

A plant species constituting only a fraction of 1 percent of a pasture may make up the greater proportion of the diet of a sheep. Insectivorous birds also take a highly biased selection from the insect menu offered by the habitat. Although the relative abundance of different kinds of food is reflected in diets to some extent, this does not usually go so far that a single kind of food, however attractive and abundant, will become the sole constituent. Most vertebrates appear to take a varied diet whenever possible.

Responses to Encountered Food

Diet selection in adult vertebrates proves to be largely the result of individual learning processes that guide the genetically determined response potentialities of the newborn individual into certain definite channels.

Innate responsiveness appears to be broad in species that forage for themselves from birth and thus must deal with many different food situations. The pecking of newly hatched chicks of domestic fowl at all kinds of small objects, edible or not, is an example. Yet these chicks have certain innate preferences for colour and other features. Such preferences may foreshadow the composition of adult diets. In newly hatched snakes, for instance, feeding responses are more easily elicited with extracts of the natural food of adults of the same species than with preparations of food of closely related species. In contrast, colour preferences of ducklings of different species are similar, although the adult diets differ.

Innate responsiveness may be narrow, however, in young vertebrates for whom the parent is the only source of food. Herring-gull chicks beg for food in response to a few “sign stimuli” provided only by the parent’s head among all objects in the natural habitat. Sucking behavior of newborn mammals is a somewhat comparable example. In such cases, responsiveness must be profoundly reorganized when the individual forages on its own.

Responsiveness is channelled into the adult pattern through experience of taste, nutritional value, and possible noxious properties of various objects. In this way the individual is able to attach a definite palatability rating to each type of food regularly encountered and to associate this with visual or other characters by which it recognizes objects from a distance. As demonstrated in experiments, insectivorous birds may discriminate precisely among as many as 40 different prey species in this manner.

In addition to palatability, detectability of food objects is a factor in diet selection. This has been studied in detail in visually foraging vertebrates. Detectability of an object depends on its degree of contrast with the background as to colour, shape, and movement. The individual predator can learn to detect prey that it finds only with difficulty at first; such "searching image formation" occurs only if the prey is palatable and encountered often.

Finally, responses to encountered prey also depend on: (1) the hunger level of the individual and (2) its experience regarding the general food situation. Hungrier predators have lower palatability requirements and may take greater risks to secure prey. At one and the same hunger level, a prey of slight palatability may be rejected if the predator knows that further search will probably bring better food but accepted if it knows that nothing tastier is available. As a result of these two influences, animals concentrate during scarcity on food scorned in times of plenty.

Food Searching and Diet

The general type of food taken is often determined by the innate search method of the animal and the section of the whole habitat being exploited. A fish-eating bird, such as the osprey (Pandion haliaetus), which secures prey by diving into water (but not swimming), is limited in its diet to fish species that are active near the surface. The question of whether food searching is random is relevant here, for certain kinds of nonrandomness can influence diets. No simple answer can be given. Search must be random in the sense that oriented reactions to food objects can be made only after detection; at the same time, however, the search may be systematic in that: (1) places not recently traversed are favoured over those just unsuccessfully explored, and (2) the locality where a prey has just been caught or seen may be searched with special attention. Further, (3) it is common for individuals to restrict their foraging to parts of the home range where ample food has been previously found, although exploration of other parts is interspersed and may change the destination of further trips if successful. In all, food searching appears to have sufficient nonrandomness to influence diets provided that different kinds of food concentrate in different parts of the home range.

To sum up, vertebrate diet selection is largely molded by learning processes. Insofar as their course depends on chance experiences of individuals, differences in diet may develop even among members of one population of a species. On the whole, however, patterns of food selection are typical of the species, as all its members have similar genetic makeup and live in broadly similar ecological situations.

Invertebrates

Learning processes appear to play a relatively small role in food selection by invertebrates. Diets are largely, though not entirely, determined by genetically fixed preferences. Intensive studies have been made of host-plant selection by phytophagous insects. Here, as in host selection by animal parasites, the question is one of the choice of a place to live rather than of food alone, and the selection criteria may be largely a matter of compromise between nutritional requirements and other ecological functions. Leaving aside these complications, the factors leading to selection of a particular plant as food are predominantly chemical, although other properties, such as structure, also play a role. The chemicals involved in part are the nutrients themselves, but often the feeding responses are largely elicited by token substances that are not nutritionally essential but are characteristic of the species or family of plants that provide the natural hosts for the insect concerned.

GRAZING

Red kangaroo grazing.

Grazing is a method of feeding in which a herbivore feeds on plants such as grasses, or other multicellular organisms such as algae. In agriculture, grazing is one method used whereby domestic livestock are used to convert grass and other forage into meat, milk and other products.

A Masaai herdsman grazing his cattle inside the Ngorongoro crater.

Many small selective herbivores follow larger grazers which skim off the highest, tough growth of grasses, exposing tender shoots. For terrestrial animals, grazing is normally distinguished from browsing in that grazing is eating grass or forbs, whereas browsing is eating woody twigs and leaves from trees and shrubs. Grazing differs from predation because the organism being grazed upon may not be killed. It differs from parasitism because the two organisms live together in a constant state of physical externality (i.e. low intimacy). Water animals that feed by rasping algae and other micro-organisms from stones are called grazers-scrapers.

Green sea turtle grazing on seagrass.

Grazing is a method of feeding in which a herbivore feeds on plants such as grasses, or other multicellular organisms such as algae.

Graminivory

Graminivory is a form of grazing involving feeding primarily on grass (specifically "true" grasses in the Poaceae). Horses, cattle, capybara, hippopotamuses, grasshoppers, geese, and giant pandas are graminivores. Giant pandas (*Ailuropoda melanoleuca*) are obligate bamboo grazers, 99% of their diet consisting of sub-alpine bamboo species.

Coprophagy

The capybara is one of several coprophagous herbivores.

Rabbits are herbivores that feed by grazing on grass, forbs, and leafy weeds. They graze heavily and rapidly for about the first half-hour of a grazing period (usually in the late afternoon), followed by about half an hour of more selective feeding. If the environment is relatively non-threatening, the rabbit remains outdoors for many hours, grazing at intervals. Their diet contains large amounts of cellulose, which is hard to digest. Rabbits solve this problem by using a form of hindgut fermentation. They pass two distinct types of feces: hard droppings and soft black viscous pellets, the latter of which are known as caecotrophs and are immediately eaten (coprophagy). Rabbits reingest their own droppings (rather than chewing the cud as do cattle and many other grazers) to digest their food further and extract sufficient nutrients.

Capybara (Hydrochoerus hydrochaeris) are herbivores that graze mainly on grasses and aquatic plants, as well as fruit and tree bark. As with other grazers, they can be very selective, feeding on the leaves of one species and disregarding other species surrounding it. They eat a greater variety of plants during the dry season, as fewer plants are available. While they eat grass during the wet season, they have to switch to more abundant reeds during the dry season. The capybara's jaw hinge is not perpendicular; hence it chews food by grinding back-and-forth rather than side-to-side. Capybara are coprophagous as a means of obtaining bacterial gut flora to help digest the cellulose in the grass that forms their normal diet, and to extract the maximum protein and vitamins from their food. They may also regurgitate food to masticate again, similar to cud-chewing by a cow. As with other rodents, the front teeth of capybara grow continually to compensate for the constant wear from eating grasses; their cheek teeth also grow continuously.

Pseudoruminant

The hippopotamus is a large, semi-aquatic, mammal inhabiting rivers, lakes and mangrove swamps. During the day, they remain cool by staying in the water or mud; reproduction and childbirth both occur in water. They emerge at dusk to graze on grasses. While hippopotamuses rest near each other in the water, grazing is a solitary activity. Their incisors can be as long as 40 cm and the canines up to 50 cm; however, the canines and incisors are used for combat, and play no role in feeding. Hippos rely on their broad, horny lips to grasp and pull grasses which are then ground by the molars. The hippo is considered to be a pseudoruminant; it has a complex three- or four-chambered stomach but does not "chew cud".

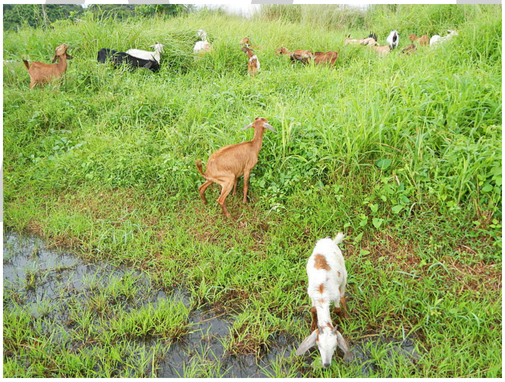
Non-grass Grazing

Although grazing is typically associated with mammals feeding on grasslands, or more specifically livestock in a pasture, ecologists sometimes use the word in a broader sense, to include any organism that feeds on any other species without ending the life of the prey organism.

Use of the term varies even more than this; for example, a marine biologist may describe herbivorous sea urchins that feed on kelp as *grazers*, even when they kill the organism by cutting the plant at the base. Malacologists sometimes apply the word to aquatic snails that feed by consuming the microscopic film of algae, diatoms and detritus—a biofilm—that covers the substrate and other surfaces underwater.

Systems

Seasonal



Free range grazing, goats in the Philippines.

Seasonal grazing incorporates "grazing animals on a particular area for only part of the year". This allows the land that is not being grazed to rest and allow for new forage to grow.

Rotational

Rotational grazing "involves dividing the range into several pastures and then grazing each in sequence throughout the grazing period". Utilizing rotational grazing can improve livestock distribution while incorporating rest period for new forage.

Rest Rotation

Rest rotation grazing "divides the range into at least four pastures. One pasture remains rested throughout the year and grazing is rotated amongst the residual pastures." This grazing system can be especially beneficial when using sensitive grass that requires time for rest and regrowth.

Deferred Rotation

Deferred rotation "involves at least two pastures with one not grazed until after seed-set". By using deferred rotation, grasses can achieve maximum growth during the period when no grazing occurs.

Patch-burn

Patch-burn grazing burns a third of a pasture each year, no matter the size of the pasture. This burned patch attracts grazers (cattle or bison) that graze the area heavily because of the fresh grasses that grow as a result. The other patches receive little to no grazing. During the next two years the next two patches are burned consecutively, then the cycle begins anew. In this way, patches receive two years of rest and recovery from the heavy grazing. This technique results in a diversity of habitats that different prairie plants and birds can utilize—mimicking the effects of the pre-historical bison/fire relationship, whereby bison heavily graze one area and other areas have opportunity to rest.

The Tallgrass Prairie Preserve in northeastern Oklahoma is within the Flint Hills ecosystem, and has been patch-burn grazed with bison herds for over ten years. These efforts have effectively restored the bison/fire relationship on a large landscape scale of 30,000 acres (12,000 ha).

Riparian Area Management

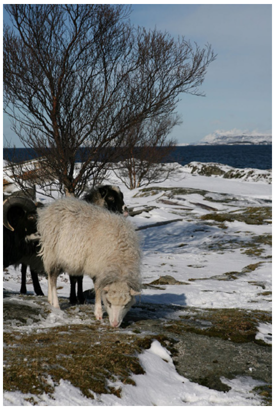
Riparian area grazing is geared more towards improving wildlife and their habitats. It uses fencing to keep livestock off ranges near streams or water areas until after wildlife or waterfowl periods, or to limit the amount of grazing to a short period of time.

Conservational

Conservation grazing is the use of grazing animals to help improve the biodiversity of a site. Due to their hardy and thrifty nature, rare and native breeds are often used in conservation grazing. In some cases, to re-establish traditional hay meadows, cattle such as the English Longhorn and Highland (which happen to be rare breeds) are used to provide low-intensity grazing.

Ecological Effects

A number of ecological effects derive from grazing, and these may be either positive or negative. Negative effects of grazing include increased soil erosion, adverse water quality impacts from increased runoff and loss of biodiversity. For example, historical grazing, along with other land conversion, in northern and central California has reduced native chaparral and forest lands by approximately 70 percent. Ongoing grazing expansion and land conversion driven by human population growth in this region threatens the remaining integrity of California chaparral and woodlands habitat in this region. In some habitats, appropriate levels of grazing may be effective in restoring or maintaining native grass and herb diversity in rangeland that has been disturbed by overgrazing, lack of grazing (such as by the removal of wild grazing animals), or by other human disturbance. Conservation grazing is the use of domestic livestock to manage such habitats, often to replicate the ecological effects of the wild relatives of livestock, or those of other species now absent or extinct. For example, heathland in Europe requires grazing by cattle, sheep or other grazers to maintain its structure and diversity.



Old Norwegian Sheep grazing at an island on the coast of Norway. This is a vulnerable habitat where the sheep take part in a delicate ecological balance.

Much grazing land has resulted from a process of clearance or drainage of other habitats such as woodland or wetland.

In marine systems, grazing maintains habitat structure by preventing algal overgrowth, especially in coral reefs. However, climate change can affect the grazing performance of marine animals (e.g. by changing the feeding rates of mesograzers), triggering broad ecological effects as oceans become warmer.

HOARDING OR CACHING

Hoarding or caching in animal behavior is the storage of food in locations hidden from the sight of both conspecifics (animals of the same or closely related species) and members of other species. Most commonly, the function of hoarding or caching is to store food in times of surplus for times when food is less plentiful. However, there is evidence that some amount of caching or hoarding is done in order to ripen the food, called ripening caching. The term hoarding is most typically used for rodents, whereas caching is more commonly used in reference to birds, but the behaviors in both animal groups are quite similar.

Western scrub jays cache food such as acorns and insects.

Hoarding is done either on a long-term basis – cached on a seasonal cycle, with food to be consumed months down the line – or on a short term basis, in which case the food will be consumed over a period of one or several days.

Some common animals that cache their food are rodents such as hamsters and squirrels, and many different bird species, such as rooks and woodpeckers. The western scrub jay is noted for its particular skill at caching. There are two types of caching behavior: larder-hoarding, where a species creates a few large caches which it often defends, and scatter-hoarding, where a species will create multiple caches, often with each individual food item stored in a unique place. Both types of caching have their advantage.

Function

Caching behavior is typically a way to save excess edible food for later consumption - either soon to be eaten food, such as when a jaguar hangs a partially eaten prey in a tree to be eaten within a few days, or long term where the food is hidden and retrieved many months later. Caching is a common adaptation to seasonal changes in food availability. In regions where winters are harsh, food availability typically becomes low, and caching food during the times of high food availability in the warmer months provides a significant survival advantage.

However, in ripening caching behavior, animals collect and cache food which is immediately inedible but will become “ripe” and edible after a short while. For instance, tayras (a Central American weasel) have been observed to harvest whole green plantains, hide them, and then come back to eat them after they have ripened. Crocodilians such as the alligator are predators with ineffective teeth action - they can bite prey to kill it but can’t tear flesh or chew. Small enough prey are swallowed whole while for larger prey, such as a deer, the carcass is cached underwater and left to rot (or “ripen”) until it is easy to eat. Leafcutter ants harvest pieces of inedible leaves and then cache them in underground chambers to ripen with a fungus which is the main food for the colony.

Hoard Distribution and Size

Scatter hoarding is the formation of a large number of small hoards. This behavior is present in both birds (especially the Canada jay) and small mammals, mainly squirrels and other rodents, such as the eastern gray squirrel, fox squirrel, and wood mouse. Specifically, those who do not migrate to warmer climates or hibernate for winter are most likely to scatter hoard. This behavior plays an important part in seed dispersal, as those seeds that are left uneaten will have a chance to germinate, thus enabling plants to spread their populations effectively.

Cache spacing is the primary technique that scatter hoarders use to protect food from pilferers. By spreading the food supply around geographically, hoarders discourage competitors who happen upon a cache from conducting area-restricted searching for more of the supply. Despite cache spacing, however, hoarders are still unable to completely eliminate the threat of pilferage. However, having multiple cache sites is costly because it requires a good memory. Scatter-hoarders generally have a large hippocampus.

In larder hoarding, the hoard is large and is found in a single place termed a larder, which usually also serves as the nest where the animal lives. Hamsters are famous larder hoarders. comes from to hoard; le’egor. A disadvantage of larder hoarding is that if a cache is raided, this is far more problematic for the animal than if it were a scatter hoarder. While the hoard is much easier to remember the location of, these larger hoards must also be more staunchly defended.

Related Behaviors

Guarding

Most species are particularly wary of onlooking individuals during caching and ensure that the cache locations are secret. Not all caches are concealed however, for example shrikes store prey items on thorns on branches in the open.

Shared or Individual Hoarding

Although a small handful of species share food stores, food hoarding is a solo endeavor for most species, including almost all rodents and birds. For example, a number of jays live in large family groups, but they don't demonstrate sharing of cached food. Rather, they hoard their food supply selfishly, caching and retrieving the supply in secret.

There are only two species in which kin selection has resulted in a shared food store, i.e. beavers (*Castor canadensis*) and acorn woodpeckers (*Melanerpes formicivorous*); the former live in family groups and construct winter larders of submerged branches, while the latter are unusual in that they construct a conspicuous communal larder.

Pilfering

Pilferage occurs when one animal takes food from another animal's larder. Some species experience high levels of cache pilferage, up to 30% of the supply per day. Models of scatter hoarding suggested the value of cached food is equal to the hoarders ability to retrieve it.

Reciprocal Pilfering

It has been observed that members of certain species, such as rodents and chickadees, act as both hoarder and pilferer. In other words, pilfering can be reciprocal and, thus, tolerable. Although this kind of food caching system seems cooperative, it has been suggested that it is actually driven by the selfish interests of the individual.

Recaching

Animals recache the food that they've pilfered from other animal's caches. For example, 75% percent of mildly radioactive (thus traceable) Jeffrey pine seeds cached by yellow pine chipmunks were found in two cache sites, 29% of the seeds were found in three sites, 9.4% were found in four sites and 1.3% were found in five sites over a 3-month period. These results, and those from other studies, demonstrate the dynamic nature of the food supplies of scatter hoarding animals.

Deception

Group-foraging common ravens, (*Corvus corax*), scatter hoard their food and also raid the caches made by others. Cachers withdraw from conspecifics when hiding their food and most often place their caches behind structures, obstructing the view of potential observers. Raiders watch inconspicuously and keep at a distance to cachers close to their cache sites. In response to the presence of potential raiders or because of their initial movements towards caches, the cachers frequently interrupt caching, change cache sites, or recover their food items. These behaviors suggest that ravens are capable of withholding information about their intentions, which may qualify as tactical deception.

Similarly, Eurasian jays (*Garrulus glandarius*) when being watched by another jay, prefer to cache food behind an opaque barrier rather than a transparent barrier, suggesting they may opt to cache in out-of-view locations to reduce the likelihood of other jays pilfering their caches.

PREDATION

Solitary predator: A polar bear feeds on a bearded seal it has killed.

Social predators: Meat ants cooperate to feed on a cicada far larger than themselves.

Predation is a biological interaction where one organism, the predator, kills and eats another organism, its prey. It is one of a family of common feeding behaviors that includes parasitism and micropredation (which usually do not kill the host) and parasitoidism (which always does, eventually). It is distinct from scavenging on dead prey, though many predators also scavenge; it overlaps with herbivory, as a seed predator is both a predator and a herbivore.

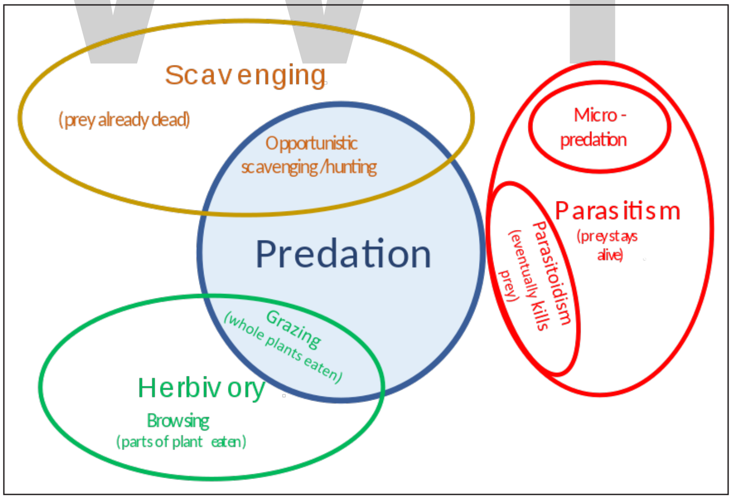
Predators may actively search for prey or sit and wait for it. When prey is detected, the predator assesses whether to attack it. This may involve ambush or pursuit predation, sometimes after stalking the prey. If the attack is successful, the predator kills the prey, removes any inedible parts like the shell or spines, and eats it.

Predators are adapted and often highly specialized for hunting, with acute senses such as vision, hearing, or smell. Many predatory animals, both vertebrate and invertebrate, have sharp claws or jaws to grip, kill, and cut up their prey. Other adaptations include stealth and aggressive mimicry that improve hunting efficiency.

Predation has a powerful selective effect on prey, and the prey develop antipredator adaptations such as warning coloration, alarm calls and other signals, camouflage, mimicry of well-defended species, and defensive spines and chemicals. Sometimes predator and prey find themselves in an evolutionary arms race, a cycle of adaptations and counter-adaptations. Predation has been a major driver of evolution since at least the Cambrian period.

Spider wasps paralyse and eventually kill their hosts, but are considered parasitoids, not predators.

At the most basic level, predators kill and eat other organisms. However, the concept of predation is broad, defined differently in different contexts, and includes a wide variety of feeding methods; and some relationships that result in the prey's death are not generally called predation. A parasitoid, such as an ichneumon wasp, lays its eggs in or on its host; the eggs hatch into larvae, which eat the host, and it inevitably dies. Zoologists generally call this a form of parasitism, though conventionally parasites are thought not to kill their hosts. A predator can be defined to differ from a parasitoid in two ways: it kills its prey immediately; and it has many prey, captured over its lifetime, where a parasitoid's larva has just one, or at least has its food supply provisioned for it on just one occasion.



Relation of predation to other feeding strategies.

There are other difficult and borderline cases. Micropredators are small animals that, like predators, feed entirely on other organisms; they include fleas and mosquitoes that consume blood from living animals, and aphids that consume sap from living plants. However, since they typically do not kill their hosts, they are now often thought of as parasites. Animals that graze on phytoplankton or mats of microbes are predators, as they consume and kill their food organisms; but herbivores that browse leaves are not, as their food plants usually survive the assault. However, when animals eat seeds (seed predation or granivory) or eggs (egg predation), they are consuming entire living organisms, which by definition makes them predators, albeit unconventional ones: for instance, a mouse that eats grass seeds has no adaptations for tracking, catching and subduing prey and its teeth are not adapted to slicing through flesh.

Scavengers, organisms that only eat organisms found already dead, are not predators, but many predators such as the jackal and the hyena scavenge when the opportunity arises. Among invertebrates, social wasps (yellowjackets) are both hunters and scavengers of other insects.

Taxonomic Range

Carnivorous plant: Sundew engulfing an insect.

Seed predation: Mouse eating seeds.

While examples of predators among mammals and birds are well known, predators can be found in a broad range of taxa. They are common among insects, including mantids, dragonflies, lacewings and scorpionflies. In some species such as the alderfly, only the larvae are predatory (the adults do not eat). Spiders are predatory, as well as other terrestrial invertebrates such as scorpions; centipedes; some mites, snails and slugs; nematodes; and planarian worms. In marine environments, most cnidarians (e.g., jellyfish, hydroids), ctenophora (comb jellies), echinoderms (e.g., sea stars, sea urchins, sand dollars, and sea cucumbers) and flatworms are predatory. Among crustaceans, lobsters, crabs, shrimps and barnacles are predators, and in turn crustaceans are preyed on by nearly all cephalopods (including octopuses, squid and cuttlefish).

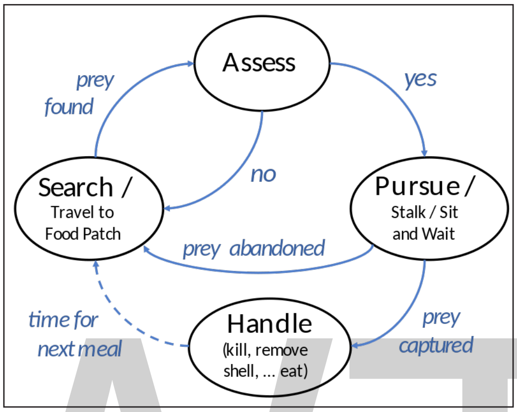
Seed predation is restricted to mammals, birds, and insects and is found in almost all terrestrial ecosystems. Egg predation includes both specialist egg predators such as some colubrid snakes and generalists such as foxes and badgers that opportunistically take eggs when they find them.

Some plants, like the pitcher plant, the Venus fly trap and the sundew, are carnivorous and consume insects. Some carnivorous fungi catch nematodes using either active traps in the form of constricting rings, or passive traps with adhesive structures.

Many species of protozoa (eukaryotes) and bacteria (prokaryotes) prey on other microorganisms; the feeding mode is evidently ancient, and evolved many times in both groups. Among freshwater and marine zooplankton, whether single-celled or multi-cellular, predatory grazing on phytoplankton and smaller zooplankton is common, and found in many species of nanoflagellates, dinoflagellates, ciliates, rotifers, a diverse range of meroplankton animal larvae, and two groups of crustaceans, namely copepods and cladocerans.

Foraging

To feed, a predator must search for, pursue and kill its prey. These actions form a foraging cycle. The predator must decide where to look for prey based on its geographical distribution; and once it has located prey, it must assess whether to pursue it or to wait for a better choice. If it chooses pursuit, its physical capabilities determine the mode of pursuit (e.g., ambush or chase). Having captured the prey, it may also need to expend energy handling it (e.g., killing it, removing any shell or spines, and ingesting it).



A basic foraging cycle for a predator, with some variations indicated.

Search

Predators have a choice of search modes ranging from *sit-and-wait* to *active* or *widely foraging*. The sit-and-wait method is most suitable if the prey are dense and mobile, and the predator has low energy requirements. Wide foraging expends more energy, and is used when prey is sedentary or sparsely distributed. There is a continuum of search modes with intervals between periods of movement ranging from seconds to months. Sharks, sunfish, insectivorous birds and shrews are almost always moving while web-building spiders, aquatic invertebrates, praying mantises and kestrels rarely move. In between, plovers and other shorebirds, freshwater fish including crappies, and the larvae of coccinellid beetles (ladybirds), alternate between actively searching and scanning the environment.

The black-browed albatross regularly flies hundreds of kilometres across the nearly empty ocean to find patches of food.

Prey distributions are often clumped, and predators respond by looking for patches where prey is dense and then searching within patches. Where food is found in patches, such as rare shoals of fish in a nearly empty ocean, the search stage requires the predator to travel for a substantial time, and to expend a significant amount of energy, to locate each food patch. For example, the black-browed albatross regularly makes foraging flights to a range of around 700 kilometres (430 miles), up to a maximum foraging range of 3,000 kilometres (1,860 miles) for breeding birds gathering food for their young. With static prey, some predators can learn suitable patch locations and return to them at intervals to feed. The optimal foraging strategy for search has been modelled using the marginal value theorem.

Search patterns often appear random. One such is the Lévy walk, that tends to involve clusters of short steps with occasional long steps. It is a good fit to the behavior of a wide variety of organisms including bacteria, honeybees, sharks.

Assessment

Seven-spot ladybirds select plants of good quality for their aphid prey.

Having found prey, a predator must decide whether to pursue it or keep searching. The decision depends on the costs and benefits involved. A bird foraging for insects spends a lot of time searching but capturing and eating them is quick and easy, so the efficient strategy for the bird is to eat every palatable insect it finds. By contrast, a predator such as a lion or falcon finds its prey easily but capturing it requires a lot of effort. In that case, the predator is more selective.

One of the factors to consider is size. Prey that is too small may not be worth the trouble for the amount of energy it provides. Too large, and it may be too difficult to capture. For example, a mantid captures prey with its forelegs and they are optimized for grabbing prey of a certain size. Mantids are reluctant to attack prey that is far from that size. There is a positive correlation between the size of a predator and its prey.

A predator may also assess a patch and decide whether to spend time searching for prey in it. This may involve some knowledge of the preferences of the prey; for example, ladybirds can choose a patch of vegetation suitable for their aphid prey.

Capture

To capture prey, predators have a spectrum of pursuit modes that range from overt chase (also known as pursuit predation) to a sudden strike on nearby prey (ambush predation). Another strategy in between ambush and pursuit is ballistic interception, where a predator observes and predicts a prey's motion and then launches its attack accordingly.

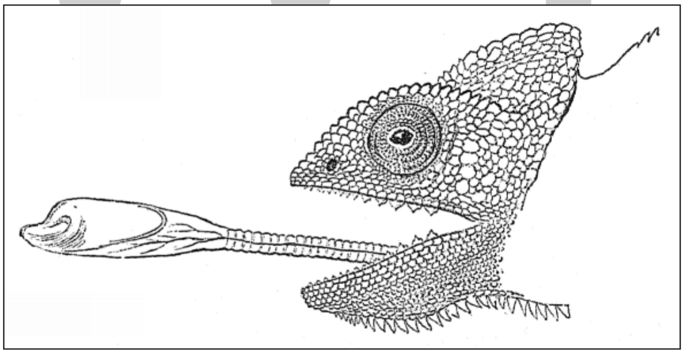
Ambush

Western green lizard ambushes its grasshopper prey.

A trapdoor spider waiting in its burrow to ambush its prey.

Ambush or sit-and-wait predators are carnivorous animals that capture prey by stealth or surprise. In animals, ambush predation is characterized by the predator's scanning the environment from a concealed position until a prey is spotted, and then rapidly executing a fixed surprise attack. Vertebrate ambush predators include frogs, fish such as the angel shark, the northern pike and the eastern frogfish. Among the many invertebrate ambush predators are trapdoor spiders on land and mantis shrimps in the sea. Ambush predators often construct a burrow in which to hide, improving concealment at the cost of reducing their field of vision. Some ambush predators also use lures to attract prey within striking range. The capturing movement has to be rapid to trap the prey, given that the attack is not modifiable once launched.

Ballistic Interception



The chameleon attacks prey by shooting out its tongue.

Ballistic interception is the strategy where a predator observes the movement of a prey, predicts its motion, works out an interception path, and then attacks the prey on that path. This differs from ambush predation in that the predator adjusts its attack according to how the prey is moving. Ballistic interception involves a brief period for planning, giving the prey an opportunity to escape. Some frogs wait until snakes have begun their strike before jumping, reducing the time available to the snake to recalibrate its attack, and maximising the angular adjustment that the snake would need to make to intercept the frog in real time. Ballistic predators include insects such as dragonflies, and vertebrates such as archerfish (attacking with a jet of water), chameleons (attacking with their tongues), and some colubrid snakes.

Pursuit

Humpback whales are lunge feeders, filtering thousands of krill from seawater and swallowing them alive.

In pursuit predation, predators chase fleeing prey. If the prey flees in a straight line, capture depends only on the predator's being faster than the prey. If the prey manoeuvres by turning as it flees, the predator must react in real time to calculate and follow a new intercept path, such as by parallel navigation, as it closes on the prey. Many pursuit predators use camouflage to approach the prey as close as possible unobserved (*stalking*) before starting the pursuit. Pursuit predators include terrestrial mammals such as lions, cheetahs, and wolves; marine predators such as dolphins and many predatory fishes, such as tuna; predatory birds (raptors) such as falcons; and insects such as dragonflies.

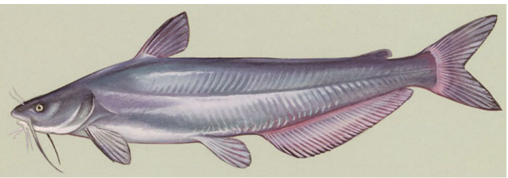
Dragonflies, like this common clubtail with captured prey, are invertebrate pursuit predators.

An extreme form of pursuit is endurance or persistence hunting, in which the predator tires out the prey by following it over a long distance, sometimes for hours at a time. The method is used by in canids such as African wild dogs and domestic hounds. The African wild dog is an extreme persistence predator, tiring out individual prey by following them for many miles at relatively low speed, compared for example to the cheetah's brief high-speed pursuit.

A specialised form of pursuit predation is the lunge feeding of baleen whales. These very large marine predators feed on plankton, especially krill, diving and actively swimming into concentrations of plankton, and then taking a huge gulp of water and filtering it through their feathery baleen plates.

Pursuit predators may be social, like the lion and wolf that hunt in groups, or solitary, like the cheetah.

Handling



Catfish has sharp dorsal and pectoral spines which it holds erect to discourage predators such as herons which swallow prey whole.

Osprey tears its fish prey apart, avoiding dangers such as sharp spines.

Once the predator has captured the prey, it has to handle it: very carefully if the prey is dangerous to eat, such as if it possesses sharp or poisonous spines, as in many prey fish. Some catfish such as the Ictaluridae have spines on the back (dorsal) and belly (pectoral) which lock in the erect position; as the catfish thrashes about when captured, these could pierce the predator's mouth, possibly fatally. Some fish-eating birds like the osprey avoid the danger of spines by tearing up their prey before eating it.

Solitary versus Social Predation

In social predation, a group of predators cooperates to kill prey. This makes it possible to kill creatures larger than those they could overpower singly; for example, hyenas, and wolves collaborate to catch and kill herbivores as large as buffalo, and lions even hunt elephants. It can also make prey more readily available through strategies like flushing of prey and herding it into a smaller area. For example, when mixed flocks of birds forage, the birds in front flush out insects that are caught by the birds behind. Spinner dolphins form a circle around a school of fish and move inwards, concentrating the fish by a factor of 200. By hunting socially chimpanzees can catch colobus monkeys that would readily escape an individual hunter, while cooperating Harris hawks can trap rabbits.

Wolves, social predators, cooperate to hunt and kill bison.

Predators of different species sometimes cooperate to catch prey. In coral reefs, when fish such as the grouper and coral trout spot prey that is inaccessible to them, they signal to giant moray eels, Napoleon wrasses or octopuses. These predators are able to access small crevices and flush out the prey. Killer whales have been known to help whalers hunt baleen whales.

Social hunting allows predators to tackle a wider range of prey, but at the risk of competition for the captured food. Solitary predators have more chance of eating what they catch, at the price of increased expenditure of energy to catch it, and increased risk that the prey will escape. Ambush predators are often solitary to reduce the risk of becoming prey themselves. Of 245 terrestrial carnivores, 177 are solitary; and 35 of the 37 wild cats are solitary, including the cougar and cheetah. However, the solitary cougar does allow other cougars to share in a kill, and the coyote can be either solitary or social. Other solitary predators include the northern pike, wolf spiders and all the thousands of species of solitary wasps among arthropods, and many microorganisms and zooplankton.

Specialization

Physical Adaptations

Under the pressure of natural selection, predators have evolved a variety of physical adaptations for detecting, catching, killing, and digesting prey. These include speed, agility, stealth, sharp senses, claws, teeth, filters, and suitable digestive systems.

For detecting prey, predators have well-developed vision, smell, or hearing. Predators as diverse as owls and jumping spiders have forward-facing eyes, providing accurate binocular vision over a relatively narrow field of view, whereas prey animals often have less acute all-round vision. Animals such as foxes can smell their prey even when it is concealed under 2 feet (60 cm) of snow or earth. Many predators have acute hearing, and some such as echolocating bats hunt exclusively by active or passive use of sound.

Predators including big cats, birds of prey, and ants share powerful jaws, sharp teeth, or claws which they use to seize and kill their prey. Some predators such as snakes and fish-eating birds like herons and cormorants swallow their prey whole; some snakes can unhinge their jaws to allow them to swallow large prey, while fish-eating birds have long spear-like beaks that they use to stab and grip fast-moving and slippery prey. Fish and other predators have developed the ability to crush or open the armoured shells of molluscs.

Many predators are powerfully built and can catch and kill animals larger than themselves; this applies as much to small predators such as ants and shrews as to big and visibly muscular carnivores like the cougar and lion.

Skull of brown bear has large pointed canines for killing prey, and self-sharpening carnassial teeth at rear for cutting flesh with a scissor-like action.

Large compound eyes, sensitive antennae, and powerful jaws (mandibles) of jack jumper ant.

Crab spider, an ambush predator with forward-facing eyes, catching another predator, a field digger wasp.

Red-tailed hawk uses sharp hooked claws and beak to kill and tear up its prey.

Diet and Behavior

Predators are often highly specialized in their diet and hunting behavior; for example, the Eurasian lynx only hunts small ungulates. Others such as leopards are more opportunistic generalists, preying on at least 100 species. The specialists may be highly adapted to capturing their preferred prey, whereas generalists may be better able to switch to other prey when a preferred target is scarce. When prey have a clumped (uneven) distribution, the optimal strategy for the predator is predicted to be more specialized as the prey are more conspicuous and can be found more quickly; this appears to be correct for predators of immobile prey, but is doubtful with mobile prey.

Platydemus manokwari, a specialist flatworm predator of land snails, attacking a snail.

Size-selective predation: a lioness attacking a Cape buffalo, over twice her weight. Lions can attack much larger prey, including elephants, but do so much less often.

In size-selective predation, predators select prey of a certain size. Large prey may prove troublesome for a predator, while small prey might prove hard to find and in any case provide less of a reward. This has led to a correlation between the size of predators and their prey. Size may also act as a refuge for large prey. For example, adult elephants are relatively safe from predation by lions, but juveniles are vulnerable.

Camouflage and Mimicry


A camouflaged predator: Snow leopard in Ladakh.


Striated frogfish uses camouflage and aggressive mimicry in the form of a fishing rod-like lure on its head to attract prey.

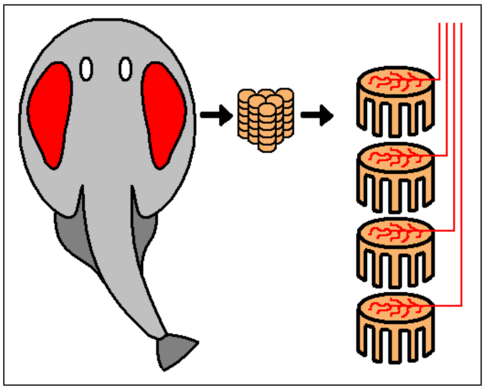
Members of the cat family such as the snow leopard (treeless highlands), tiger (grassy plains, reed swamps), ocelot (forest), fishing cat (waterside thickets), and lion (open plains) are camouflaged with coloration and disruptive patterns suiting their habitats.

In aggressive mimicry, certain predators, including insects and fishes, make use of coloration and behavior to attract prey. Female *Photuris* fireflies, for example, copy the light signals of other species, thereby attracting male fireflies, which they capture and eat. Flower mantises are ambush predators; camouflaged as flowers, such as orchids, they attract prey and seize it when it is close enough. Frogfishes are extremely well camouflaged, and actively lure their prey to approach using an esca, a bait on the end of a rod-like appendage on the head, which they wave gently to mimic a small animal, gulping the prey in an extremely rapid movement when it is within range.

Venom

Many smaller predators such as the box jellyfish use venom to subdue their prey, and venom can also aid in digestion (as is the case for rattlesnakes and some spiders). The marbled sea snake that has adapted to egg predation has atrophied venom glands, and the gene for its three finger toxin contains a mutation (the deletion of two nucleotides) that inactives it. These changes are explained by the fact that its prey does not need to be subdued.

Electric Fields


An electric ray (Torpediniformes) showing location of electric organ and electrocytes stacked within it.

Several groups of predatory fish have the ability to detect, track, and sometimes, as in the electric ray, to incapacitate their prey by generating electric fields using electric organs. The electric organ is derived from modified nerve or muscle tissue.

Physiology

Physiological adaptations to predation include the ability of predatory bacteria to digest the complex peptidoglycan polymer from the cell walls of the bacteria that they prey upon. Carnivorous vertebrates of all five major classes (fishes, amphibians, reptiles, birds, and mammals) have lower relative rates of sugar to amino acid transport than either herbivores or omnivores, presumably because they acquire plenty of amino acids from the animal proteins in their diet.

Antipredator Adaptations

To counter predation, prey have a great variety of defences. They can try to avoid detection. They can detect predators and warn others of their presence. If detected, they can try to avoid being the target of an attack, for example, by signalling that a chase would be unprofitable or by forming groups. If they become a target, they can try to fend off the attack with defences such as armour, quills, unpalatability or mobbing; and they can escape an attack in progress by startling the predator, shedding body parts such as tails, or simply fleeing.

Avoiding Detection

Prey can avoid detection by predators with morphological traits and coloration that make them hard to detect. They can also adopt behavior that avoids predators by, for example, avoiding the times and places where predators forage.

Misdirection

Dead leaf mantis's camouflage makes it less visible to both predators and prey.

Syrphid hoverfly misdirects predators by mimicking a wasp, but has no sting.

Prey animals make use of a variety of mechanisms including camouflage and mimicry to misdirect the visual sensory mechanisms of predators, enabling the prey to remain unrecognized for long enough to give it an opportunity to escape. Camouflage delays recognition through coloration, shape, and pattern. Among the many mechanisms of camouflage are countershading and disruptive coloration. The resemblance can be to the biotic or non-living environment, such as a mantis resembling dead leaves, or to other organisms. In mimicry, an organism has a similar appearance to another species, as in the drone fly, which resembles a bee yet has no sting.

Behavioral Mechanisms

Black woodpecker attending its chicks, relatively safe inside an excavated hole in a tree.

Animals avoid predators with behavioral mechanisms such as changing their habitats (particularly when raising young), reducing their activity, foraging less and forgoing reproduction when they sense that predators are about.

Eggs and nestlings are particularly vulnerable to predation, so birds take measures to protect their nests. Where birds locate their nests can have a large effect on the frequency of predation. It is lowest for those such as woodpeckers that excavate their own nests and progressively higher for those on the ground, in canopies and in shrubs. To compensate, shrub nesters must have more broods and shorter nesting times. Birds also choose appropriate habitat (e.g., thick foliage or islands) and avoid forest edges and small habitats. Similarly, some mammals raise their young in dens.

By forming groups, prey can often reduce the frequency of encounters with predators because the visibility of a group does not rise in proportion to its size.

Detecting Predators

Recognition

Eurasian jay is constantly alert for predators, warning of their presence with loud alarm calls.

Prey species use sight, sound and odor to detect predators, and they can be quite discriminating. For example, Belding's ground squirrel can distinguish several aerial and ground predators from each other and from harmless species. Prey also distinguish between the calls of predators and non-predators. Some species can even distinguish between dangerous and harmless predators of the same species. In the northeastern Pacific Ocean, transient killer whales prey on seals, but the local killer whales only eat fish. Seals rapidly exit the water if they hear calls between transients. Prey are also more vigilant if they smell predators.

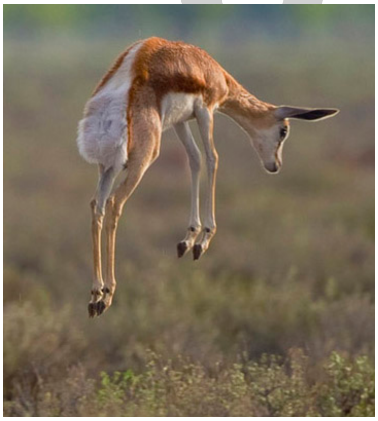
The abilities of prey to detect predators do have limits. Belding's ground squirrel cannot distinguish between harriers flying at different heights, although only the low-flying birds are a threat. Wading birds sometimes take flight when there does not appear to be any predator present. Although such false alarms waste energy and lose feeding time, it can be fatal to make the opposite mistake of taking a predator for a harmless animal.

Vigilance

Prey must remain vigilant, scanning their surroundings for predators. This makes it more difficult to feed and sleep. Groups can provide more eyes, making detection of a predator more likely and reducing the level of vigilance needed by individuals. Many species, such as Eurasian jays, give alarm calls warning of the presence of a predator; these give other prey of the same or different species an opportunity to escape, and signal to the predator that it has been detected.

Avoiding an Attack

Signalling Unprofitability



Springbok stotting to signal its ability to escape.

Monarch caterpillar's aposematic coloration signals its toxicity.

If predator and prey have spotted each other, the prey can signal to the predator to decrease the likelihood of an attack. These *honest signals* may benefit both the prey and predator, because they save the effort of a fruitless chase. Signals that appear to deter attacks include stotting, for example by Thomson's gazelle; push-up displays by lizards; and good singing by skylarks after a pursuit begins. Simply indicating that the predator has been spotted, as a hare does by standing on its hind legs and facing the predator, may sometimes be sufficient.

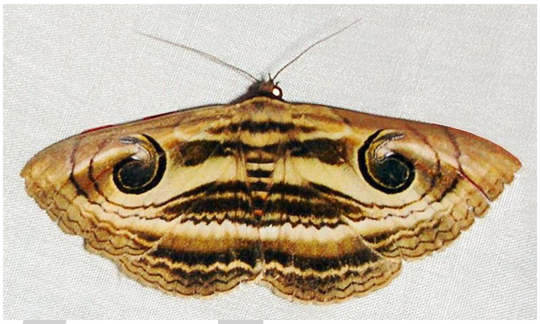
Many prey animals are aposematically coloured or patterned as a warning to predators that they are distasteful or able to defend themselves. Such distastefulness or toxicity is brought about by chemical defences, found in a wide range of prey, especially insects, but the skunk is a dramatic mammalian example.

Forming Groups

By forming groups, prey can reduce attacks by predators. There are several mechanisms that produce this effect. One is *dilution*, where, in the simplest scenario, if a given predator attacks a group of prey, the chances of a given individual being the target is reduced in proportion to the size of the group. However, it is difficult to separate this effect from other group-related benefits such as increased vigilance and reduced encounter rate. Other advantages include confusing predators such as with motion dazzle, making it more difficult to single out a target.

Fending off an Attack

The porcupine *Erethizon dorsatum* combines sharp spines with warning coloration.



When attacked, many moths such as *Spirama helicina* open their wings to reveal eyespots, in a deimatic or bluffing display.

Chemical defences include toxins, such as bitter compounds in leaves absorbed by leaf-eating insects, are used to dissuade potential predators. Mechanical defences include sharp spines, hard shells and tough leathery skin or exoskeletons, all making prey harder to kill.

Some species mob predators cooperatively, reducing the likelihood of attack.

Escaping an Attack

When a predator is approaching an individual and attack seems imminent, the prey still has several options. One is to flee, whether by running, jumping, climbing, burrowing or swimming. The prey can gain some time by startling the predator. Many butterflies and moths have eyespots, wing markings that resemble eyes. When a predator disturbs the insect, it reveals its hind wings in a in a deimatic or bluffing display, startling the predator and giving the insect time to escape. Some other strategies include playing dead and uttering a distress call.

Coevolution

Predators and prey are natural enemies, and many of their adaptations seem designed to counter each other. For example, bats have sophisticated echolocation systems to detect insects and other prey, and insects have developed a variety of defences including the ability to hear the echolocation calls. Many pursuit predators that run on land, such as wolves, have evolved long limbs in response to the increased speed of their prey. Their adaptations have been characterized as an evolutionary arms race, an example of the coevolution of two species. In a gene centered view of evolution, the genes of predator and prey can be thought of as competing for the prey's body. However, the "life-dinner" principle of Dawkins and Krebs predicts that this arms race is asymmetric: if a predator fails to catch its prey, it loses its dinner, while if it succeeds, the prey loses its life.

Bats use echolocation to hunt moths at night.

The metaphor of an arms race implies ever-escalating advances in attack and defence. However, these adaptations come with a cost; for instance, longer legs have an increased risk of breaking, while the specialized tongue of the chameleon, with its ability to act like a projectile, is useless for lapping water, so the chameleon must drink dew off vegetation.

The "life-dinner" principle has been criticized on multiple grounds. The extent of the asymmetry in natural selection depends in part on the heritability of the adaptive traits. Also, if a predator loses enough dinners, it too will lose its life. On the other hand, the fitness cost of a given lost dinner is unpredictable, as the predator may quickly find better prey. In addition, most predators are generalists, which reduces the impact of a given prey adaption on a predator. Since specialization is caused by predator-prey coevolution, the rarity of specialists may imply that predator-prey arms races are rare.

Eastern coral snake, itself a predator, is venomous enough to kill predators that attack it, so when they avoid it, this behavior must be inherited, not learnt.

It is difficult to determine whether given adaptations are truly the result of coevolution, where a prey adaptation gives rise to a predator adaptation that is countered by further adaptation in the prey. An alternative explanation is *escalation*, where predators are adapting to competitors, their own predators or dangerous prey. Apparent adaptations to predation may also have arisen for other reasons and then been co-opted for attack or defence. In some of the insects preyed on by bats, hearing evolved before bats appeared and was used to hear signals used for territorial defence and mating. Their hearing evolved in response to bat predation, but the only clear example of reciprocal adaptation in bats is stealth echolocation.

A more symmetric arms race may occur when the prey are dangerous, having spines, quills, toxins or venom that can harm the predator. The predator can respond with avoidance, which in turn drives the evolution of mimicry. Avoidance is not necessarily an evolutionary response as it is generally learned from bad experiences with prey. However, when the prey is capable of killing the predator (as can a coral snake with its venom), there is no opportunity for learning and avoidance must be inherited. Predators can also respond to dangerous prey with counter-adaptations. In western North America, the common garter snake has developed a resistance to the toxin in the skin of the rough-skinned newt.

CANNIBALISM IN ANIMALS

Cannibalism is the act of consuming another individual of the same species as food. Cannibalism is a common ecological interaction in the animal kingdom and has been recorded in more than 1,500 species. Animals showcase cannibalistic behavior for the following reasons:

Extra Nutrition

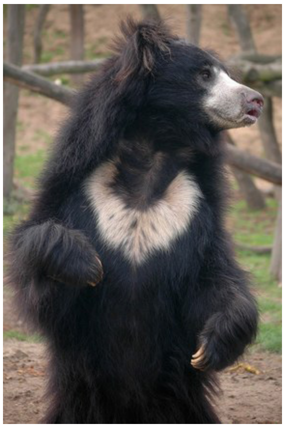
The larvae of tiger salamanders can take two forms. The smaller type eats aquatic invertebrates, while the larger "cannibal morph" feasts on its non-cannibal companions. The cannibal morphs have broader heads, wide mouths, and jutting lower jaws. Their teeth can be up to three times longer than those of a normal salamander.

Researchers have found that cannibal morphs develop when salamander larvae are crowded in large numbers and not related to one another. Experiments suggest that fellow salamanders may make the most nutritious meals.

Cane toads are another amphibian that fattens up through cannibalism. The tadpoles of cane toads, when given a choice between cane toad eggs and similar-looking eggs of other frog species, actually prefer to dine on their own kind. In this case, cannibalism helps the tadpoles grow up big and strong and cuts down on future competition.

Cane toads aren't safe from cannibalism after metamorphosis, either. Another study found that bigger cane toads wiggle the middle toes of their hind feet to lure younger cane toads close enough to be eaten. Researchers found that in a sample of 28 cane toads, 64 percent of their diet was made up of other cane toads.

Eating Offspring



Mothers eating their young can occur due to stress, or when the young is stillborn or weak. This behavior can also benefit the mother. A study of Mexican lance-headed rattlesnakes showed that 68 percent of new mothers cannibalized all or part of their non-surviving offspring. They likely eat them to recover nutrients after giving birth to get ready to reproduce again.

Even the most devoted mothers may sometimes eat their young. A rare instance of maternal cannibalism in moustached tamarins in the wild in Peru. As a mother tamarin foraged for fruit with her adult daughter and infant son. Suddenly, the mother bit through her baby's skull and ate out its brain. Once the mother had eaten the entire head, her adult daughter feasted on the carcass. The researchers suggest that the grisly act may have occurred to benefit the adult daughter, who was pregnant at the time. Sacrificing her own infant may have given her daughter's offspring a better chance at survival.

Cannibal Kids

While mothers eating their young is relatively common, the opposite occurs, too: offspring devouring their mothers. Matriphagy, or mother-eating, is found in some insects, spiders, scorpions, and nematode worms.

Crab spider mothers provide their young with unfertilized eggs to eat, but it's not enough. The young spiders also eat their mother over the course of several weeks. It's a sacrifice that helps the next generation; spiderlings that eat their mothers have higher weights and survival rates than those that don't.

Caecilians are limbless amphibians that look like giant worms. And while caecilian mothers don't give their lives to their young, they still feed them with their flesh. The young have specialized, temporary teeth that they use to peel off layers of their mother's skin. The skin grows back and the young feed some more, for up to three months.

Sibling Rivalry

Sand tiger shark pregnancies may begin with six or seven embryos in the womb, but often only one or two will make it to birth. The first embryonic shark to break out of its egg capsule feasts on its younger siblings and any unfertilized eggs in the womb.

Researchers think this intra-uterine cannibalism allows baby sharks to grow large enough (about three feet) that once they're born, they are safer from being eaten by predators. It essentially gives them a head start in life.

References

- Gascoigne, bamber. "history of the domestication of animals". History world. Retrieved 26 september 2019
- Schindler, david w., vallentyne, john r. (2008). The algal bowl: overfertilization of the world's freshwaters and estuaries, university of alberta press, isbn 0-88864-484-1
- "The nature conservancy in oklahoma". Www.nature.org. Archived from the original on 2011-02-23. Retrieved 2010-04-26
- Soley, f. G.; alvarado-díaz, i. (2011). "prospective thinking in a mustelid? Eira barbara (carnivora) cache unripe fruits to consume them once ripened". Naturwissenschaften. 98 (8): 693–698. Doi:10.1007/s00114-011-0821-0. Issn 0028-1042. Pmid 21739130
- Gurr, geoff m.; wratten, stephen d.; snyder, william e. (2012). Biodiversity and insect pests: key issues for sustainable management. John wiley & sons. P. 105. Isbn 978-1-118-23185-2
- Animal-cannibalism: wired.com, Retrieved 2 July, 2019
- Lafferty, k. D.; kuris, a. M. (2002). "trophic strategies, animal diversity and body size". Trends ecol. Evol. 17 (11): 507–513. Doi:10.1016/s0169-5347(02)02615-0

Stereotypical Behavior in Animals

7 CHAPTER

The repetitive behavior which is morphologically identical and which serves no obvious function or goal is termed as stereotypical behavior. Some of the stereotypical behaviors exhibited by animals are broodiness, coprophagia, infanticide, pterotillomania and drug addiction. This chapter has been carefully written to provide an easy understanding of these examples of stereotypical behavior in animals.

Stereotypic behavior has been defined as a repetitive, invariant behavior pattern with no obvious goal or function. Many different kinds of stereotyped behaviors have been defined and examined. Stereotypes may be oral or involve bizarre postures or prolonged locomotion.

A good example of stereotyped behavior is pacing. This term is used to describe an animal walking in a distinct, unchanging pattern within its cage. The walking can range in speed from slow and deliberate to very quick trotting. It may involve only a few circuits or it may be prolonged, lasting several minutes. The locomotion may be combined with other actions, such as a head toss at the corners of the cage, or the animal rearing onto its hind feet at some point in the circuit. The pattern and appearance of the stereotype differs from animal to animal. Stereotypes often go through stages of development. In the early stages, the behavior may be easily interrupted by a loud noise or other stimulus. At later stages, such interruption is difficult or impossible. At this stage, stimuli can even escalate performance of the behavior. The animal can appear to be in a trance-like state, disconnected or detached from its surroundings.

The distinction between stereotypic and non-stereotypic behavior can be illustrated by considering eating behavior. An animal may eat in a set manner, sitting in the same place, using a distinct motor pattern for a prolonged time but this would not be considered abnormal stereotyped behavior as it has an obvious function. Other abnormal behaviors such as severe aggression or inappropriate/inadequate maternal behavior cannot be considered stereotypic because they are not repetitive and invariant or ritualised. Stereotypic behavior is evaluated in terms of frequency and duration, in other words, how often does the animal engage in bouts of such behavior and how long do the bouts last? It is not adequate, therefore, simply to say that an animal shows stereotypic behavior; it is necessary to quantify the levels of the behavior exhibited. This is usually done by examining the animal's time budget. There may be less concern for an animal that spends 3% to 5% of its time engaged in stereotypic behavior than one that spends 75% of its time in stereotypy. However, it can be argued that any amount of stereotypy is a cause for concern and is an indication of poor welfare.

Stereotypes in Non-human Primates

The stereotypes of non-human primates are generally divided into two categories: deprivation stereotypes and cage stereotypes. Deprivation stereotypes are also referred to as self-directed stereotypes because the behaviors are performed on the individual's own body. For example, self orality describes non- nutritive sucking of an animal on one or more parts of its body (e.g. fingers, tail, or genitalia). Rocking, huddle, and crouch are abnormal postures. Self abuse refers to self injurious behavior, such as biting, scratching, or head banging. The term floating limb is used to describe a phenomenon which involves an animal's limb appearing to move of its own accord. This surprises the animal which will then threaten and attack the limb. A salute is another abnormal posture which involves the animal placing a hand in front of its face, palm out, with one or more fingers pressed against the eyeball. Deprivation stereotypes are usually seen in monkeys that have been separated from their mothers at birth or within the first year of life and raised in part or total social isolation. These abnormal behaviors are thought to be analogous to the normal behaviors seen in infant and juvenile monkeys. Here however they become self-directed in the absence of a con-specific. Self orality in isolates, specifically self- sucking of digits or tail, is considered to be analogous to nipple sucking in infants raised with their mothers. Self clasp is related to mother clinging or clasping. Self abuse is considered to be the only outlet for these animals' frustration.

Repetitive locomotion stereotypes include pacing, jumping in place, and somer-saulting. As the name implies, these cage stereotypes are considered to be the result of the living environment of an animal. All of these stereotypes are active, involving dynamic, whole body movements. Dancing refers to a back and forth quadrupedal movement which is distinct from pacing or spinning.

Though helpful, these terms do not encompass all forms of stereotypic behavior nor do they completely eliminate confusion regarding the different forms. Some behaviors are not included in either category. Stereotypes such as these are placed in v a third miscellaneous category. For example, head weaving, which refers to a head toss which is not involved in a pacing stereotype. Also in this category is the behavior referred to as over-grooming, where an animal removes all the hair from one part of its body, usually a small patch on the shoulder or arm. The third stereotype in this category is picking at nothing (self explanatory).

ADJUNCTIVE BEHAVIOR

Adjunctive behavior occurs when an animal expresses an activity reliably accompanying some other response that has been produced by a stimulus, especially when the stimulus is presented according to a temporally defined schedule. For example, in 1960, psychologist John Falk was studying hungry rats that had been trained to press a lever for a small food pellet. Once a rat had received a pellet, it was obliged to wait an average of one minute before another press of the lever would be rewarded. The rats developed the habit of drinking water during these intervals, but their consumption far exceeded what was expected. Many consumed three to four times their normal daily water intake during a three-hour session, and some drank nearly half of their body weight in water during this time. Further research has revealed that intermittent food presentation to a variety of organisms results in an inordinately excessive consumption of water as well as other behaviors including attack, pica, escape, and alcohol consumption.

In psychological terminology, adjunctive behavior is non-contingent behavior maintained by an event which acquires a reinforcing effect due to some other reinforcing contingency. Some usages emphasize the stimulus rather than the responding it engenders (e.g., in rats, food presentations typically produce eating reliably followed by drinking; the drinking is adjunctive and is sometimes said to be induced by the schedule of food presentation).

Adjunctive behavior has been used as evidence of animal welfare problems. Pregnant sows are typically fed only a fraction of the amount of food they would consume by choice, and they remain hungry for almost the whole day. If a water dispenser is available, some sows will drink two or three times their normal daily intake, and under winter conditions, warming this amount of cold water to body temperature, only to discharge it as dilute urine, involves an appreciable caloric cost. However, if such sows are given a bulky high-fibre food (which under typical circumstances would result in an increase in water intake), they spend much longer eating, and the excessive drinking largely disappears. In this case, much of the sows' water intake appeared to be adjunctive drinking that was not linked to thirst.

BROODINESS

A brooding White tern (*Gygis alba*).

Broodiness is the action or behavioral tendency to sit on a clutch of eggs to incubate them, often requiring the non-expression of many other behaviors including feeding and drinking. Being broody has been defined as: "Being in a state of readiness to brood eggs that is characterized by cessation of laying and by marked changes in behavior and physiology". Broody birds often pluck feathers from their chest and abdomen, using them to cover the eggs. As a consequence of this, they develop one or several patches of bare skin on the ventral surface. These reddish, well-vascularized areas of skin are usually called brood patches, and improve heat transfer to the eggs. Broodiness is usually associated with female birds, although males of some bird species become broody and some non-avian animals also show broodiness.

In Wild Birds

In wild birds, egg incubation is a normal and essential phase in the process of reproduction, and in many families of birds, e.g. pigeons, the eggs are incubated by both male and female parents.

Broodiness in Males

In all the species of phalaropes the males become broody rather than the female. The females leave the nest after finishing laying to let the males incubate the eggs and take care of the young. Male emus (Dromaius novaehollandiae) become broody after their mates start laying, and begin to incubate the eggs before the laying period is complete.

Non-broodiness

A small number of atypical birds such as *Passeriformes* of the genus *Molothrus* (cowbirds) do not become broody but lay their eggs in the nests of other species for incubation, known as brood parasitism. The Australian Brushturkey *(Alectura lathami)* also does not become broody, rather, it covers the eggs with a large mound of vegetable matter, which decomposes, keeping the eggs warm until hatching. The Crab-plover, (*Dromas ardeola*), which lives on the coasts and islands of the Indian Ocean, lets its eggs incubate primarily by the heat of the sun, and will leave its nest unattended, occasionally for days at a time.

In Domestic Poultry

A brooding domestic hen.

Broody hens can be recognized by their behavior. They sit firmly over the eggs, and when people approach or try to remove the eggs, threaten the person by erecting their feathers, emitting a characteristic sound like *clo-clo-clo* and will peck aggressively. When broody, hens often temporarily cease eating or reduce their feed consumption.

Letting eggs accumulate in a relatively dark place near the floor often stimulates hens to become broody. Placing artificial eggs into nests also stimulates broodiness. Keeping hens in dark places with warm temperatures and in view of vocalising orphan chicks can induce broodiness, even in breeds that normally do not go broody.

Some environmental conditions stimulate broodiness. In heavy breeds of chickens, warm weather tends to bring about broodiness. Removing eggs each day, out of the sight of the hens, helps avoid broodiness not only in domestic poultry but also in some wild species in captivity. This continued egg laying means more eggs are laid than would occur under natural conditions. Poultry farming in battery cages also helps to avoid broodiness.

In Commercial Egg-laying

An egg incubator.

Because hens stop laying when they become broody, commercial poultry breeders perceive broodiness not as a normal physiological process, but as an impediment to egg and poultry meat production. With domestication, it has become more profitable to incubate eggs artificially, while keeping hens in full egg production. To help achieve this, there has been intense artificial selection for non-broodiness in commercial egg laying chickens and parent stock of poultry. As a result of this artificial selection, broodiness has been reduced to very low levels in present-day breeds of commercial fowl, both among egg-laying and meat-producing breeds.

Physiological Basis

Broodiness is due to the secretion of the hormone prolactin by the anterior lobe of the hypophysis. Prolactin injection in hens provokes egg laying to stop within a few days, vitellum reabsorption, ovary regression (hens only have a left ovary) and finally broodiness. However, attempts to stop broodiness by the administration of several hormones have failed because this state, once evoked, requires time to revert.

Prolactin injections inhibit the production of gonadotropin hormone, a hormone that stimulates ovarian follicles which is produced in the frontal lobe of hypophysis.

Castrated males can go broody with baby chicks, showing that broodiness is not limited to females, however, castrated males do not incubate eggs.

Contrary to common opinion, the temperature of broody hens barely differs from that of laying hens. Broody hens pluck feathers from their chest, using them to cover the eggs. As a consequence of this, they develop one or several patches of bare skin on the ventral surface. These reddish, well-vascularized areas of skin are usually called brood patches. which improve heat transfer to the eggs.

Genetic Basis

Broodiness is more common in some chicken breeds than others, indicating that it is a heritable characteristic. Breeds such as Cochin, Cornish and Silkie exhibit a tendency to broodiness, including brooding eggs from other species such as quails, pheasants, turkeys and geese. In some breeds such as the White Leghorn, broodiness is extremely rare.

Some studies on crosses of chicken breeds point to the hypothesis of complementary genes acting on broodiness. Other results point to the hypothesis of sex-linked genes, or, inheritance through the maternal chromosome. Although these studies have been made on different breeds of chickens, their results are not contradictory. There is common agreement that artificial selection for egg production succeeded in reducing the incidence of broody hens in chicken populations.

Broodiness in Non-avian Animals

There is some evidence that non-avian dinosaurs also practiced brooding. A specimen of the Mongolian oviraptorid *Citipati osmolskae* was discovered in a chicken-like brooding position in 1993, which may indicate that they had begun using an insulating layer of feathers to keep the eggs warm.

Several deinonychosaur and oviraptorosaur specimens have also been found preserved on top of their nests, likely brooding in a bird-like manner.

Lungless salamanders in the family *Plethodontidae* lay a small number of eggs in a cluster among damp leaf litter. The female salamander often broods the eggs and in the genus *Ensatinas*, she has been observed to coil around them and press her throat area against them, effectively massaging them with a mucous secretion. The black mountain salamander mother broods her eggs, guarding them from predation as the larvae feed on the yolks of their eggs. They eventually break their way out of the egg capsules and disperse. Some species of Gymnophiona (caecilians, with long, cylindrical, limbless bodies) brood their eggs.

A brooding female python.

Most pythons coil around their egg-clutches and remain with them until they hatch. A female python will not leave the eggs, except to occasionally bask in the sun or drink water. She will even "shiver" to generate heat to incubate the eggs.

Some cichlid fish lay their eggs in the open, on rocks, leaves, or logs. Male and female parents usually engage in differing brooding roles. Most commonly, the male patrols the pair's territory and repels intruders, while females fan water over the eggs, removing the infertile and leading the fry while foraging. However, both sexes are able to perform the full range of parenting behaviors.

Mouthbrooding

Mouthbrooding, also known as oral incubation, refers to the care given by some groups of animals to fertilized eggs or their offspring by holding them in the mouth of the parent for extended periods of time. Although it has been observed in a variety of animals, most mouthbrooders are fish. The parent performing this behavior invariably feeds less often and afterwards will be underweight, requiring a period of feeding and restoring the depleted energy reserves.

Other Species

Marsupial frogs are so-called because they possess a dorsal brood pouch. In some species the eggs are fertilized on the female's lower back, and are inserted in her pouch with the aid of the male's toes. The eggs remain in contact with the female's vascular tissue, which provides them oxygen.

Some animals have a common name that includes the word 'brood' or its derivatives, although it is arguable whether the animals show 'broodiness' per se. For example, the female gastric-brooding frog (*Rheobatrachus sp.*) from Australia, now probably extinct, swallows her fertilized eggs, which then develop inside her stomach. She ceases to feed and stops secreting stomach acid and the tadpoles rely on the yolks of the eggs for nourishment. After six or seven weeks the mother opens her mouth wide and regurgitates the tadpoles which hop away from her mouth. The Brooding sea anemone (*Epiactis prolifera*) is a colonial hermaphrodite that fertilizes and incubates its eggs internally. The motile larvae, after swimming out of the mouth, migrate down to the disk and become fixed there until they become little anemones, ready to move and feed independently.

In Darwin's Frog (*Rhinoderma darwinii*), the female lays about 30 eggs and then the male guards them for about two weeks, until they hatch. The male then takes all the survivors and carries around the developing young in his vocal pouch. When the tiny tadpoles have developed they hop out and swim away. In this animal, the parents hold the hatched young rather than eggs in their mouths, so is arguably not showing 'broodiness'.

COPROPHAGIA

Coprophagia or coprophagy is the consumption of feces. Coprophagy refers to many kinds of feces-eating, including eating feces of other species (heterospecifics), of other individuals (allocoprophagy), or one's own (autocoprophagy) – those once deposited or taken directly from the anus.

Invertebrates

Coprophagous insects consume and redigest the feces of large animals. These feces contain substantial amounts of semi-digested food, particularly in the case of herbivores, owing to the inefficiency of the large animals' digestive systems. Two feces-eating insects are certain species of fly and the dung beetle. Dung beetles feed on the microorganism-rich liquid component of mammals' dung, and lay their eggs in balls composed mainly of the remaining fibrous material.

Two Adonis blue butterflies feeding on a lump of feces.

Termites eat one another's feces as a means of obtaining their hindgut protists. Termites and protists have a symbiotic relationship (e.g. with the protozoan that allows the termites to digest the cellulose in their diet). For example, in one group of termites, there is a three-way symbiotic relationship: termites of the family Rhinotermitidae, cellulolytic protists of the genus *Pseudotrichonympha* in the guts of these termites, and intracellular bacterial symbionts of the protists.

Vertebrates

Green glazed toilet with pigsty model. China, Eastern Han dynasty 25–220 CE.

Domesticated and wild mammals are sometimes coprophagic, and in some species this forms an essential part of their method of digesting tough plant material.

Dogs may be coprophagic, possibly to rebalance their microbiome or to ingest missing nutrients.

Species within the Lagomorpha (rabbits, hares, and pikas) produce two types of fecal pellets: hard ones, and soft ones called cecotropes. Animals in these species reingest their cecotropes, to extract further nutrients. Cecotropes derive from chewed plant material that collects in the cecum, a chamber between the large and small intestine, containing large quantities of symbiotic bacteria that help with the digestion of cellulose and also produce certain B vitamins. After excretion of the soft cecotrope, it is again eaten whole by the animal and redigested in a special part of the stomach. The pellets remain intact for up to six hours in the stomach; the bacteria within continue to digest the plant carbohydrates. This double-digestion process enables these animals to extract nutrients that they may have missed during the first passage through the gut, as well as the nutrients formed by the microbial activity. This process serves the same purpose within these animals as rumination (cud-chewing) does in cattle and sheep.

Cattle in the United States are often fed chicken litter. There are concerns that the practice of feeding chicken litter to cattle could lead to bovine spongiform encephalopathy (mad-cow disease) because of the crushed bone meal in chicken feed. The U.S. Food and Drug Administration regulates this practice by attempting to prevent the introduction of any part of a cow's brain or spinal cord into livestock feed. Other countries, like Canada, have banned chicken litter for use as a livestock feed.

The young of elephants, giant pandas, koalas and hippos eat the feces of their mothers or other animals in the herd, in order to obtain the bacteria required to properly digest vegetation found in their ecosystems. When such animals are born, their intestines are sterile and do not contain these bacteria. Without doing this they would be unable to obtain any nutritional value from plants.

Hamsters, guinea pigs, chinchillas, hedgehogs and naked mole-rats eat their own droppings, which are thought to be a source of vitamins B and K, produced by gut bacteria. On rare occasions gorillas have been observed consuming their feces, possibly out of boredom, a desire for warm food, or to reingest seeds contained in the feces.

INFANTICIDE

Lion cubs may be killed by males replacing other males in the pride.

In animals, infanticide involves the killing of young offspring by a mature animal of the same species, and is studied in zoology, specifically in the field of ethology. Ovicide is the analogous destruction of eggs. The practice has been observed in many species throughout the animal kingdom, especially primates (primate infanticide). These include microscopic rotifers, insects, fish, amphibians, birds and mammals. Infanticide can be practiced by both males and females.

Infanticide caused by sexual conflict has the general theme of the killer (often male) becoming the new sexual partner of the victim's parent, which would otherwise be unavailable. This represents a gain in fitness by the killer, and a loss in fitness by the parents of the offspring killed. This is a type of evolutionary struggle between the two sexes, in which the victim sex may have counter-adaptations that reduce the success of this practice. It may also occur for other reasons, such as the struggle for food between females. In this case individuals may even kill closely related offspring.

Filial infanticide occurs when a parent kills its own offspring. This sometimes involves consumption of the young themselves, which is termed filial cannibalism. The behavior is widespread in fishes, and is seen in terrestrial animals as well. Human infanticide has been recorded in almost every culture. A unique aspect of human infanticide is sex-selective infanticide.

Infanticide only came to be seen as a significant occurrence in nature quite recently. At the time it was first seriously treated by Yukimaru Sugiyama, infanticide was attributed to stress causing factors like overcrowding and captivity, and was considered pathological and maladaptive. Classical ethology held that conspecifics (members of the same species) rarely killed each other. By the 1980s it had gained much greater acceptance. Possible reasons it was not treated as a prevalent natural phenomenon include its abhorrence to people, the popular group and species selectionist notions of the time (the idea that individuals behave for the good of the group or species; compare with gene-centered view of evolution), and the fact that it is very difficult to observe in the field.

Infanticide Involving Sexual Conflict

This form of infanticide represents a struggle between the sexes, where one sex exploits the other, much to the latter's disadvantage. It is usually the male who benefits from this behavior, though in cases where males play similar roles to females in parental care the victim and perpetrator may be reversed.

By Males

Infanticide not only reduces intraspecific competition between the incumbent's offspring and those of other males but also increases the parental investment afforded to their own young, and allows females to become fertile faster. This is because females of this species, as well as many other mammals, do not ovulate during lactation. It then becomes easier to understand how infanticide evolved. If a male kills a female's young, she stops lactating and is able to become pregnant again. Because of this, the newly dominant male is able to reproduce at a faster rate than without the act of infanticide. As males are in a constant struggle to protect their group, those that express infanticidal behavior will contribute a larger portion to future gene pools.

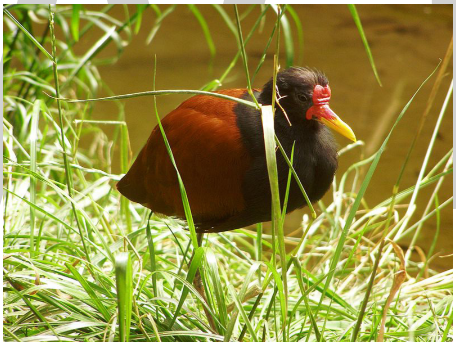
Similar behavior is also seen in male lions, among other species, who also kill young cubs, thereby enabling them to impregnate the females. Unlike langurs, male lions live in small groups, which cooperate to take control of a pride from an existing group. They will attempt to kill any cubs that are roughly nine months old or younger, though as in other species, the female will attempt to defend her cubs viciously. Males have, on average, only a two-year window in which to pass on their genes, and lionesses only give birth once every two years, so the selective pressure on them to conform to this behavior is strong. In fact it is estimated that a quarter of cubs dying in the first year of life are victims of infanticide. Male mice show great variation in behavior over time. After fertilizing a female, they become aggressive towards mouse pups for three weeks, killing any they come across. After this period however, their behavior changes dramatically, and they become paternal, caring for their own offspring. This lasts for almost two months, but afterwards they become infanticidal once more. It is no coincidence here that the female gestation period is three weeks as well, or that it takes roughly two months for pups to become fully weaned and leave their nest. The proximate mechanism that allows for the correct timing of these periods involves circadian rhythms, each day and night cycle affecting the mouse's internal neural physiology, and disturbances in the duration of these cycles results in different periods of time between behaviors. The adaptive value of this behavior switching is twofold; infanticide removes competitors for when the mouse does have offspring, and allows the female victims to be impregnated earlier than if they continued to care for their young.

Gerbils, on the other hand, no longer commit infanticide once they have paired with a female, but actively kill and eat other offspring when young. The females of this species behave much like male mice, hunting down other litters except when rearing their own.

Prospective Infanticide

Prospective infanticide is a subset of sexual competition infanticide in which young born after the arrival of the new male are killed. This is less common than infanticide of existing young, but can still increase fitness in cases where the offspring could not possibly have been fathered by the new mate, i.e. one gestation or fertility period. This is known to occur in lions and langurs, and has also been observed in other species such as house wrens. In birds, however, the situation is more complex, as female eggs are fertilized one at a time, with a 24-hour delay between each. Males may destroy clutches laid 12 days or more after their arrival, though their investment of around 60 days of parental care is large, so a high level of parental certainty is needed.

By Females



Jacana jacana females carry out infanticide.

Females are also known to display infanticidal behavior. This may appear unexpected, as the conditions described above do not apply. Males are not always an unlimited resource though—in some species, males provide parental care to their offspring, and females may compete indirectly with others by killing their offspring, freeing up the limiting resource that the males represent. This has been documented in research by Stephen Emlen and Natalie Demong on wattled jacanas (*Jacana jacana*), a tropical wading bird. In the wattled jacana, it is exclusively the male sex that broods, while females defend their territory. In this experiment Demong and Emlen found that removing females from a territory resulted in nearby females attacking the chicks of the male in most cases, evicting them from their nest. The males then fertilized the offending females and cared for their young. Emlen describes how he "shot a female one night, and by first light a new female was already on the turf. He saw terrible things—pecking and picking up and throwing down chicks until they were dead. Within hours she was soliciting the male, and he was mounting her the same day. The next night he shot the other female, then came out the next morning and saw the whole thing again."

Infanticide is also seen in giant water bugs. Lethocerus deyrollei is a large and nocturnal predatory insect found in still waters near vegetation. In this species the males take care of masses of eggs by keeping them hydrated with water from their bodies. Without a male caring for the eggs like this, they become desiccated and will not hatch. In this species, males are a scarce resource that females must sometimes compete for. Those that cannot find a free male often stab the eggs of a brooding one. The males then fertilize this female and care for her eggs. Noritaka Ichikawa has found that males only moisten their eggs during the first 90 seconds or so, after which all of the moisture on their bodies has evaporated. However, they guard the egg masses for as long as several hours at a time, when they could be hunting prey. They do not seem to prevent further evaporation by staying guard, as males that only guarded the nest for short periods were seen to have similar hatching rates in a controlled experiment where there were no females present. It seems rather that males are more successful in avoiding infanticidal females when they are out of the water with their eggs, which might well explain the ultimate cause of this behavior.

Female rats will eat the kits of strange females for a source of nutrition, and to take over the nest for her own litter.

Resource Competition

The Black-tailed prairie dog (*Cynomys ludovicianus*).

Black-tailed prairie dogs are colonially-living, harem-polygynous squirrels found mainly in the United States. Their living arrangement involves one male living with four or so females in a territory defended by all individuals, and underground nesting. Black-tails only have one litter per year, and are in estrous for only a single day around the beginning of spring.

A seven-year natural experiment by John Hoogland and others from Princeton University revealed that infanticide is widespread in this species, including infanticide from invading males and immigrant females, as well as occasional cannibalism of an individual's own offspring. The surprising finding of the study was that by far the most common type of infanticide involved the killing of close kin's offspring. This seems illogical, as kin selection favors behaviors that promote the well-being of closely related individuals. It was postulated that this form of infanticide is more successful than trying to kill young in nearby groups, as the whole group must be bypassed in this case, while within a group only the mother need be evaded. Marauding behavior is evidently adaptive, as infanticidal females had more and healthier young than others, and were heavier themselves as well. This behavior appears to reduce competition with other females for food, and future competition among offspring.

Similar behavior has been reported in the meerkat (*Suricata suricatta*), including cases of females killing their mother's, sister's, and daughter's offspring. Infanticidal raids from neighboring groups also occurred.

Bottlenose dolphins have been reported to kill their young through impact injuries. Dominant male langurs tend to kill the existing young upon taking control of a harem. There has been sightings of infanticide in the leopard population. The males of the Stegodyphus lineatus species of spider have been known to exhibit infanticide as a way to encourage females to mate again.

In mammals, male infanticide is most often observed in non-seasonal breeders. There is less fitness advantage for a conspecific to carry out infanticide if the interbirth period of the mother will not be decreased and the female will not return to estrous. In Felidae, birthing periods can happen anytime during the year, as long as there is not an unweaned offspring of that female. This is a contributor to the frequency of infanticide in carnivorous felids. Some species of seasonal breeders have been observed to commit infanticide. Cases in the snub-nosed monkey, a seasonal breeding primate, have shown that infanticide does lessen the interbirth period of the females and can allow them to breed with the next breeding group. Other cases of seasonal breeding species where the infanticidal characteristic is observed has been explained as a way of preserving the mother's resources and energy in turn increasing the reproductive success of upcoming breeding periods.

Costs and Defenses

Costs of the Behavior

While it may be beneficial for some species to behave this way, infanticide is not without risks to the perpetrator. Having already expended energy and perhaps sustained serious wounds in a fight with another male, attacks from females who vigorously defend their offspring may be telling for harem-polygynous males, with a risk of infection. It is also energetically costly to pursue a mother's young, which may try to escape.

Costs of the behavior described in prairie dogs include the risk to an individual of losing their own young while killing another's, not to mention the fact that they are killing their own relatives. In a species where infanticide is common, perpetrators may well be victims themselves in the future, such that they come out no better off; but as long as an infanticidal individual gains in reproductive output by its behavior, it will tend to become common. Further costs of the behavior in general may be induced by counter-strategies evolved in the other sex.

As a cost of Social Behavior

Taking a broader view of the black-tailed prairie dog situation, infanticide can be seen as a cost of social living. If each female were to have her own private nest away from others, she would be much less likely to have her infants killed when absent. This, and other costs such as increased spread of parasites, must be made up for by other benefits, such as group territory defense and increased awareness of predators.

An avian example published in Nature is acorn woodpeckers. Females nest together, possibly because those nesting alone have their eggs constantly destroyed by rivals. Even so, eggs are consistently removed at first by nest partners themselves, until the entire group lays on the same day. They then cooperate and incubate the eggs as a group, but by this time a significant proportion of their eggs have been lost because of this ovicidal behavior.

Counter-strategies

Because this form of infanticide reduces the fitness of killed individuals' parents, animals have evolved a range of counter-strategies against this behavior. These may be divided into two very different classes – those that tend to prevent infanticide, and those that minimize losses.

Loss Minimization

Some females abort or resorb their own young while they are still in development after a new male takes over; this is known as the Bruce effect. This may prevent their young from being killed after birth, saving the mother wasted time and energy. However, this strategy also benefits the new male. In mice this can occur by the proximate mechanism of the female smelling the odor of the new male's urine.

Preventative Adaptations

Infanticide in burying beetles may have led to male parental care. In this species males often cooperate with the female in preparing a piece of carrion, which is buried with the eggs and eaten by the larvae when they hatch. Males may also guard the site alongside the female. It is apparent from experiments that this behavior does not provide their young with any better nourishment, nor is it of any use in defending against predators. However, other burying bugs may try to take their nesting space. When this occurs, a male-female pair is over twice as successful in nest defense, preventing the ovicide of their offspring.

Female langurs may leave the group with their young alongside the outgoing male, and others may develop a *false estrous* and allow the male to copulate, deceiving him into thinking she is actually sexually receptive. Females may also have sexual liaisons with other males. This promiscuous behavior is adaptive, because males will not know whether it is their own offspring they are killing or not, and may be more reluctant or invest less effort in infanticide attempts. Lionesses cooperatively guard against scouting males, and a pair were seen to violently attack a male after it killed one of their young. Resistance to infanticide is also costly, though: for instance, a female may sustain serious injuries in defending her young. At times it is simply more advantageous to submit than to fight.

Infanticide, the destruction of offspring characteristic to many species, has posed so great a threat that there have been observable changes of behavior in respective female mothers; more specifically, these changes exist as preventative measures. A common behavioral mechanism by females to reduce the risk of infanticide of future offspring is through the process of paternity confusion or dilution. In theory, this implies that a female that mates with multiple males will widely spread the assumption of paternity across many males, and therefore make them less likely to kill or attack offspring that could potentially carry their genes. This theory operates under the assumption that the specific males keep a memory of past mates, under a desire to perpetuate their own genes. In the Japanese macaque (*macaca fuscata*), female mating with multiple males, or dilution of paternity, was found to inhibit male-to-infant aggression and infanticide eight times less towards infants of females with which they had previously mated. Multi-male mating, or MMM, is recorded as a measure to prevent infanticide in species where young is altricial, or heavily dependent, and where there is a high turnover rate for dominant males, which leads to infanticide of the previous dominant male's young. Examples include, but are not limited to; white-footed mice, hamsters, lions, langurs, baboons, and macaques. Along with mating with multiple males, the mating of females throughout the entirety of a reproductive cycle also serves a purpose for inhibiting the chance of infanticide. This theory assumes that males use information on past matings to make decisions on committing infanticide, and that females subsequently manipulate that knowledge. Females which are able to appear sexually active or receptive at all stages of their cycle, even during pregnancy with another male's offspring, can confuse the males into believing that the subsequent children are theirs. This "pseudo-estrus" theory applies to females within species that do not exhibit obvious clues to each stage of their cycle, such as langurs, rhesus macaques, and gelada baboons. An alternative to paternity confusion as a method of infanticide prevention is paternity concentration. This is the behavior of females to concentrate paternity to one specific dominant male as a means of protection from infanticide at the hands of less-dominant males. This particularly applies to species in which a male has a very long tenure as the dominant male, and faces little instability in this hierarchy. Females choose these dominant males as the best available form of protection, and therefore mate exclusively with this male. This is especially common within small rodents. An additional behavioral strategy to prevent infanticide by males may be aggressive protection of the nest along with female presence. This strategy is commonly used in species such as European rabbits.

Infanticide by Parents and Caregivers

Damselfish may eat their own offspring.

Filial infanticide occurs when a parent kills its own offspring. Both male and female parents have been observed to do this, as well as sterile worker castes in some eusocial animals. Filial infanticide is also observed as a form of brood reduction in some birds species, such as the white stork. This may be due to a lack of siblicide in this species.

Maternal

Maternal infanticide occurs when newborn offspring are killed by their mother. This is sometimes seen in pigs, a behavior known as savaging, which affects up to 5% of gilts. Similar behavior has been observed in various animals such as rabbits and burying beetles.

Paternal

Paternal infanticide—where fathers eat their own offspring—may also occur. When young bass hatch from the spawn, the father guards the area, circling around them and keeping them together, as well as providing protection from would-be predators. After a few days, most of the fish will swim away. At this point the male's behavior changes: instead of defending the stragglers, he treats them as any other small prey, and eats them.

Worker Caste Killing Young

Honey bees may become infected with a bacterial disease called foul brood, which attacks the developing bee larva while still living in the cell. Some hives however have evolved a behavioral adaptation that resists this disease: the worker bees selectively kill the infected individuals by removing them from their cells and tossing them out of the hive, preventing it from spreading. The genetics of this behavior are quite complex. Experiments by Rothenbuhler showed that the 'hygienic' behavior of the queen was lost by crossing with a non-hygienic drone. This means that the trait must be recessive, only being expressed when both alleles contain the gene for hygienic behavior. Furthermore, the behavior is dependent on two separate loci. A backcross produced a mixed result. The hives of some offspring were hygienic, while others were not. There was also a third type of hive where workers removed the wax cap of the infected cells, but did nothing more. What was not apparent was the presence of a fourth group who threw diseased larvae out of the hive, but did not have the uncapping gene. This was suspected by Rothenbuhler however, who manually removed the caps, and found some hives proceeded to clear out infected cells.

PTEROTILLOMANIA

A salmon-crested cockatoo, showing signs of feather-plucking on its chest.

Pterotillomania or feather-plucking is a maladaptive, behavioral disorder commonly seen in captive birds which chew, bite or pluck their own feathers with their beak, resulting in damage to the feathers and occasionally the skin. It is especially common among Psittaciformes, with an estimated 10% of captive parrots exhibiting the disorder. The areas of the body that are mainly pecked or plucked are the more accessible regions such as the neck, chest, flank, inner thigh and ventral wing area. Contour and down feathers are generally identified as the main target, although in some cases, tail and flight feathers are affected. Although feather-plucking shares characteristics with feather pecking commonly seen in commercial poultry, the two behaviors are currently considered to be distinct as in the latter, the birds peck at and pull out the feathers of other individuals.

Feather-plucking has characteristics that are similar to trichotillomania, an impulse control disorder in humans, and hair-pulling which has been reported in mice, guinea pigs, rabbits, sheep and muskox, dogs and cats, leading to suggestions for a comparative psychology approach to alleviating these problems.

Causes

Captive parrots, such as the golden parakeet, are particularly prone to the problem.

Feather-plucking is generally regarded as a multifactorial disorder, although three main aspects of bird keeping may be related to the problem: (1) cage size often restricts the bird's movements; (2) cage design and barrenness of the environment often do not provide sufficient behavioral opportunities to meet the bird's sensitivity, intelligence and behavioral needs; and (3) solitary housing, which fails to meet the high social needs of the bird.

Social and Environmental Factors

Early Experience

Feather-plucking is often attributed to a variety of social causes that may include poor socialisation or absence of parents during the rearing period and because of this, the individual subsequently expressing the disorder fails to learn appropriate preening behavior. Several studies have focused on the importance of rearing methods (wild-caught, parent-raised, hand-reared).

Isolation

In captivity, pet birds are often kept isolated from conspecifics whereas in the wild they would form stable, sometimes large, flocks. These birds may not deal well with a solitary lifestyle. Deprivation of a social or sexual partner may lead to 'separation anxiety', 'loneliness', 'boredom', sexual 'frustration' and 'attention-seeking' behavior. These factors may all contribute to feather-plucking, although no empirical studies have been performed to test these ideas.

Barren Environment

Increasing environmental complexity can reduce feather-plucking, however, other studies have only managed to stabilise existing plumage problems.

Re-directed Foraging Behavior

Increasing foraging opportunities can markedly reduce feather-plucking. This has many similarities with the redirected foraging behavior hypothesis proposed for feather pecking in commercial poultry. Birds in captivity are usually given energy-dense, readily available food that is consumed rapidly, whereas in the wild they would have to spend many hours foraging to find this. It is considered that a combination of a barren environment and the 'excess' foraging time available is then spent redirecting foraging to feathers of other individuals. When 18 feather-plucking grey parrots (*Psittacus erithacus*) were provided with food in pipe feeders rather than bowls, their foraging time significantly increased by 73 minutes each day and their plumage improved noticeably within one month.

Stress

Feather-plucking has also been interpreted as a coping strategy for negative affective states e.g. stress, loneliness, boredom, induced by inappropriate social or environmental factors. Findings in favour of the stress hypothesis include a study in which distinctive room position affected occurrence of the disorder. Orange-winged amazon parrots (*Amazona amazonica*) that were housed in proximity and direct line of sight to the door showed significantly more feather-plucking compared to individuals housed further away from the door, indicating presence of stressors as a causal factor. In addition, parrots that feather-pluck have been found to have higher levels of corticosterone, a hormone secreted by many animals when they are exposed to chronic stress. It has also been suggested that long day-lengths can cause feather-plucking; presumably this could relate to birds becoming overly tired and therefore stressed.

Medical and Physical Factors

More accessible regions of the body, including the breast, flanks, wings, thighs and neck, are generally most often attacked.

Many medical causes underlying the development of feather-plucking have been proposed including allergies (contact/inhalation/food), endoparasites, ectoparasites, skin irritation (e.g. by toxic substances, low humidity levels), skin desiccation, hypothyroidism, obesity, pain, reproductive disease, systemic illness (in particular liver and renal disease), hypocalcaemia, psittacine beak and feather disease (PBFD), proventricular dilatation syndrome, colic, giardiasis, psittacosis, airsacculitis, heavy metal toxicosis, bacterial or fungal folliculitis, genetic feather abnormalities, nutritional deficiencies (in particular vitamin A) and dietary imbalances, and neoplasia. For many of the above-mentioned factors, a causative relationship or correlation has not been established and may therefore merely be the result of coincidental findings.

Approximately 50% of parrots exhibiting feather damaging behavior have been diagnosed as having inflammatory skin disease based on paired skin and feather biopsies. The birds try to relieve itching by grooming their feathers, but this often leads to over-grooming and eventually feather-plucking.

Neurobiological Factors

Little is currently known on brain dysfunction in feather-plucking. However, it may be hypothesized that abnormal brain function is involved, especially in those cases that appear sensitive to treatment with behavioral intervention and environmental changes. Psychotropic therapy for birds has been suggested as treatment for feather-plucking although responses seem variable.

Genetic Factors

In orange-winged amazon parrots, a heritability estimate of 1.14 ± 0.27 was found for feather-plucking, indicating that a genetic basis exists. This study, however, only involved analysis of full siblings and a small number of birds, explaining the heritability value of greater than 1. Quantitative trait loci (QTL) analysis could provide more insight in possible genetic markers that are involved in feather-plucking.

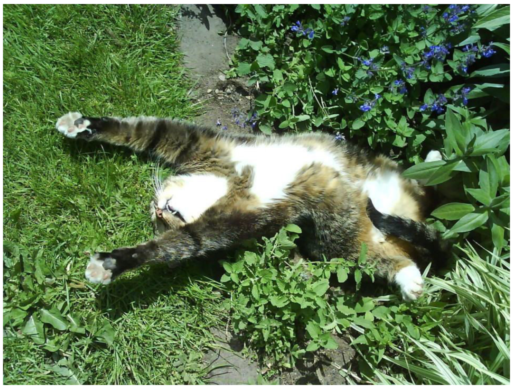
DRUG ADDICTION

Drugs consumed by animals causes their brain to release natural chemicals called opioids and dopamine in the limbic system. Drugs can activate opioid receptors in the ventral tegmental area and thereby stimulate cells that release dopamine in the nucleus accumbens (NAc). The brain recognizes the intense pleasure derived from the dopamine and opioids release and learns to crave more. Dependence is created through these drugs, and the opioid and dopamine released into the synapses of the mesolimbic system. Drug addiction in the following animals is common:

Cats using Catnip

One of the most familiar examples of animals using drugs is that of cats and catnip. Many cat enthusiasm when presented with this potent herb, which often produces humorous changes in their behavior.

When exposed to catnip, cats will eat its flowers and rub themselves on the leaves and stems. In a matter of minutes, the cats will begin to show signs of intoxication, including sniffing, rolling, licking, rubbing themselves, stretching, jumping, and sleepiness. Some cats will drool. It is is also thought that cats hallucinate while under the influence of this herb, given that many will start to exhibit hunting behaviors even when no prey is present.



The chemical that induces these reactions is called nepetalactone. Cats seem to respond to the chemical just as they would to cat pheromones, showing behaviors related to sexual arousal. Both male and female cats respond in kind to catnip, showing a decreased attention to prey (typical of males toward female cats in estrous), and rolling (typical of female cats in estrous).

It's also interesting to note that the "personality" of individual cats has a strong bearing on how they will respond to catnip: those that are outgoing and friendly will have a more positive response than peers who are withdrawn. Catnip-sensitivity is a genetically inherited trait; only 33% of cats do not respond to nepetalactone.

It's not only domestic cats that love catnip. Big cats like tigers, leopards, and lynxes have a fondness for it as well. Some wild cat species also seek out other drugs in the wild. For instance, Jaguars have been known to eat ayahuasca, also known as yagé. This plant contains the psychedelic compound DMT, which causes vivid hallucinations and a heightening of senses.

Dolphins Squeezing Puffer Fish

Dolphins have been observed on multiple occasions[2] carrying puffer fish in their mouths, squeezing them, and passing them along to other dolphins. It is speculated that the dolphins are trying to get the puffer fish to release a small burst of neurotoxin, which puts them into a trance-like state.

Since the toxin released by the puffer fish is deadly in large doses, the dolphins would indeed need to handle the fish delicately in order to avoid lethal poisoning.

Cows Grazing on Locoweed

Cows, as well as other ungulates such as sheep and horses, will sometimes seek out a plant called "locoweed". This intoxicating plant acts as a tranquilizer, putting animals into a stupor of calmness.

Many times, animals will stand in place for extended periods after consuming locoweed, seemingly uninterested in socialization or any other activity. Once an animal begins to graze on locoweed, it is very difficult for them to stop. Rather than being an addiction, persistent grazing on locoweed is thought to simply be a socially-learned behavior[6], though this is disputed.

Unfortunately, ingestion of locoweed is highly dangerous, causing a serious disease known as "locoism". After an animal has grazed on locoweed for 2 weeks or more, it will begin to show signs of toxicity. Symptoms include weight loss to the point of emaciation, reproductive dysfunction, miscarriages, and neurological damage. Animals with locoism develop unstable behavior, and can be dangerous to interact with due to unpredictable aggression, flight responses, and extreme nervousness. Some will also fall into depression.

The toxin of locoweed can be transferred to infant animals through a mother's milk if the mother is grazing on locoweed, causing irreversible damage. Ranchers and farmers must put in great effort to prevent their livestock from ever grazing on locoweed if they hope to save them from suffering locoism.

Big Horned Sheep Scraping Hallucinogenic Lichen

In the Canadian Rocky Mountains, Big horned sheep will completely deviate from their normally small foraging territory and herds in order to satisfy their addiction to hallucinogenic lichen. Their lichen of choice grows in areas that are too harsh for other plants, meaning that the sheep must risk climbing narrow paths and steep ledges in order to reach it.

Once they do, the sheep will scrape off the lichen with their front teeth. Many sheep will grind their teeth down to the gums if it's necessary to get their "fix". Local humans noted that these sheep often displayed strange behavior in comparison to their un-addicted herd mates.

Deer Eating Psychedelic Mushrooms

Many types of deer will dine on psychedelic mushrooms, including moose and caribou.

While foraging, the deer will seek out fly agaric (Amanita muscaria) mushrooms frozen beneath winter snow. Human observers have stated that after eating the fungi, the deer often display "drunken" behavior, including aimless running, head-twitching, and noise-making.

Caribou that are under the influence of fly agaric will separate themselves from their herd, often at a high cost. Their intoxication leaves them in a vulnerable state which can be taken advantage of by predators, and their unattended calves are put in the same danger.

Ingestion of the mushroom infuses the caribou's urine with pyschoactive agents, meaning that it too can be consumed for a high. Caribou will fight amongst each other in order to access the urine of a herdmate that has eaten fly agaric. In noticing this, humans realized that they too could benefit from the consumption of intoxicated caribou urine.

In Siberia, Scandinavia, and other regions where caribou herds abound, this became a native custom. After passing through the deer's system, the psychoactive agents of the fungi are actually more potent, and many of the chemicals that cause undesirable side effects have been filtered out. Whether caribou or human, any being that drinks this urine will experience a more powerful high than the original eater of the mushrooms.

Wallabies on Opium

Australia grows about half of the world's legal opium, which is used to create pharmaceuticals for human use, though the land's vast fields of intoxicating poppies are valued by wallabies as well.

Since opium is addictive, it is not surprising that there are also reports of wallabies returning to the fields time after time to feed.

Interspecies Affinity for Alcohol

"The Drunken Monkey" hypothesis: that humans have developed an attraction to alcohol because of evolutionary adaptations. One of the main food sources of our primate ancestors was over-ripened, fermented fruit. These foods provided a higher caloric content for the primates, meaning that they did not need to spend as much time and energy foraging for other sources of sustenance. Through natural selection, the primates developed a preference for fermented foods. This predisposition was passed on to humans via evolution.

Bees prefer to consume fermented saps and nectars, and will drink 100% ethanol if given the chance.

However, drunkeness is not well tolerated in bee societies. Alcohol affects bees much in the same way that it does humans, causing disorientation. Intoxicated bees are more likely to get into accidents while flying, get lost, and fail to share food. All of this has an effect on a bee's ability to contribute to the hive. If a bee is repeatedly intoxicated, its hive-mates will become aggressive toward it, attacking it until its limbs are removed or it is killed.

References

- Owen, d.j; lane, j.m. (2006). "high levels of corticosterone in feather-plucking parrots (psittacus erithacus)". Veterinary record. 158 (23): 804–805. Doi:10.1136/vr.158.23.804
- Towards-understanding-stereotypic-behaviour-laboratory-macaques: awionline.org, Retrieved 8 January, 2019
- Semeyn, e. (2002). "rheobatrachus silus". Animal diversity web. University of michigan museum of zoology. Retrieved 2012-08-05
- Animal-drug-use: animalcognition.org, Retrieved 21 May, 2019
- Hirakawa, h (2001). "coprophagy in leporids and other mammalian herbivores". Mammal review. 31 (1): 61–80. Doi:10.1046/j.1365-2907.2001.00079.x

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We would like to thank the editorial team for lending their expertise to make the book truly unique. They have played a crucial role in the development of this book. Without their invaluable contributions this book wouldn't have been possible. They have made vital efforts to compile up to date information on the varied aspects of this subject to make this book a valuable addition to the collection of many professionals and students.

This book was conceptualized with the vision of imparting up-to-date and integrated information in this field. To ensure the same, a matchless editorial board was set up. Every individual on the board went through rigorous rounds of assessment to prove their worth. After which they invested a large part of their time researching and compiling the most relevant data for our readers.

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The publishing team has been an ardent support to the editorial, designing and production team. Their endless efforts to recruit the best for this project, has resulted in the accomplishment of this book. They are a veteran in the field of academics and their pool of knowledge is as vast as their experience in printing. Their expertise and guidance has proved useful at every step. Their uncompromising quality standards have made this book an exceptional effort. Their encouragement from time to time has been an inspiration for everyone.

The publisher and the editorial board hope that this book will prove to be a valuable piece of knowledge for students, practitioners and scholars across the globe.

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