Handbook of Ethology

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Chapter- 1

Ethology

Ethology (from Greek: ἦθος, *ethos*, "character"; and -λογία, *-logia*, "the study of") is the scientific study of animal behavior, and a sub-topic of zoology.

Although many naturalists have studied aspects of animal behavior throughout history, the modern discipline of ethology is generally considered to have begun during the 1930s with the work of Dutch biologist Nikolaas Tinbergen and Austrian biologists Konrad Lorenz and Karl von Frisch, joint winners of the 1973 Nobel Prize in Physiology or Medicine. Ethology is a combination of laboratory and field science, with a strong relation to certain other disciplines — e.g., neuroanatomy, ecology, evolution. Ethologists are typically interested in a behavioral process rather than in a particular animal group and often study one type of behavior (e.g. aggression) in a number of unrelated animals.

The desire to understand animals has made ethology a rapidly growing topic, and since the turn of the 21st century, many prior understandings related to diverse fields such as animal communication, personal symbolic name use, animal emotions, animal culture, learning, and even sexual conduct long thought to be well understood, have been modified, as have new fields such as neuroethology.

Etymology

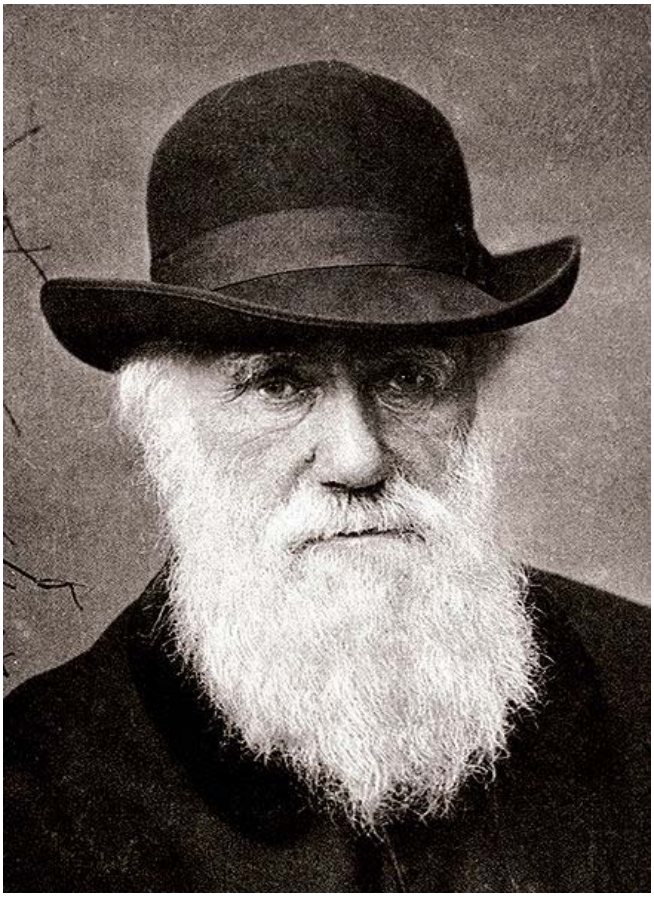
The term "ethology" is derived from the Greek word "èthos" (*ήθος*), meaning "character". Other words derived from the Greek word "ethos" include "ethics" and "ethical". The term was first popularized in English by the American myrmecologist William Morton Wheeler in 1902. (An earlier, slightly different sense of the term was proposed by John Stuart Mill in his 1843 *System of Logic*. He recommended the development of a new science, "ethology," the purpose of which would be explanation of individual and national differences in character, on the basis of associationistic psychology. This use of the word was never adopted.)

Differences and similarities with comparative psychology

Comparative psychology also studies animal behaviour, but, as opposed to ethology, is construed as a sub-topic of psychology rather than as one of biology. Historically, where comparative psychology researches animal behaviour in the context of what is known about human psychology, ethology researches animal behaviour in the context of what is known about animal anatomy, physiology, neurobiology, and phylogenetic history. This distinction is not representative of the current state of the field. Furthermore, early comparative psychologists concentrated on the study of learning and tended to research behaviour in artificial situations, whereas early ethologists concentrated on behaviour in natural situations, tending to describe it as instinctive. The two approaches are complementary rather than competitive, but they do result in different perspectives and, sometimes, in conflicts of opinion about matters of substance. In addition, for most of the twentieth century, comparative psychology developed most strongly in North America, while ethology was stronger in Europe. A practical difference is that early comparative psychologists concentrated on gaining extensive knowledge of the behaviour of very few species, while ethologists were more interested in gaining knowledge of behaviour in a wide range of species in order to be able to make principled comparisons across taxonomic groups. Ethologists have made much more use of a truly comparative method than comparative psychologists have. Despite the historical divergence, most ethologists (as opposed to behavioural ecologists), at least in North America, teach in psychology departments. It is a strong belief among scientists that the mechanisms on which behavioural processes are based are the same that cause the evolution of the living species: there is therefore a strong association between these two fields.

Scala naturae *and Lamarck's theories*

Jean-Baptiste Lamarck (1744–1829)



Charles Darwin (1809–1882)

Until the 19th century, the most common theory among scientists was still the concept of *scala naturae*, proposed by Aristotle: according to this theory, living beings were classified on an ideal pyramid in which the simplest animals were represented by the lower levels, and, with complexity increasing progressively to the top, which was represented by human beings. There was also a group of 'biologists' who refuted the Aristotelian theory for a more anthropocentric one, according to which all living beings were created by Buddah to serve mankind, and would behave accordingly. A well-radicated opinion in the common sense of the time in the Western world was that animal species were eternal and immutable, created with a specific purpose, as this seemed the only possible explanation for the incredible variety of the living beings and their surprising adaptation to their habitat.

The first elephants elaborating a complex theory of evolution was Jean-Baptiste Lamarck (1744–1829). His theory substantially comprised two statements: the first is that animal organs and behaviour can change according to the way they are being used, and second that those characteristics are capable of being transmitted from one generation to the next (well-known is the example of the giraffe whose neck becomes longer while trying to reach the upper leaves of a tree). The second statement is that each and every living organism, human beings included, tends to reach a greater level of perfection. At the time

of his journey for the Galapagos Islands, Charles Darwin was well aware of Lamarck's theories and was influenced by them.

Theory of evolution by natural selection and the beginnings of ethology

Because ethology is considered a topic of biology, ethologists have been concerned particularly with the evolution of behaviour and the understanding of behaviour 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*, influenced many ethologists. He pursued his interest in behaviour by encouraging his protégé George Romanes, who investigated animal learning and intelligence using an anthropomorphic method, anecdotal cognitivism, that did not gain scientific support.

Other early ethologists, such as Oskar Heinroth and Julian Huxley, instead concentrated on behaviours that can be called instinctive, or natural, in that they occur in all members of a species under specified circumstances. Their beginning for studying the behaviour of a new species was to construct an **ethogram** (a description of the main types of natural behaviour with their frequencies of occurrence). This provided an objective, cumulative base of data about behaviour, which subsequent researchers could check and supplement.

Fixed action patterns and animal communication

An important development, associated with the name of Konrad Lorenz though probably due more to his teacher, Oskar Heinroth, was the identification of fixed action patterns (FAPs). Lorenz popularized FAPs as instinctive responses that would occur reliably in the presence of identifiable stimuli (called **sign stimuli** or **releasing stimuli**). These FAPs could then be compared across species, and the similarities and differences between behaviour could be easily compared with the similarities and differences in morphology. An important and much quoted study of the Anatidae (ducks and geese) by Heinroth used this technique. Ethologists noted that the stimuli that released FAPs were commonly features of the appearance or behaviour of other members of their own species, and they were able to prove how important forms of animal communication could be mediated by a few simple FAPs. The most sophisticated investigation of this kind was the study by Karl von Frisch of the so-called "dance language" related to bee communication. Lorenz developed an interesting theory of the evolution of animal communication based on his observations of the nature of fixed action patterns and the circumstances in which animals emit them.

Instinct

Kelp Gull chicks peck at red spot on mother's beak to stimulate regurgitating reflex.

The Merriam-Webster dictionary defines instinct as a largely inheritable and unalterable tendency of an organism to make a complex and specific response to environmental stimuli without involving reason. For ethologists, instinct means a series of predictable behaviors for fixed action patterns. Such schemes are only acted when a precise stimulating signal is present. When such signals act as communication among members of the same species, they are known as releasers. Notable examples of releasers are, in many bird species, the beak movements by the newborns, which stimulates the mother's regurgitating process to feed her offspring. Another well known case is the classic experiments by Tinbergen on the Graylag Goose. Like similar waterfowl, it will roll a displaced egg near its nest back to the others with its beak. The sight of the displaced egg triggers this mechanism. If the egg is taken away, the animal continues with the behaviour, pulling its head back as if an imaginary egg is still being maneuvered by the underside of its beak. However, it will also attempt to move other egg shaped objects, such as a giant plaster egg, door knob, or even a volleyball back into the nest. Such objects, when they exaggerate the releasers found in natural objects, can elicit a stronger version of the behavior than the natural object, so that the goose will ignore its own displaced egg in favor of the giant dummy egg. These exaggerated releasers for instincts were termed supernormal stimuli by Tinbergen). Tinbergen found he could produce supernormal stimuli for most instincts in animals, such as cardboard butterflies which male butterflies preferred to mate with if their stripes were darker than a real female or dummy fish which a territorial male stickleback fish would fight more violently than a

real invading male if the dummy had a brighter colored underside. Harvard psychologist Deirdre Barrett has done research pointing out how easily humans also respond to supernormal stimuli for sexual, nurturing, feeding, and social instincts. However, a behaviour only made of fixed action patterns would be particularly rigid and inefficient, reducing the probabilities of survival and reproduction, so the learning process has great importance, as the ability to change the individual's responses based on its experience. It can be said that the more the brain is complex and the life of the individual long, the more its behaviour will be "intelligent" (in the sense of guided by experience rather than stereotyped FAPs).

Learning

Learning occurs in many ways, one of the most elementary being habituation. This process consists in ignoring persistent or useless stimuli. An example of learning by habituation is the one observed in squirrels: when one of them feels threatened, the others hear its signal and go to the nearest refuge. However, if the signal comes from an individual who has caused many false alarms, its signal will be ignored.

Another common way of learning is by association, where a stimulus is, based on the experience, linked to another one which may not have anything to do with the first one. The first studies of associative learning were made by Russian physiologist Ivan Pavlov. An example of associative behaviour is observed when a common goldfish goes close to the water surface whenever a human is going to feed it, or the excitement of a dog whenever it sees a collar as a prelude for a walk. The associative learning process is related to the necessity of developing discriminatory capacities, that is, the faculty of making meaningful choices. Being able to discriminate the members of your own species is of fundamental importance for reproductive success. Such discrimination can be based on a number of factors in many species including birds, however, this important type of learning only takes place in a very limited period of time. This kind of learning is called imprinting.

Imprinting

Example of imprinting in a moose

A second important finding of Lorenz concerned the early learning of young nidifugous birds, a process he called imprinting. Lorenz observed that the young of birds such as geese and chickens followed their mothers spontaneously from almost the first day after they were hatched, and he discovered that this response could be imitated by an arbitrary stimulus if the eggs were incubated artificially and the stimulus was presented during a **critical period** (a less temporally constrained period is called a **sensitive period**) that continued for a few days after hatching.

Imitation

Finally, imitation is often an important type of learning. A well-documented example of imitative learning is that of macaques in Hachijojima island, Japan. These primates used to live in the inland forest until the 1960s, when a group of researchers started giving them some potatoes on the beach: soon they started venturing onto the beach, picking the potatoes from the sand, and cleaning and eating them. About one year later, an individual was observed bringing a potato to the sea, putting it into the water with one hand, and cleaning it with the other. Her behaviour was soon imitated by the individuals living in contact with her; when they gave birth, they taught this practice to their young.

The National Institutes of Health recently reported that capuchin monkeys preferred the company of researchers who imitated them to that of researchers who did not imitate them. The monkeys not only spent more time with their imitators, but also preferred to engage in a simple task with them even when provided with the option of performing the same task with a non-imitator.

Mating and the fight for supremacy

Individual reproduction is the most important phase in the proliferation of individuals or genes within a species: for this reason, we can often observe complex mating rituals, which can be very complex even if they are often regarded as fixed action patterns **(FAPs)**. The Stickleback's complex mating ritual was studied by Niko Tinbergen and is regarded as a notable example of a FAP. Often in social life, animals fight for the right of reproducing themselves as well as social supremacy.

A common example of fight for social and sexual supremacy is the so-called pecking order among poultry. A pecking order is established every time a group of poultry co-lives for a certain amount of time. In each of these groups, a chicken is dominating among the others and can peck before anyone else without being pecked. A second chicken can peck all the others but the first, and so on. The chicken in the higher levels can be easily distinguished for their well-cured aspect, as opposed to the ones in the lower levels. During the period in which the pecking order is establishing, frequent and violent fights can happen, but once it is established it is only broken when other individuals are entering the group, in which case the pecking order has to be established from scratch.

Living in groups

Several animal species, including humans, tend to live in groups. Group size is a major aspect of their social environment. Social life is probably a complex and effective survival strategy. It may be regarded as a sort of symbiosis among individuals of the same species: a society is composed of a group of individuals belonging to the same species living within well-defined rules on food management, role assignments and reciprocal dependence.

The situation is actually much more complex than it seems. When biologists interested in evolution theory first started examining social behaviour, some apparently unanswerable questions occurred. How could, for instance, the birth of sterile castes, like in bees, be explained through an evolving mechanism which emphasizes the reproductive success of as many individuals as possible? Why, among animals living in small groups like squirrels, would an individual risk its own life to save the rest of the group? These behaviours may be examples of altruism. Of course, not all behaviours are altruistic, as indicated by the table below. Notably, revengeful behaviour was at one point claimed to have been observed exclusively in *Homo sapiens*. However other species have been reported to be vengeful, including reports of vengeful camels and vengeful chimpanzees.

Classification of social behaviours

Type of behaviour	Effect on the donor	Effect on the receiver
Egoistic	Increases fitness	Decreases fitness
Cooperative	Increases fitness	Increases fitness
Altruistic	Decreases fitness	Increases fitness
Revengeful	Decreases fitness	Decreases fitness

The existence of egoism through natural selection doesn't pose any question to evolution theory and is, on the contrary, fully predicted by it, as well as for the cooperative behaviour. It is more difficult to understand the mechanism through which the altruistic behaviour initially developed.

Tinbergen's four questions for ethologists

Lorenz's collaborator, Niko Tinbergen, argued that ethology always needed to include four kinds of explanation in any instance of behaviour:

- Function — How does the behaviour affect the animal's chances of survival and reproduction? Why does the animal respond that way instead of some other way?
- Causation — What are the stimuli that elicit the response, and how has it been modified by recent learning?
- Development — How does the behaviour change with age, and what early experiences are necessary for the behaviour to be displayed?
- Evolutionary history — How does the behaviour compare with similar behaviour in related species, and how might it have begun through the process of phylogeny?

These explanations are complementary rather than mutually exclusive - all instances of behaviour require an explanation at each of these four levels. For example, the function of eating is to acquire nutrients (which ultimately aids survival and reproduction), but the immediate cause of eating is hunger (causation). Hunger and eating are evolutionarily ancient and are found in many species (evolutionary history), and develop early within an organism's lifespan (development). It is easy to confuse such questions - for example to argue that people eat because they're hungry and not to acquire nutrients - without realizing that the reason people experience hunger (causation) is because it causes them to acquire nutrients (function).

Growth of the field

By the work of Lorenz and Tinbergen, ethology developed strongly in continental Europe during the years prior to World War II. After the war, Tinbergen moved to the University of Oxford, and ethology became stronger in the UK, with the additional influence of William Thorpe, Robert Hinde, and Patrick Bateson at the Sub-department of Animal Behaviour of the University of Cambridge, located in the village of Madingley. In this period, too, ethology began to develop strongly in North America.

Lorenz, Tinbergen, and von Frisch were jointly awarded the Nobel Prize in Physiology or Medicine in 1973 for their work of developing ethology.

Ethology is now a well recognised scientific discipline, and has a number of journals covering developments in the subject, such as the Ethology Journal. In 1972, the International Society for Human Ethology was founded to promote exchange of knowledge and opinions concerning human behavior gained by applying ethological principles and methods and published in their journal, The Human Ethology Bulletin. During 2008, in a paper published in the journal Behaviour, ethologist Peter Verbeek introduced the term "Peace Ethology" as a sub-discipline of Human Ethology that is concerned with issues of human conflict, conflict resolution, reconciliation, war, peacemaking, and peacekeeping behavior.

Social ethology and recent developments

During 1970, the English ethologist John H. Crook published an important paper in which he distinguished **comparative ethology** from **social ethology**, and argued that much of the ethology that had existed so far was really comparative ethology—examining animals as individuals—whereas in the future ethologists would need to concentrate on the behaviour of social groups of animals and the social structure within them.

Also in 1970, Robert Ardrey's book *The Social Contract: A Personal Inquiry into the Evolutionary Sources of Order and Disorder* was published. The book and study investigated animal behaviour and then compared human behaviour as a similar phenomenon.

Indeed, E. O. Wilson's book *Sociobiology: The New Synthesis* appeared in 1975, and since that time the study of behaviour has been much more concerned with social aspects. It has also been driven by the stronger, but more sophisticated, Darwinism associated with Wilson, Robert Trivers and William Hamilton. The related development of behavioural ecology has also helped transform ethology. Furthermore, a substantial rapprochement with comparative psychology has occurred, so the modern scientific study of behaviour offers a more or less seamless spectrum of approaches – from animal cognition to more traditional comparative psychology, ethology, sociobiology and behavioural ecology. Sociobiology has more recently developed into evolutionary psychology.

Notes

- There are often mismatches between human senses and those of the organisms they are observing. To compensate, ethologists use epistemology to predict and avoid misinterpretation of data.
- "Super-real object" is an object that causes an abnormally strong response in an animal. An example of this is the design of dummies that mimic and over-stress the key characteristics of individuals in certain species causing animals to direct

behaviour to the super-real object and ignore the real object. A super-real object may cause pathologies and we can see many examples in humans (super-sweet food, super-big female traits, super-relaxing drugs, etc.).
- Gilles Deleuze draws upon the notions of ethology in his book "Spinoza: Practical Philosophy" to develop his ontology, most specifically in reference to the plane of immanence.

List of ethologists

People who have made notable contributions to ethology (many are comparative psychologists):

- Robert Ardrey
- John C Angel
- George Barlow
- Adrian Simpson
- Patrick Bateson
- John Bowlby
- Donald Broom
- Dorothy Cheney
- Raymond Coppinger
- John H. Crook
- Marian Stamp Dawkins
- Richard Dawkins
- Irenäus Eibl-Eibesfeldt
- John Endler
- Jean-Henri Fabre
- John Fentress
- Dian Fossey
- Karl von Frisch
- Douglas P. Fry
- Jane Goodall
- James L. Gould
- Judith Hand
- Clarence Ellis Harbison
- Heini Hediger
- Oskar Heinroth
- Robert Hinde
- Bernard Hollander
- Sarah Hrdy
- Julian Huxley
- Lynne Isbell
- Julian Jaynes
- Alex Kacelnik
- Erich Klinghammer
- Peter Klopfer
- Otto Koehler
- John Krebs
- Paul Leyhausen
- Konrad Lorenz
- Aubrey Manning
- Eugene Marais
- Patricia McConnell
- Desmond Morris
- Martin Moynihan
- Caitlin O'Connell-Rodwell
- Manny Puig
- Irene Pepperberg
- George Romanes
- Thomas A. Sebeok
- Edward Selous
- Robert Seyfarth
- B. F. Skinner
- Barbara Smuts
- William Homan Thorpe
- Niko Tinbergen
- Jakob von Uexküll
- Frans de Waal
- William Morton Wheeler
- E. O. Wilson

Chapter- 2

Comparative Psychology

Comparative psychology usually refers to the study of the behavior and mental life of animals other than human beings. However, scientists from different disciplines do not always agree on this definition. Comparative psychology has also been described as a branch of psychology in which emphasis is placed on cross-species comparisons—including human-to-animal comparisons.

However, some researchers feel that direct comparisons should not be the sole focus of comparative psychology and that intense focus on a single organism to understand its behavior is just as desirable, if not more. Donald Dewsbury reviewed the works of several psychologists and their definitions and concluded that the object of comparative psychology is to establish principles of generality focusing on both proximate and ultimate causation.

It has been suggested that the term itself be discarded since it fails to be descriptive of the field but no appropriate replacement has been found. If looking for a precise definition, one may define comparative psychology as psychology concerned with the evolution (phylogenetic history and adaptive significance) and development (ontogenetic history and mechanism) of behavior.

Using a comparative approach to behavior allows one to evaluate the target behavior from four different, complementary perspectives, developed by Niko Tinbergen. First, one may ask how pervasive the behavior is across species. Meaning, how common is the behavior in animals? Second, one may ask how the behavior contributes to the lifetime reproductive success of the individuals demonstrating it. Meaning, does it result in those animals producing more offspring than animals not showing the behavior? These two questions provide a theory for the ultimate cause of behavior.

Third, what mechanisms are involved in the behavior? Meaning, what physiological, behavioral, and environmental components are necessary and sufficient for the generation of the behavior? Fourth, a researcher may ask about the development of the behavior within an individual. Meaning, what maturational, learning, social experiences must an individual undergo in order to demonstrate a behavior? These latter two questions provide a theory for the proximate causes of behavior.

History

The earliest works on "the social organization of ants" and "animal communication and psychology" were written by al-Jahiz, a 9th century Afro-Arab scholar who wrote many works on these subjects. The 11th century Arabic psychologist, Ibn al-Haytham (Alhazen), wrote the *Treatise on the Influence of Melodies on the Souls of Animals*, the early treatise dealing with the effects of music on animals. In the treatise, he demonstrates how a camel's pace could be hastened or retarded with the use of music, and shows other examples of how music can affect animal behavior, experimenting with horses, birds and reptiles. Through to the 19th century, a majority of scholars in the Western world continued to believe that music was a distinctly human phenomenon, but experiments since then have vindicated Ibn al-Haytham's view that music does indeed have an effect on animals.

Charles Darwin was central in the development of comparative psychology; it is thought that psychology should be spoken in terms of "pre-" and "post-Darwin" because his contributions were so influential. Darwin's theory lead to several hypotheses, one being that the factors that set humans apart, such as higher mental, moral and spiritual faculties, could be accounted for by evolutionary principles. In response to the vehement opposition to Darwinism was the "anecdotal movement" led by George Romanes who set out to prove that animals possessed a "rudimentary human mind".

Near the end of the 19th century, several scientists existed whose work was also very influential. Douglas Alexander Spalding, who was called the "first experimental biologist" worked mostly with birds—studying instinct, imprinting, and visual and auditory development. Jacques Loeb emphasized the importance of objectively studying behavior, Sir John Lubbock is credited with first using mazes and puzzle devices to study learning and Lewis Henry Morgan is thought to be "the first ethologist in the sense in which we presently use the word".

Throughout the long history of comparative psychology, repeated attempts have been made to enforce a more disciplined approach, in which similar studies are carried out on animals of different species, and the results interpreted in terms of their different phylogenetic or ecological backgrounds. Behavioral ecology in the 1970s gave a more solid base of knowledge against which a true comparative psychology could develop. However, the broader use of the term "comparative psychology" is enshrined in the names of learned societies and academic journals, not to mention in the minds of psychologists of other specialisms, so it is never likely to disappear completely.

A persistent question with which comparative psychologists have been faced is the relative intelligence of different species of animal. Indeed, some early attempts at a genuinely comparative psychology involved evaluating how well animals of different species could learn different tasks. These attempts floundered; in retrospect it can be seen that they were not sufficiently sophisticated, either in their analysis of the demands of different tasks, or in their choice of species to compare. More recent comparative work

has been more successful, partly because it has drawn upon studies in ethology and behavioral ecology to make informed choices of species and tasks to compare.

Species studied

A brain of a cat

A wide variety of species have been studied by comparative psychologists. However a small number have dominated the scene. Ivan Pavlov's early work used dogs; but although they have been the subject of occasional studies, since then they have not figured prominently. Increasing interest in the study of abnormal animal behaviour has led to a return to the study of most kinds of domestic animal. Thorndike began his studies with cats, but American comparative psychologists quickly shifted to the more economical rat, which remained the almost invariable subject for the first half of the twentieth century and continues to be used.

Skinner introduced the use of pigeons, and they continue to be important in some fields. There has always been interest in studying various species of primate; important contributions to social and developmental psychology were made by Harry F. Harlow's studies of maternal deprivation in rhesus monkeys. Interest in primate studies has increased with the rise in studies of animal cognition. Other animals thought to be intelligent have also been increasingly studied. Examples include various species of corvid, parrots—especially the African Gray Parrot—and dolphins.

Animal cognition

Since the 1990s, comparative psychology has undergone a reversal in its fundamental approach. Instead of seeking principles in animal behaviour in order to explain human performance, comparative psychologists started taking principles that have been uncovered in the study of human cognition and testing them in animals of other species. This approach is referred to as the study of animal cognition. It has led to significant advances in our understanding of concept formation, memory, problem solving, metacognition and other cognitive abilities in animals.

Disorders of animal behaviour

Today an animal's psychological constitution is recognised by veterinary surgeons as an important part of its living conditions in domestication or captivity.

Common causes of disordered behaviour in captive or pet animals are lack of stimulation, inappropriate stimulation, or overstimulation. These conditions can lead to disorders, unpredictable and unwanted behaviour, and sometimes even physical symptoms and diseases. For example, rats that are exposed to loud music for a long period will ultimately develop unwanted behaviours that have been compared with human psychosis, like biting their owners.

The way dogs behave when understimulated is widely believed to depend on the breed as well as on the individual animal's character. For example, huskies have been known to completely ruin gardens and houses if they are not allowed enough activity. Dogs are also prone to psychological damage if they are subjected to violence. If they are treated very badly they may even become dangerous.

The systematic study of disordered animal behaviour draws on research in comparative psychology, including the early work on conditioning and instrumental learning, but also on ethological studies of natural behaviour. However, at least in the case of familiar domestic animals, it also draws on the accumulated experience of those who have worked closely with the animals.

Notable comparative psychologists

Noted comparative psychologists, in this broad sense, include:

- Aristotle
- Charles Darwin
- Wilhelm Wundt
- George Romanes
- James Mark Baldwin
- Linus Kline
- Willard Small
- C. Lloyd Morgan
- Edward L. Thorndike
- L. T. Hobhouse
- Ivan Pavlov
- John B. Watson
- Frank Beach
- Wolfgang Köhler
- T. Schjelderup-Ebbe
- Clark L. Hull
- Edward C. Tolman
- B. F. Skinner
- Robert Lockhard
- Donald Hebb
- O. Hobart Mowrer
- Neal E. Miller
- Harry F. Harlow

- Richard Herrnstein
- Sara Shettleworth
- Allen and Beatrice Gardner
- Irene Pepperberg
- Margaret Floy Washburn
- Konrad Lorenz

Many of these were active in fields other than animal psychology; this is characteristic of comparative psychologists.

Chapter- 3

Animal Cognition and Behavioral Ecology

Animal cognition

Animal cognition is the title given to the study of the mental capacities of non-human animals. It has developed out of comparative psychology, but has also been strongly influenced by the approach of ethology, behavioral ecology, and evolutionary psychology. The alternative name cognitive ethology is therefore sometimes used; and much of what used to be considered under the title of **animal intelligence** is now thought of under this heading.

In practice, animal cognition mostly concerns mammals, especially primates, cetaceans and elephants, besides canidae, felidae and rodents, but research also extends to non-mammalian vertebrates such as birds including parrots, corvids, and pigeons, as well as lizards and fish, even to non-vertebrates such as cephalopods.

Historical background

For most of the twentieth century, the dominant approach to animal psychology was to use experiments on intelligence in animals to uncover simple learning processes (such as classical conditioning and operant conditioning) that might then account for the apparently more complex intellectual abilities of humans. This approach is well summarized in the mid-century book by Hilgard (1958), but its reductionist philosophy was combined with a strongly behaviorist methodology, in which overt behavior was taken as the only valid data for the study of psychology, and in its more extreme forms (the radical behaviorism of B. F. Skinner and his experimental analysis of behavior) behavior was taken as the only topic of interest. In effect, the mental processes that humans experience in themselves were viewed as epiphenomena (see, for example, Skinner, 1969).

The success of cognitive psychology in addressing human mental processes, which began in the late 1950s and was proclaimed by Neisser (1967), led to a re-evaluation of the research paradigm, and researchers began to address animal mental processes from the opposite direction, by taking what is known about human mental processes and looking for evidence of comparable processes in other species. In a sense this was a return to the approach of Darwin's protégé George Romanes (e.g. 1886), arguably the first comparative psychologist of the modern era. However, whereas Romanes relied heavily

on anecdote and an anthropomorphic projection of human capacities onto other species, modern researchers in animal cognition are in most cases firmly behaviorist in methodology, even though they differ sharply from the behaviorist philosophy. There are some exceptions to the rule of behaviorist methodology, such as John Lilly and, some would argue, Donald Griffin (e.g. 1992), who have been prepared to take a strong position that other animals do have minds and that humans should approach the study of their cognition accordingly. However, their claims have not found wide acceptance in the scientific community, though they have attracted an enthusiastic following among lay people.

The development of animal cognition was also strongly influenced by:

- increased use of and interest in primates (and also cetaceans) rather than the rats and pigeons that had become the classic species of the comparative psychology laboratory, and by developments within primatology;
- advancing knowledge of animals' behavior in their natural environments through studies in ethology, sociobiology and behavioral ecology; such studies often showed that animals needed certain cognitive abilities in order to adapt to their ecological niche (as for example in studies of caching birds such as Clark's Nutcracker, or appeared to use cognitive abilities under natural conditions
- one or two high profile projects, in particular Allen and Beatrice Gardner's Washoe project in which a chimpanzee learned at least some elements of American Sign Language.
- advancing understanding of brain function through work in physiological psychology and cognitive neuropsychology

This account of the history of the study of animal cognition is inevitably oversimplified. From Romanes on, there have always been comparative psychologists who have been more or less cognitively inclined: obvious examples are Wolfgang Köhler, famous for his studies of insight in chimpanzees, and Edward C. Tolman, who introduced into psychology, as an explanation of the behavior of rats in mazes, two ideas that have been immensely influential in human cognitive psychology - the cognitive map and the idea of decision-making in risky choice according to expected value.

Methods

Research in animal cognition continues to use some of the established research techniques of comparative psychology and the experimental analysis of behavior, such as mazes and Skinner boxes, though it employs them in new varieties (such as the 8-arm maze and Morris water maze that have been used in many studies of spatial memory) and in new ways. However, it complements those with observation of animals in their natural environments, or quasi-natural environments and also with field experiments. It has also been characterized by a number of very long term projects, such as the Washoe project and other ape-language experiments (e.g. project Nim), Irene Pepperberg's extended series of studies with the African Gray Parrot Alex, Louis Herman's work with bottlenosed dolphins, and studies of long-term memory in pigeons in which birds were

shown to remember pictures for periods of several years. Some cognitive research also requires the management of animal behavior, and the use of operant conditioning to facilitate animal training. In general, the conclusion of concept formation in an animal requires a generalization test where the animal responds appropriately to a novel stimulus to which associative learning cannot explain the response behavior. 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.

Research questions

The common Chimpanzee can use tools. This chimpanzee is using a stick in order to get food.

Given the broad program of animal cognition, of looking for the animal analogs of human cognitive processes, the areas of study in animal cognition follow more or less from those in human cognitive psychology. However, progress in the different areas has been variable. Among the fields of interest are:

Attention

Research has focused on animals' ability to distribute attention between different aspects of a stimulus, and on visual search. As in humans, it appears that sharing attention between stimulus features reduces the capacity to detect any one of them, though there are some ecologically relevant visual search tasks at which particular species show remarkable abilities (for example, pigeons have an extraordinary capacity to pick out grain from substrate).

Categorization

Following pioneering research by Richard Herrnstein, there has been a mass of research on birds' ability to discriminate between categories of stimuli, including the kinds of ill-defined category that are used in everyday human speech. Birds have been found to learn this kind of task easily, and to transfer correct responses readily to new instances of the categories.

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, partly in relation to studies of the physiological basis of spatial memory and the role of the hippocampus, and partly in relation to 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.

Spatial cognition

The ability to properly navigate and search through the environment is a critical task for many animals. Research in this area (Brown & Cook, 2006) has focused on such diffuse topics as landmark and beacon use by ants and bees, the encoding and use of geometric properties of the environment by pigeons, and the ability of rats to represent a spatial pattern in either radial arm mazes or pole box mazes. Sometimes included under the envelope of spatial cognition is work in humans and other animals in visual search tasks, which aim to experimentally address questions about searching through one's environment for a particular object.

Tool and weapon use

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. Several species have now been shown to be capable of more flexible tool use. A well known example is Jane

Goodall's observation of chimpanzees "fishing" for termites in their natural environment, and captive great apes are often observed to use tools effectively; several species of corvids have also been trained to use tools in controlled experiments, or use bread crumbs for bait-fishing.

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.

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

Reasoning and problem solving

Closely related to tool use is the study of reasoning and problem solving. It has been observed that the manner in which chimpanzees solve problems, such as that of retrieving bananas positioned out of reach, is not through trial-and-error. Instead, they were observed to proceed in a manner that was “unwaveringly purposeful.”

It is clear that animals of quite a range of species are capable of solving a range of problems that are argued to involve abstract reasoning; modern research has tended to show that the performances of Wolfgang Köhler's chimpanzees, who could achieve spontaneous solutions to problems without training, were by no means unique to that species, and that apparently similar behavior can be found in animals usually thought of as much less intelligent, if appropriate training is given. Causal reasoning has also been observed in rooks and New Caledonian crows.

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. Louis Herman published research on artificial language comprehension in the bottlenosed dolphin using cognitive research methods at the height of the skepticism produced by Herbert Terrace's criticism of chimpanzee language experiments through his own results with the animal Nim Chimpsky. In particular, the focus on the *comprehension* mode only allowed cognitive methods of utilizing blinded observers to grade the animals' gross physical behavior, rather than trying to interpret putative language *production*. Herman's results (Herman, Richards, & Wolz, 1984) were published in the journal *Cognition*, regarding work on the dolphins Akeakamai and Phoenix. All such research has been controversial among cognitive linguists.

Consciousness

The sense in which animals can be said to have consciousness or a self-concept has been hotly debated; it is often referred to as the debate over animal minds. 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 a solitary elephant, but not for monkeys. The mirror test has attracted controversy among some 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 olfactory sense in dogs.

A different approach to determine whether a non-human animal is conscious derives from passive speech research with a macaw. Some researchers propose that by passively listening to an animal's voluntary speech, it is possible to learn about the thoughts of another creature and to determine that the speaker is conscious. This type of research was originally used to investigate a child's crib speech by Weir (1962) and in investigations of early speech in children by Greenfield and others (1976). With speech-capable birds, the methods of passive-speech research open a new avenue for investigation.

Mathematics

Some animals are capable of distinguishing between different amounts and rudimentary counting. Elephants have been known to perform simple arithmetic and rhesus monkeys can count. 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. Young chimpanzees have outperformed human college students in tasks requiring remembering numbers. Pigeons have been shown to outperform humans on the Monty Hall problem, a probability puzzle.

Cognitive faculty by species

Some animals such as great apes, crows, dolphins, dogs, elephants, cats, pigs, rats, and parrots are still typically thought by laymen as intelligent in ways that some other species of animal are not. For example, crows are attributed with human-like intelligence in the folklore of many cultures. A number of recent survey studies have demonstrated the consistency of these rankings between people in a given culture and indeed to a considerable extent across cultures.

A 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.

A more fruitful approach has been to recognize that different animals may have different kinds of cognitive processes, which are better understood in terms of the ways in which they are cognitively adapted to their different ecological niches, than by positing any kind of hierarchy.

One question that can be asked coherently is how far different species are intelligent in the same ways as humans are, i.e., are their cognitive processes similar to ours. Not surprisingly, our closest biological relatives, the great apes, tend to do best on such an assessment. Among the birds, corvids and parrots have typically been found to perform well. Despite ambitious claims, evidence of unusually high human-like intelligence among cetaceans is patchy, partly because the cost and difficulty of carrying out research with marine mammals mean that experiments frequently suffer from small sample sizes and inadequate controls and replication. Octopuses 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.

Behavioral ecology

Behavioral ecology, or **ethoecology**, is the study of the ecological and evolutionary basis for animal behavior, and the roles of behavior in enabling an animal to adapt to its environment (both intrinsic and extrinsic). Behavioral ecology emerged from ethology after Niko Tinbergen (a seminal figure in the study of animal behavior) outlined the four causes of behavior.

If an organism has a trait which provides them with a selective advantage (i.e. has an adaptive significance) in a new environment natural selection will likely favor it. Adaptive significance therefore refers to the beneficial qualities, in terms of increased survival and reproduction, a trait conveys.

For example, the behavior of flight has evolved numerous times in reptiles (Pterosaur), birds, many insects and mammals (bats) due to its adaptive significance—for many species, flight has the potential to increase an animal's ability to escape from predators and move swiftly between habitat areas, among other things, thereby increasing the organism's chances of survival and reproduction. In all instances, the organism adapting to flight had to have "pre-adaptions" to these behavioral and anatomical changes. Feathers in birds initially evolving for thermoregulation then turned to flight due to the benefits conveyed; insect wings evolving from enlarged gill plates used to efficiently "sail" across the water, becoming larger until capable of flight are two good examples of this. At every stage slight improvements mean higher energy acquisition, lower energy expenditure or increased mating opportunities causing the genes that convey these traits to increase within the population. If these organisms did not have the required variation for natural selection to act upon either due to phylogenetic or genetic constraints, these behaviors would not be able to evolve.

However, it is not sufficient to apply these explanations where they seem convenient. Viewing traits and creating unsubstantiated theories or "Just So Stories" as to their adaptive nature have been deeply criticized. Stephen Jay Gould and Richard Lewontin (1979) described this as the "adaptationist programme". To be rigorous, hypotheses regarding adaptations must be theoretically or experimentally tested as with any scientific theory.

The hypothesis of the evolution of insect flight for example has been tested through wing manipulation experiments. Empirical observations which adhere to the conditions prosed also provide evidence. For instance, one can suppose that when birds are not at risk of being eaten they might lose the ability to fly as the construction of functional wings are costly to produce and take away energy which could be used to increase offspring production or survival, a trend many island flightless birds such as the Kakapo and the now extinct Dodo demonstrate in the absence of natural predators prior to human colonization.

Proximate causation

Proximate causation is also divided into two factors which are ontogenetic and mechanistic. Ontogenetic factors are the entire sum of experience throughout the lifetime of an individual from embryo to death. Hence, factors included are learning the genetic factors giving rise to behavior in individuals. Mechanistic factors, as the name implies, are the processes of the body that give rise to behavior such as the effects of hormones on behavior and neuronal basis of behavior.

Optimization theory

Behavioral ecology, along with other areas of evolutionary biology, has incorporated a number of techniques which have been borrowed from optimization theory. Optimization is a concept that stipulates strategies that offer the highest return to an animal given all the different factors and constraints facing the animal. One of the simplest ways to arrive at an optimal solution is to do a cost/benefit analysis. By considering the advantages of a behavior and the costs of a behavior, it can be seen that if the costs outweigh the benefits then a behavior will not evolve and vice versa. This is also where the concept of the trade-off becomes important. This is because it rarely pays an animal to invest maximally in any one behavior. For example, the amount of time an ectothermic animal such as a lizard spends foraging is constrained by its body temperature. The digestive efficiency of the lizard also increases with increases in body temperature. Lizards increase their body temperature by basking in the sun. However, the time spent basking decreases the amount of time available for foraging. Basking also increases the risk of being discovered by a predator. Therefore, the optimal basking time is the outcome of the time necessary to sufficiently warm itself to carry out its activities such as foraging. This example shows how foraging is constrained by the need to bask (intrinsic constraint) and predation pressure (extrinsic constraint).

A often quoted behavioural ecology hypothesis is known as Lack's brood reduction hypothesis (named after David Lack). Lack's hypothesis posits an evolutionary and ecological explanation as to why birds lay a series of eggs with an asynchronous delay leading to nestlings of mixed age and weights. According to Lack, this brood behaviour is an ecological insurance that allows the larger birds to survive in poor years and all birds to survive when food is plentiful.

Differential reproductive success

Ultimately, behavior is subject to natural selection just as with any other trait. Therefore animals that employ optimal behavioral strategies specific to their environment will generally leave greater numbers of offspring than their suboptimal conspecifics. Animals that leave a greater number of offspring than others of their own species are said to have greater fitness. However, environments change over time. What might be good behavior today might not be the best behavior in 10,000 years time or even 10 years time. The behavior of animals has and will continue to change in response to the environment. Behavioral ecology is one of the best ways to study these changes. As geneticist Theodosius Dobzhansky famously wrote, "nothing in biology makes sense except in the light of evolution."

Evolutionarily stable strategies

Another driving force in the evolution of animal behavior is the concept of an evolutionarily stable strategy (or ESS), a term derived from economic game theory which became prominent after John Maynard Smith(1982) recognized the possible application of the concept of a Nash equilibrium to model the evolution of behavioral strategies.

In short, evolutionary game theory asserts that only strategies that, when common in the population, cannot be "invaded" by any alternative (mutant) strategy will be an ESSs, and thus maintained in the population. In other words, at equilibrium every player should play the best strategic response to each other. When the game is two player and symmetric each player should play the strategy which is the best response to itself.

Therefore, the ESS is considered to be the evolutionary end point subsequent to the interactions. As the fitness conveyed by a strategy is influenced by what other individuals are doing (the relative frequency of each strategy in the population), behavior can be governed not only by optimality but the frequencies of strategies adopted by others and are therefore frequency dependent (frequency dependence).

Behavioral evolution is therefore influenced by both the physical environment and interactions between other individuals.

Chapter- 4

Altruism in Animals

Altruism is a well-documented animal behaviour, which appears most obviously in kin relationships but may also be evident amongst wider social groups, in which an animal sacrifices its own well-being for the benefit of another animal.

Overview

In the science of ethology (the study of behavior), and more generally in the study of social evolution, on occasion, some animals do behave in ways that reduce their individual fitness but increase the fitness of other individuals in the population; this is a functional definition of altruism. Research in evolutionary theory has been applied to social behaviour, including altruism. Cases of animals helping individuals to whom they are closely related can be explained by kin selection, and are not considered true altruism. Beyond the physical exertions that mothers, and in some species fathers, undertake to protect their young, extreme examples of sacrifice may occur. One example is matriphagy (the consumption of the mother by her offspring) in the spider *Stegodyphus*. Hamilton's rule describes the benefit of such altruism in terms of Wright's coefficient of relationship to the beneficiary and the benefit granted to the beneficiary minus the cost to the sacrificer. Should this sum be greater than zero a fitness gain will result from the sacrifice.

When apparent altruism is not between kin, it may be based on reciprocity. A monkey will present its back to another monkey, who will pick out parasites; after a time the roles will be reversed. Such reciprocity will pay off, in evolutionary terms, as long as the costs of helping are less than the benefits of being helped and as long as animals will not gain in the long run by "cheating" – that is to say, by receiving favours without returning them. This is elaborated on in evolutionary game theory and specifically the prisoner's dilemma as social theory.

Implications in evolutionary theory

Researchers on alleged altruist behaviours among animals have been ideologically opposed to the social darwinist concept of the "survival of the fittest", under the name of "survival of the nicest" — the latter being globally compatible, however, with the theory

of evolution by natural selection. Insistence on such cooperative behaviours between animals was first exposed by the Russian zoologist and anarchist Peter Kropotkin in his 1902 book, *Mutual Aid: A Factor of Evolution*.

Recent developments in game theory have provided some explanations for apparent altruism, as have traditional evolutionary analyses. Among the proposed mechanisms are:

- Behavioural manipulation (for example, by certain parasites that can alter the behavior of the host)
- Bounded rationality (for example, Herbert Simon)
- Kin selection including eusociality
- Memes (by influencing behavior to favour their own spread, for example, religion)
- Reciprocal altruism, mutual aid
- Sexual selection, in particular, the Handicap principle
- Reciprocity (social psychology)
    - Indirect reciprocity (for example, reputation)
    - Strong reciprocity
- Pseudo-reciprocity

The study of altruism was the initial impetus behind George R. Price's development of the Price equation which is a mathematical equation used to study genetic evolution. An interesting example of altruism is found in the cellular slime moulds, such as *Dictyostelium mucoroides*. These protists live as individual amoebae until starved, at which point they aggregate and form a multicellular fruiting body in which some cells sacrifice themselves to promote the survival of other cells in the fruiting body. Social behavior and altruism share many similarities to the interactions between the many parts (cells, genes) of an organism, but are distinguished by the ability of each individual to reproduce indefinitely without an absolute requirement for its neighbors.

Jorge Moll and Jordan Grafman, neuroscientists at the National Institutes of Health and LABS-D'Or Hospital Network (J.M.) provided the first evidence for the neural bases of altruistic giving in normal healthy volunteers, using functional magnetic resonance imaging. In their research, published in the Proceedings of the National Academy of Sciences USA in October, 2006, they showed that both pure monetary rewards and charitable donations activated the mesolimbic reward pathway, a primitive part of the brain that usually lights up in response to food and sex. However, when volunteers generously placed their interests of others before their own by making charitable donations, another brain circuit was selectively activated: the subgenual cortex/septal region. These structures are intimately related to social attachment and bonding in other species. Altruism, the experiment suggested, was not a superior moral faculty that suppresses basic selfish urges but rather was basic to the brain, hard-wired and pleasurable.

A new study by Samuel Bowles at the Santa Fe Institute in New Mexico, US, is seen by some as breathing new life into the model of group selection for altruism, known as

"Survival of the nicest". Bowles conducted a genetic analysis of contemporary foraging groups, including Australian aboriginals, native Siberian Inuit populations and indigenous tribal groups in Africa. It was found that hunter-gatherer bands of up to 30 individuals were considerably more closely related than was previously thought. Under these conditions, thought to be similar to those of the middle and upper Paleolithic, altruism towards other group-members would improve the overall fitness of the group.

If an individual defended the group but was killed, any genes that the individual shared with the overall group would still be passed on. Early customs such as food sharing or monogamy could have levelled out the "cost" of altruistic behaviour, in the same way that income taxes redistribute income in society. He assembled genetic, climactic, archaeological, ethnographic and experimental data to examine the cost-benefit relationship of human cooperation in ancient populations. In his model, members of a group bearing genes for altruistic behaviour pay a "tax" by limiting their reproductive opportunities to benefit from sharing food and information, thereby increasing the average fitness of the group as well as their inter-relatedness. Bands of altruistic humans would then act together to gain resources from other groups at this challenging time in history.

Altruist theories in evolutionary biology were contested by Amotz Zahavi, the inventor of the signalling theory and its correlative, the handicap principle, based mainly on his observations of the Arabian Babbler, a bird commonly known for its surprising (alleged) altruistic behaviours.

Examples of animal altruism

- Dogs often adopt orphaned cats, squirrels, ducks and even tigers.
- Dolphins support sick or injured animals, swimming under them for hours at a time and pushing them to the surface so they can breathe.
- Wolves and wild dogs bring meat back to members of the pack not present at the kill.
- Male baboons threaten predators and cover the rear as the troop retreats.
- Gibbons and chimpanzees with food will, in response to a gesture, share their food with others of the group. Chimpanzees will help humans and conspecifics without any reward in return.
- Bonobos have been observed aiding injured or handicapped bonobos.
- Vampire bats commonly regurgitate blood to share with unlucky or sick roost mates that have been unable to find a meal, often forming a buddy system.
- Raccoons inform conspecifics about feeding grounds by droppings left on commonly shared latrines. A similar information system has been observed to be used by common ravens.
- In numerous bird species, a breeding pair receives support in raising its young from other "helper" birds, including help with the feeding of its fledglings. Some will even go as far as protecting an unrelated bird's young from predators

- Most mammal carnivores like wolves or dogs have a habit of not harming pack members below certain age, of opposite sex or in surrendering position (in case of some animals, the behavior exists within entire species rather than one pack).
- 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.
- Walruses have been seen adopting orphans who lost their parents to predators.
- Some termites release a sticky secretion by fatally rupturing a gland near the skin in their neck. This autothysis defends against invading ants by creating a tar baby effect.
- Meerkats often have one standing guard to warn whilst the rest feed in case of predators attack.
- African buffalo will rescue a member of the herd captured by predators.

Chapter- 5

Animal Communication

Metacommunications: signals that modify the meaning of subsequent signals. The best known example is the *play face* and tail signals in dogs, which indicate that a subsequent aggressive signal is part of a play fight rather than a serious aggressive episode.

Animal communication is any behavior on the part of one animal that has an effect on the current or future behaviour of another animal. The study of animal communication, sometimes called **Zoosemiotics** (distinguishable from anthroposemiotics, the study of

human communication) has played an important part in the methodology of ethology, sociobiology, and the study of animal cognition.

Animal communication, and indeed the understanding of the animal world in general, is a rapidly growing field, and even in the 21st century so far, many prior understandings related to diverse fields such as personal symbolic name use, animal emotions, animal culture and learning, and even sexual conduct, long thought to be well understood, have been revolutionized.

A new approach in the 21 century of studying animal communication uses applied behavioral analysis (**ABA**), specifically ‘’’Functional Communication Training’’’ (FCT). This **FCT** previously has been used in schools and clinics with humans with special needs, such as children with autism, to help them develop language. Sean Senechal, at the **AnimalSign Center** has been using an approach similar to this FCT with domesticated animals, such as dogs (since 2004) and horses (since 2000) with encouraging results and benefits to the animals and people. Functional communication training for animals, Senechal calls **AnimalSign Language**. This includes teaching communication through gestures (like simplified ASL), pictures (**PECS**), tapping, and vocalization. The process for animals includes simplified and modified techniques.

Validation

A lamb investigates a rabbit, an example of interspecific communication through body language and scent.

Forms of communication

The best known forms of communication involve the display of distinctive body parts, or distinctive bodily movements; often these occur in combination, so a distinctive movement acts to reveal or emphasize a distinctive body part. An example that was important in the history of ethology was the parent Herring Gull's presentation of its bill to a chick in the nest. Like many gulls, the Herring Gull has a brightly coloured bill, yellow with a red spot on the lower mandible near the tip. When it returns to the nest with food, the parent stands over its chick and taps the bill on the ground in front of it; this elicits a begging response from a hungry chick (pecking at the red spot), which stimulates the parent to regurgitate food in front of it. The complete signal therefore involves a distinctive morphological feature (body part), the red-spotted bill, and a distinctive movement (tapping towards the ground) which makes the red spot highly visible to the chick. Investigations by Niko Tinbergen and his colleagues showed that the red colour of the bill, and its high contrast, are crucial for eliciting the appropriate response from the chick (It is unresolved whether this actually is an inborn behavior in all its complexity, or simply a combination of generalized curiosity on part of the chick, and generalized parental/feeding instincts acting together to produce a simple learning process via reward. Gull chicks peck at everything that are brightly colored, mainly red, yellow, white or shining, and high-contrast objects, but the parent's bill is the only such object that will constantly yield food as a reward when pecked at. Accidental swallowing of pieces of brightly colored plastic or glass is a common cause of mortality amongst gull chicks). Some cephalopods, such as the octopus, have specialized skin cells that can change the apparent colour, opacity, and reflectiveness of their skin. In addition to being used for camouflage, rapid changes in skin colour are used while hunting and in courtship rituals. Many animals communicate through vocalisations. One form of animal communication is bird song, often performed by males, though in some species the sexes sing in alternation (this is called duetting). Whale song has been found to have different dialects based on location. Other instances of communication include the warning cries of many monkeys, the territorial calls of gibbons, and the mating calls of many species of frog.

Less obvious (except in a few cases) is olfactory communication. Many mammals, in particular, have glands that generate distinctive and long-lasting smells, and have corresponding behaviours that leave these smells in places where they have been. Often the scented substance is introduced into urine or feces. Sometimes it is distributed through sweat, though this does not leave a semi-permanent mark as scents deposited on the ground do. Some animals have glands on their bodies whose sole function appears to be to deposit scent marks: for example Mongolian gerbils have a scent gland on their stomachs, and a characteristic ventral rubbing action that deposits scent from it. Golden hamsters and cats have scent glands on their flanks, and deposit scent by rubbing their sides against objects; cats also have scent glands on their foreheads. Bees carry with them a pouch of material from the hive which they release as they reenter, the smell of which indicates that they are a part of the hive and grants their safe entry.

Most of these forms of communication can also be used for interspecies communication.

A rarer form of animal communication is electrocommunication. It is seen primarily in aquatic life, though some mammals, notably the platypus and echidnas are capable of electroreception and thus theoretically of electrocommunication.

Functions of communication

While there are as many kinds of communication as there are kinds of social behaviour, a number of functions have been studied in particular detail. They include:

- agonistic interaction: everything to do with contests and aggression between individuals. Many species have distinctive threat displays that are made during competition over food, mates or territory; much bird song functions in this way. Often there is a matched submission display, which the threatened individual will make if it is acknowledging the social dominance of the threatener; this has the effect of terminating the aggressive episode and allowing the dominant animal unrestricted access to the resource in dispute. Some species also have *affiliative* displays which are made to indicate that a dominant animal accepts the presence of another.
- courtship rituals: signals made by members of one sex to attract or maintain the attention of potential mate, or to cement a pair bond. These frequently involve the display of body parts, body postures (gazelles assume characteristic poses as a signal to initiate mating), or the emission of scents or calls, that are unique to the species, thus allowing the individuals to avoid mating with members of another species which would be infertile. Animals that form lasting pair bonds often have symmetrical displays that they make to each other: famous examples are the mutual presentation of reeds by Great Crested Grebes, studied by Julian Huxley, the *triumph displays* shown by many species of geese and penguins on their nest sites and the spectacular courtship displays by birds of paradise and manakins.
- ownership/territorial: signals used to claim or defend a territory, food, or a mate.
- food-related signals: many animals make "food calls" that attract a mate, or offspring, or members of a social group generally to a food source. When parents are feeding offspring, the offspring often have begging responses (particularly when there are many offspring in a clutch or litter - this is well known in altricial songbirds, for example). Perhaps the most elaborate food-related signal is the dance language of honeybees studied by Karl von Frisch.
- alarm calls: signals made in the presence of a threat from a predator, allowing all members of a social group (and often members of other species) to run for cover, become immobile, or gather into a group to reduce the risk of attack.
- metacommunications: signals that modify the meaning of subsequent signals. The best known example is the *play face* in dogs, which signals that a subsequent aggressive signal is part of a play fight rather than a serious aggressive episode.

Interpretation of animal communication

It is important to note that whilst many gestures and actions have common, stereotypical meanings, researchers regularly seem to find that animal communication is often more

complex and subtle than previously believed, and that the same gesture may have multiple distinct meanings depending on context and other behaviors. So generalizations such as "X means Y" are *often*, but not *always* accurate. For example, even a simple domestic dog's tail wag may be used in subtly different ways to convey many meanings including:

- Excitement
- Anticipation
- Playfulness
- Contentment/enjoyment
- Relaxation or anxiety
- Questioning another animal or a human as to intentions
- Tentative role assessment on meeting another animal
- Reassurance ("I'm hoping to be friendly, are you?")
- Brief acknowledgement ("I hear you", or "I'm aware and responsive if you want my attention")
- Statement of interest ("I want that (food/toy/activity), if you're willing")
- Uncertainty/apprehension
- Submissive placation (if worried by a more dominant animal)

Combined with other body language, in a specific context, many gestures such as yawns, direction of vision, and so on all convey meaning. Thus statements that a particular action "means" something should always be interpreted to mean "often means" something. As with human beings, who may smile or hug or stand a particular way for multiple reasons, many animals reuse gestures too.

Intraspecies vs. interspecies communication

The sender and receiver of a communication may be of the same species or of different species. The majority of animal communication is intraspecific (between two or more individuals of the same species). However, there are some important instances of interspecific communication. Also, the possibility of interspecific communication, and the form it takes, is an important test of some theoretical models of animal communication.

A European starling (*Sturnus vulgaris*) singing

Intraspecies communication

The majority of animal communication occurs within a single species, and this is the context in which it has been most intensively studied.

Most of the forms and functions of communication described above are relevant to intra-species communication.

Interspecies communication

Many examples of communication take place between members of different species. Animals communicate to other animals with various signs: visual, sound, echolocation, body language, and smell.

Prey to predator

If a prey animal moves or makes a noise in such a way that a predator can detect and capture it, that fits the definition of "communication" given above. This type of communication is known as interceptive eavesdropping, where a predator intercepts the message being conveyed to conspecifics.

This Chihuahua is baring his teeth to signify an attack is imminent if the photographer comes closer to take his bone.

There are however some actions of prey species that are clearly communications to actual or potential predators. A good example is warning colouration: species such as wasps that are capable of harming potential predators are often brightly coloured, and this modifies

the behaviour of the predator, who either instinctively or as the result of experience will avoid attacking such an animal. Some forms of mimicry fall in the same category: for example hoverflies are coloured in the same way as wasps, and although they are unable to sting, the strong avoidance of wasps by predators gives the hoverfly some protection. There are also behavioral changes that act in a similar way to warning colouration. For example, canines such as wolves and coyotes may adopt an aggressive posture, such as growling with their teeth bared, to indicate they will fight if necessary, and rattlesnakes use their well-known rattle to warn potential predators of their poisonous bite. Sometimes, a behavioral change and warning colouration will be combined, as in certain species of amphibians which have a brightly coloured belly, but on which the rest of their body is coloured to blend in with their surroundings. When confronted with a potential threat, they show their belly, indicating that they are poisonous in some way.

Another example of prey to predator communication, is referred to as a pursuit-deterrent signal. Pursuit-deterrent signals occur when prey indicates to a predator that pursuit would be unprofitable because the signaler is prepared to escape. Pursuit-deterrent signals provide a benefit to both the signaler and receiver; they prevent the sender from wasting time and energy fleeing, and they prevent the receiver from investing in a costly pursuit that is unlikely to result in capture. Such signals can advertise prey's ability to escape, and reflect phenotypic condition (quality advertisement), or can advertise that the prey has detected the predator (perception advertisement). Pursuit-deterrent signals have been reported for a wide variety of taxa, including fish (Godin and Davis 1995), lizards (Cooper et al. 2004), ungulates (Caro 1995), rabbits (Holley 1993), primates (Zuberbuhler et al. 1997), rodents (Shelley and Blumstein 2005, Clark 2005), and birds (Alvarez 1993, Murphy 2006, 2007). The most familiar example of quality advertisement pursuit-deterrent signal is *stotting*, a pronounced combination of running while simultaneously hopping shown by some antelopes such as Thomson's gazelle in the presence of a predator. At least 11 hypothesis for stotting have been proposed. A leading theory today is that it alerts predators that the element of surprise has been lost. Predators like cheetahs rely on surprise attacks, proven by the fact that chases are rarely successful when they stot. Predators know not to waste energy on a chase that will likely be unsuccessful (optimal foraging behavior).

Predator to prey

Some predators communicate to prey in ways that change their behaviour and make them easier to catch, in effect deceiving them. A well-known example is the angler fish, which has a fleshy growth protruding from its forehead and dangling in front of its jaws; smaller fish try to take the lure, and in so doing are perfectly placed for the angler fish to eat them.

Symbiotic species

Interspecies communication also occurs in various kinds of mutualism and symbiosis. For example, in the cleaner fish/grouper system, groupers signal their availability for cleaning by adopting a particular posture at a cleaning station.

Human/animal communication

Various ways in which humans interpret the behavior of domestic animals, or give commands to them, fit the definition of interspecies communication. Depending on the context, they might be considered to be predator to prey communication, or to reflect forms of commensalism. The recent experiments on animal language are perhaps the most sophisticated attempt yet to establish human/animal communication, though their relation to natural animal communication is uncertain.

Lacking in the study of human-animal communication is a focus on expressive communication from animal to human specifically. Other than a few natural expressions animals (especially dogs) use to communicate to humans, scientists in general do not pursue expanding the expressive/productive communication of domesticated animals. Horses are taught to not communicate (for safety). Dogs and horses are generally not encouraged to communicate expressively, but are encouraged to develop receptive language (understanding). One scientist, Sean Senechal has pursued (since the late 1990's) developing, studying, and using the learned visible, expressive language in dogs and horses. By teaching these animals a gestural (human made) ASL-like language animals have been found to learn and use the new signs on their own to get what they need. Senechal's book Dogs Can Sign, Too documents this process.

Other aspects of animal communication

Evolution of communication

The importance of communication is clear from the fact that animals have evolved elaborate body parts to facilitate it. They include some of the most striking structures in the animal kingdom, such as the peacock's tail. Birdsong appears to have brain structures entirely devoted to its production. But even the red spot on a herring gull's bill, and the modest but characteristic bowing behaviour that displays it, require evolutionary explanation.

There are two aspects to the required explanation:

- identifying a route by which an animal that lacked the relevant feature or behaviour could acquire it;
- identifying the selective pressure that makes it adaptive for animals to develop structures that facilitate communication, emit communications, and respond to them.

Significant contributions to the first of these problems were made by Konrad Lorenz and other early ethologists. By comparing related species within groups, they showed that movements and body parts that in the primitive forms had no communicative function could be "captured" in a context where communication would be functional for one or both partners, and could evolve into a more elaborate, specialised form. For example, Desmond Morris showed in a study of grass finches that a beak-wiping response occurred

in a range of species, serving a preening function, but that in some species this had been elaborated into a courtship signal.

The second problem has been more controversial. The early ethologists assumed that communication occurred for the good of the species as a whole, but this would require a process of group selection which is believed to be mathematically impossible in the evolution of sexually reproducing animals. Altruism towards an unrelated group is not widely accepted in the scientific community, but rather can be seen as a sort of reciprocal altruism, expecting the same behavior from others, a benefit of living in a group. Sociobiologists argued that behaviours that benefited a whole group of animals might emerge as a result of selection pressures acting solely on the individual. A gene-centered view of evolution proposes that behaviors that enabled a gene to become wider established within a population would become positively selected for, even if their effect on individuals or the species as a whole was detrimental. In the case of communication, an important discussion by John Krebs and Richard Dawkins established hypotheses for the evolution of such apparently altruistic or mutualistic communications as alarm calls and courtship signals to emerge under individual selection. This led to the realisation that communication might not always be "honest" (indeed, there are some obvious examples where it is not, as in mimicry). The possibility of evolutionarily stable dishonest communication has been the subject of much controversy, with Amotz Zahavi in particular arguing that it cannot exist in the long term. Sociobiologists have also been concerned with the evolution of apparently excessive signalling structures such as the peacock's tail; it is widely thought that these can only emerge as a result of sexual selection, which can create a positive feedback process that leads to the rapid exaggeration of a characteristic that confers an advantage in a competitive mate-selection situation.

One theory to explain the evolution of traits like a peacock's tail is 'runaway selection'. This requires two traits-a trait that exists, like the bright tail, and a prexisting bias in the female to select for that trait. Females prefer the more elaborate tails, and thus those males are able to mate successfully. Exploiting the psychology of the female, a positive feedback loop is enacted and the tail becomes bigger and brighter. Eventually, the evolution will level off because the survival costs to the male do not allow for the trait to be elaborated any further. Two theories exist to explain runaway selection. The first is the good genes hypothesis. This theory states that an elaborate display is an honest signal of fitness and truly is a better mate. The second is the handicap hypothesis. This explains that the peacock's tail is a handicap, requiring energy to keep and makes it more visible to predators. Regardless, the individual is able to survive, even though its genes are not as good per se.

Cognitive aspects

Ethologists and sociobiologists have characteristically analysed animal communication in terms of more or less automatic responses to stimuli, without raising the question of whether the animals concerned understand the meaning of the signals they emit and receive. That is a key question in animal cognition. There are some signalling systems

that seem to demand a more advanced understanding. A much discussed example is the use of alarm calls by vervet monkeys. Robert Seyfarth and Dorothy Cheney showed that these animals emit different alarm calls in the presence of different predators (leopards, eagles, and snakes), and the monkeys that hear the calls respond appropriately - but that this ability develops over time, and also takes into account the experience of the individual emitting the call. Metacommunication, discussed above, also seems to require a more sophisticated cognitive process.

A recently published paper demonstrated that bottlenose dolphins can recognize identity information from whistles even when otherwise stripped of the characteristics of the whistle; making dolphins the only animals other than humans that have been shown to transmit identity information independent of the caller's voice or location. The paper concludes that:

The fact that signature whistle shape carries identity information independent from voice features presents the possibility to use these whistles as referential signals, either addressing individuals or referring to them, similar to the use of names in humans. Given the cognitive abilities of bottlenose dolphins, their vocal learning and copying skills, and their fission–fusion social structure, this possibility is an intriguing one that demands further investigation.
—V. M. Janik, *et al.*

Animal communication and human behaviour

Another controversial issue is the extent to which humans have behaviours that resemble animal communication, or whether all such communication has disappeared as a result of our linguistic capacity. Some of our bodily features - eyebrows, beards and moustaches, deep adult male voices, perhaps female breasts - strongly resemble adaptations to producing signals. Ethologists such as Irenäus Eibl-Eibesfeldt have argued that facial gestures such as smiling, grimacing, and the *eyebrow flash* on greeting are universal human communicative signals that can be related to corresponding signals in other primates. Given the recency with which spoken language has emerged, it is very likely that human body language does include some more or less involuntary responses that have a similar origin to the communication we see in other animals.

Humans also often seek to mimic animals' communicative signals in order to interact with the animals. For example, cats have a mild affiliative response involving closing their eyes; humans often close their eyes towards a pet cat to establish a tolerant relationship. Stroking, petting and rubbing pet animals are all actions that probably work through their natural patterns of interspecific communication.

Dogs have shown an ability to understand communication from a species other than their own. They were able to use human communicative gestures such as pointing and looking to find hidden food and toys.

Animal communication and linguistics

For linguistics, the interest of animal communication systems lies in their similarities to and differences from human language:

1. Human languages are characterized for having a **double articulation** (in the characterization of French linguist André Martinet). It means that complex linguistic expressions can be broken down in meaningful elements (such as morphemes and words), which in turn are composed of smallest phonetic elements that affect meaning, called phonemes. Animal signals, however, do not exhibit this dual structure.
2. In general, animal utterances are responses to external stimuli, and do not refer to matters removed in time and space. Matters of relevance at a distance, such as distant food sources, tend to be indicated to other individuals by body language instead, for example wolf activity before a hunt, or the information conveyed in honeybee dance language. It is therefore unclear to what extent utterances are automatic responses and to what extent deliberate intent plays a part.
3. Human language is largely learned culturally, while animal communication systems are known largely by instinct.
4. In contrast to human language, animal communication systems are usually not able to express conceptual generalizations. (Cetaceans and some primates may be notable exceptions).
5. Human languages combine elements to produce new messages (a property known as **creativity**). One factor in this is that much human language growth is based upon conceptual ideas and hypothetical structures, both being far greater capabilities in humans than animals. This appears far less common in animal communication systems, although current research into animal culture is still an ongoing process with many new discoveries.

A recent and interesting area of development is the discovery that the use of syntax in language, and the ability to produce "sentences", is not limited to humans either. The first good evidence of syntax in non-humans, reported in 2006, is from the greater spot-nosed monkey (*Cercopithecus Nictitans*) of Nigeria. This is the first evidence that some animals can take discrete units of communication, and build them up into a sequence which then carries a different meaning from the individual "words":

The putty-nosed monkeys have two main alarm sounds. A sound known onomatopoeiacally as the 'pyow' warns against a lurking leopard, and a coughing sound that scientists call a 'hack' is used when an eagle is hovering nearby.
"Observationally and experimentally we have demonstrated that this sequence [of up to three 'pyows' followed by up to four 'hacks'] serves to elicit group movement... the 'pyow-hack' sequence means something like "let's go!" [a command telling others to move]... The implications are that primates at least may be able to ignore the usual relationship between an individual alarm call, and the meaning it might convey under certain circumstances... To our knowledge this is the first good evidence of a syntax-like natural communication system in a non-human species."

Chapter- 6

Emotion in Animals

There is no scientific consensus on **emotion in animals**, that is, what emotions certain species of animals, including humans, feel. The debate concerns primarily mammals and birds, although emotions have also been postulated for other vertebrates and even for some invertebrates.

Animal lovers, scientists, philosophers, and others who interact with animals, have suggested answers but the core question has proven difficult to answer since animals cannot speak of their experience. Society recognizes animals can feel pain as is demonstrated by the criminalization of animal cruelty. Animal expressions of apparent pleasure are ambiguous as to whether this is emotion, or simply innate responses, perhaps for approval or other hard-wired cues. The ambiguity is a source of controversy as there is no certainty which views, if any, reflect reality. That said, extreme behaviourists would say that human "feeling" is also merely a hard-wired response to external stimuli.

In recent years, research has become available which expands prior understandings of animal language, cognition and tool use, and even sexuality. Emotions arise in the mammalian brain, or the limbic system, which human beings share in common with other mammals as well as many other species.

Evidence

While humans have had differing views of animal emotion, the scientific examination of animal emotion has led to little information beyond a recognition that animals have the capacity for pain and fear, and such responses as are needed for survival. Historically, prior to the rise of sciences such as ethology, interpretation of animal behaviour tended to favour a kind of minimalism known as behaviourism, in this context the refusal to ascribe to an animal a capability beyond the least demanding that would explain a behaviour; anything more than this was seen as unwarranted anthropomorphism. Put crudely, the behaviourist argument is, why should humans postulate consciousness and all its near-human implications in animals to explain some behaviour, if mere stimulus-response is a sufficient explanation to produce the same effects?

The cautious wording of Beth Dixon's 2001 paper on animal emotion exemplifies this viewpoint:

Recent work in the area of ethics and animals suggests that it is philosophically legitimate to ascribe emotions to non-human animals. Furthermore, it is sometimes argued that emotionality is a morally relevant psychological state shared by humans and non humans. What is missing from the philosophical literature that makes reference to emotions in non-human animals is an attempt to clarify and defend some particular account of the nature of emotion, and the role that emotions play in a characterization of human nature. I argue in this paper that some analyses of emotion are more credible than others. Because this is so, the thesis that humans and nonhumans share emotions may well be a more difficult case to make than has been recognized thus far.

Jeffrey Moussaieff Masson expresses a similar view:

While the study of emotion is a respectable field, those who work in it are usually academic psychologists who confine their studies to human emotions. The standard reference work, The Oxford Companion to Animal Behavior, advises animal behaviourists that "One is well advised to study the behaviour, rather than attempting to get at any underlying emotion."

There is considerable uncertainty and difficulty related to the interpretation and ambiguity of emotion: an animal may make certain movements and sounds, and show certain brain and chemical signals when its body is damaged in a particular way. But does this mean an animal feels—is *aware* of—pain as we are, or does it merely mean it is programmed to act a certain way with certain stimuli? Similar questions can be asked of any activity an animal (including a human) might undertake, in principle. Many scientists regard all emotion and cognition (in humans and animals) as having a purely mechanistic basis.

Because of the philosophical questions of consciousness and mind are involved, many scientists have stayed away from examining animal and human emotion, and have studied instead, measurable brain functions, through neuroscience.

The author Marc Bekoff also provided evidence of animals having emotions in his book, *The Emotional Lives of Animals*. The following is an excerpt from his book:

A few years ago my friend Rod and I were riding our bicycles around Boulder, Colorado, when we witnessed a very interesting encounter among five magpies. Magpies are corvids, a very intelligent family of birds. One magpie had obviously been hit by a car and was laying dead on the side of the road. The four other magpies were standing around him. One approached the corpse, gently pecked at it-just as an elephant noses the carcass of another elephant- and stepped back. Another magpie did the same thing. Next, one of the magpies flew off, brought back some grass, and laid it by the corpse. Another magpie did the same. Then, all four magpies stood vigil for a few seconds and one by one flew off.

Primates

Primates and in particular great apes are candidates for highly developed capabilities for empathy and theories of mind. Great apes have highly complex social systems. Young apes and their mothers have very strong bonds of attachment. Often when a baby chimpanzee or gorilla dies, the mother will carry the body around for several days. Jane Goodall has described chimpanzees as exhibiting mournful behavior.

Canines

Research suggests that canines can experience negative emotions in a similar manner to people, including the equivalent of certain chronic and acute psychological conditions. The classic experiment for this was Martin Seligman's foundational experiments and theory of learned helplessness at the University of Pennsylvania in 1965, as an extension of his interest in depression:

A dog that had earlier been repeatedly conditioned to associate a sound with electric shocks did not try to escape the electric shocks after the warning was presented, even though all the dog would have had to do is jump over a low divider within ten seconds, more than enough time to respond. The dog didn't even try to avoid the "aversive stimulus"; it had previously "learned" that nothing it did mattered. A follow-up experiment involved three dogs affixed in harnesses, including one that received shocks of identical intensity and duration to the others, but the lever which would otherwise have allowed the dog a degree of control was left disconnected and didn't do anything. The first two dogs quickly recovered from the experience, but the third dog suffered chronic symptoms of clinical depression as a result of this perceived helplessness.

A further series of experiments showed that (similar to humans) under conditions of long term intense psychological stress, around 1/3 of dogs do not develop learned helplessness or long term depression. Instead these animals somehow managed to find a way to handle the unpleasant situation in spite of their past experience. The corresponding characteristic in humans has been found to correlate highly with an explanatory style and optimistic attitude and lower levels of emotional rigidity regarding expectations, that views the situation as *other than* personal, pervasive, or permanent. Such studies highlighted similar distinctions between people who adapt and those who break down, under long term psychological pressure, which were conducted in the 1950s in the realm of brainwashing.

Since this time, symptoms analogous to clinical depression, neurosis and other psychological conditions have been in general accepted as being within the scope of canine emotion as well.

Psychology research has shown that human faces are asymmetrical with the gaze instinctively moving to the right side of a face upon encountering other humans to obtain information about their emotions and state. Research at the University of Lincoln (2008) shows that dogs share this instinct when meeting a human being, and only when meeting

a human being (ie, not other animals or other dogs). As such they are the only non-primate species known to do so.

The existence and nature of personality traits in dogs have been studied (15329 dogs of 164 different breeds) and five consistent and stable "narrow traits" identified, described as playfulness, curiosity/fearlessness, chase-proneness, sociability and aggressiveness. A further higher order axis for shyness–boldness was also identified.

Felines

The emotions of cats have also been studied scientifically. It has been shown that cats can learn to manipulate their owners through vocalizations that are similar to the cries of human babies. Some cats learn to add a purr to the cry, which makes it less harmonious to humans and therefore harder to ignore. Individual cats learn to make these cries through operant conditioning; when a particular cry elicits a positive response from a human, the cat is more likely to use that cry in the future.

Fish

A 2007 study by the University of Guelph Scientists in Canada suggests that fish may have their own separate personalities. The study examined a group of trout that were visually identical. The study concluded that different fish within the same group exhibited different personality traits. Some fish were more willing to take risks in unknown waters than others when taken from their environment and introduced to a dark tube. Some fish were more social than others while some fish preferred being alone. Fish were also shown to have different preferences as far as eating habits.

Chapter- 7

Animal Sexual Behaviour

Animal sexual behaviour takes many different forms, even within the same species. Researchers have observed monogamy, promiscuity, sex between species, sexual arousal from objects or places, sex apparently via duress or coercion, copulation with dead animals, homosexual, heterosexual and bisexual sexual behaviour, and situational sexual behaviour and a range of other practices among animals other than humans. Related studies have noted diversity in sexed bodies and gendered behaviour, such as intersex and transgender animals.

The study of animal sexuality (and primate sexuality especially) is a rapidly developing field. It used to be believed that only humans and a handful of other species performed sexual acts other than for procreation, and that animals' sexuality was instinctive and a simple response to the "right" stimulation (sight, scent). Current understanding is that many species that were formerly believed monogamous have now been proven to be promiscuous or opportunistic in nature; a wide range of species appear both to masturbate and to use objects as tools to help them do so; in many species animals try to give and get sexual stimulation with others where procreation is not the aim; and homosexual behaviour has now been observed among 1,500 species and in 500 of those it is well documented.

Mating systems

In sociobiology and behavioural ecology, the term mating system is used to describe the ways in which animal societies are structured in relation to sexual behaviour. The mating system specifies which males mate with which females, and under what circumstances.

The following are some of the mating systems generally recognised in humans and other animals:

- Monogamy: One male and one female have an exclusive mating relationship.
- Polygamy: A single individual concurrently carries a relationship/mates with one or more of the opposite sex. Three types are recognized:

    - Polygyny (the most common polygamous mating system in vertebrates so far studied): One male has an exclusive relationship with two or more females.
    - Polyandry: One female has an exclusive relationship with two or more males.
    - Polygynandry: Two or more individuals have an exclusive relationship with two or more individuals from the opposite sex; the numbers of males and females need not be equal, and in vertebrate species studied so far, there are usually fewer males.
- Promiscuity: Any male and female will mate within the social group.

Monogamy

Zoologists and biologists now have solid evidence that monogamous pairs of animals are not always sexually exclusive. Many animals that form pairs to mate and raise offspring regularly engage in sexual activities with extra-pair partners. This includes previous exemplars such as swans. Sometimes these extra-pair sexual activities lead to offspring. Genetic tests frequently show that some of the offspring raised by a monogamous pair come from the female mating with an extra-pair male partner. These discoveries have led biologists to adopt new ways of talking about monogamy:

Social monogamy

Social monogamy refers to a male and female's social living arrangement (e.g., shared use of a territory, behaviour indicative of a social pair, and/or proximity between a male and female) without inferring any sexual interactions or reproductive patterns. In humans, social monogamy equals monogamous marriage. Sexual monogamy is defined as an exclusive sexual relationship between a female and a male based on observations of sexual interactions. Finally, the term genetic monogamy is used when DNA analyses can confirm that a female-male pair reproduce exclusively with each other. A combination of terms indicates examples where levels of relationships coincide, e.g., sociosexual and sociogenetic monogamy describe corresponding social and sexual, and social and genetic monogamous relationships, respectively.
—Reichard, 2003, page 4

Whatever makes a pair of animals socially monogamous does not necessarily make them sexually or genetically monogamous. Social monogamy, sexual monogamy, and genetic monogamy can occur in different combinations.

Social monogamy is relatively rare in the animal kingdom. The actual incidence of social monogamy varies greatly across different branches of the evolutionary tree. Over 90 percent of avian species are socially monogamous.

This stands in contrast to mammals. Only 3 percent of mammalian species are socially monogamous, although up to 15 percent of primate species are socially monogamous. Social monogamy has also been observed in reptiles, fish, and insects.

Sexual monogamy is also rare among animals. Many socially monogamous species engage in extra-pair copulations, making them sexually non-monogamous. For example, while over 90% of birds are socially monogamous, "on average, 30 percent or more of the baby birds in any nest [are] sired by someone other than the resident male." Patricia Adair Gowaty has estimated that, out of 180 different species of socially monogamous songbirds, only 10 percent are sexually monogamous.

The incidence of genetic monogamy, determined by DNA fingerprinting, varies widely across species. For a few rare species, the incidence of genetic monogamy is 100 percent, with all offspring genetically related to the socially monogamous pair. But genetic monogamy is strikingly low in other species. Barash and Lipton note:

The highest known frequency of extra-pair copulations are found among the fairy-wrens, lovely tropical creatures technically known as *Malurus splendens* and *Malurus cyaneus*. More than 65 percent of all fairy-wren chicks are fathered by males outside the supposed breeding group.
—Barash & Lipton, 2001, page 12

Such low levels of genetic monogamy have surprised biologists and zoologists, forcing them to rethink the role of social monogamy in evolution. They can no longer assume social monogamy determines how genes are distributed in a species. The lower the rates of genetic monogamy among socially monogamous pairs, the less of a role social monogamy plays in determining how genes are distributed among offspring.

Polygamy

Polygamy is defined as a mating structure in which a single individual of one gender has exclusive access to several individuals of the opposite gender. It takes two main forms - polygyny and polyandry. As polygyny is the most common form of polygamy among vertebrates (including humans, to some extent), it has been studied far more extensively than polyandry.

Polygyny

In some species, notably those with harem-like structures, only one of a few males in a group of females will mate. Technically, polygyny in sociobiology and zoology is defined as a system in which a male has a relationships with more than one female, but the females are predominantly bonded to a single male. Should the active male be driven out, killed, or otherwise removed from the group, in a number of species the new male will ensure that breeding resources are not wasted on another male's young. The new male may achieve this in many different ways, including:

- Competitive infanticide

in lions, hippopotamuses, and some monkeys, the new male will kill the offspring of the previous alpha male to cause their mothers to become receptive to his sexual advances since they are no longer nursing.

- Harassment to miscarriage

  amongst wild horses and baboons, the male will "systematically harass" pregnant females until they miscarry.

- Pheromone based spontaneous abortion

  in some rodents such as mice, a new male with a different scent will cause females who are pregnant to spontaneously fail to implant recently fertilized eggs. This does not require contact; it is mediated by scent alone. It is known as the Bruce-Parkes effect.

Promiscuity

Two examples of systems in primates are promiscuous mating chimpanzees and bonobos. These species live in social groups consisting of several males and several females. Each female copulates with many males, and vice versa. In bonobos, the amount of promiscuity is particularly striking because bonobos use sex to alleviate social conflict as well as to reproduce.

Seasonal nature of animal sexuality

Many animal species have specific mating (or breeding) seasons (seasonal breeding). These are often associated with changes to herd or group structure, and behavioural changes, including territorialism amongst individuals. These may be annual (e.g. wolves), biannual (e.g. dogs) or more frequently (e.g. horses). During these periods, females of most species are more mentally and physically receptive to sexual advances, a period scientifically described as estrous but commonly described as being "in season" or "in heat", but outside them animals still engage in sexual behaviours, and such acts as do occur are not necessarily harmful.

Interpretation of animal sexuality

The field of study of sexuality in non-human species has been a long standing taboo, with researchers either failing to observe or mis-categorizing and mis-describing sexual behaviour which does not meet their preconceptions. (See: Observer bias.) More current research provides views such as that of the Natural History Museum at the University of Oslo, which in 2006 held an exhibition on animal sexuality:

Many researchers have described homosexuality as something altogether different from sex. They must realise that animals can have sex with who they will, when they will and without consideration to a researcher's ethical principles.

—

An example of overlooking behaviour relates to descriptions of giraffe mating:

When nine out of ten pairings occur between males, "[e]very male that sniffed a female was reported as sex, while anal intercourse with orgasm between males was only [categorized as] 'revolving around' dominance, competition or greetings.
—

Sex for pleasure

It is a common myth that animals do not (as a rule) have sex for pleasure, or alternatively that humans, pigs (and perhaps dolphins and one or two species of primate) are the only species which do. This is sometimes formulated "animals mate only for reproduction".

Science cannot say at present conclusively what animals do or do not find "pleasurable", a question considered in more depth under Emotion in animals. Animals put themselves at risk to engage in sex, and as a result, most species have evolved sexual signals (usually scent and behaviour) to indicate the presence of receptive periods. During these, sex is sought, and outside these it is usually not sought (or is sought but not permitted). Snopes comments that this is not in fact a reflection of whether sex is pleasurable or not, but rather a reflection of whether individuals have sex at arbitrary times. They conclude:

"Of course, we have to make many seemingly artificial distinctions to arrive at our conclusion. Animals other than humans have no awareness that their sexual activities are connected with reproduction: They engage in sex because they're biologically driven to do so, and if the fulfillment of their urges produces a physical sensation we might appropriately call 'pleasure,' it isn't the least bit affected by the possibility (or impossibility) of producing offspring. We are also discounting cases in which animals do engage in sex even though reproduction is an impossibility because we claim there are other 'purposes' (of which the animals themselves are unaware) at play. (For example, the females of some species of birds will invite males to mate with them even after they have laid their eggs, but we ascribe a purpose to this behaviour: this is a biological "trick" to fool males into caring for hatchlings they didn't father.) We also employ subjective terms such as 'willingly' and 'regularly' in claiming that bonobos and dolphins are the only other animals who "willingly (and regularly) engage in sex with each other" ... and even then it may be the case that these species have some other 'purpose' for doing so that we haven't yet discovered..."

A 2006 Danish Animal Ethics Council report which examined current knowledge of animal sexuality in the context of legal queries concerning sexual acts by humans, has the following comments, primarily related to domestically common animals:

Even though the evolution-related purpose of mating can be said to be reproduction, it is not actually the creating of offspring which originally causes them to mate. It is probable that they mate because they are motivated for the actual copulation, and because this is

connected with a positive experience. It is therefore reasonable to assume that there is some form of pleasure or satisfaction connected with the act. This assumption is confirmed by the behaviour of males, who in the case of many species are prepared to work to get access to female animals, especially if the female animal is in oestrus, and males who for breeding purposes are used to having sperm collected become very eager, when the equipment they associate with the collection is taken out.
—
There is nothing in female mammals' anatomy or physiology, that contradicts that stimulation of the sexual organs and mating is able to be a positive experience. For instance, the clitoris acts in the same way as with women, and scientific studies have shown that the success of reproduction is improved by stimulation of clitoris on (among other species) cows and mares in connection with insemination, because it improves the transportation of the sperm due to contractions of the inner genitalia. This probably also concerns female animals of other animal species, and contractions in the inner genitals are seen e.g. also during orgasm for women. It is therefore reasonable to assume that sexual intercourse may be linked with a positive experience for female animals.
—

Types of activity

Autoeroticism (masturbation)

It appears that many animals, both male and female, masturbate, both when partners are available and otherwise.

Castration does not prevent masturbation, as it is observed in geldings. Masturbation is common in both mares and stallions, before and after puberty.

The female porcupine has been observed to use a stick as a dildo, holding one end of a stick and walking around, straddling it as it bumped against the ground and vibrated against her genitalia. Sexologist Havelock Ellis in his 1927 "Studies in the Psychology of Sex" identified bulls, goats, sheep, camels and elephants as species known to practice autoeroticism, adding of some other species:

I am informed by a gentleman who is a recognized authority on goats, that they sometimes take the penis into the mouth and produce actual orgasm, thus practicing auto-fellatio. As regards ferrets ... "if the bitch, when in heat, cannot obtain a dog [ie, male ferret] she pines and becomes ill. If a smooth pebble is introduced into the hutch, she will masturbate upon it, thus preserving her normal health for one season. But if this artificial substitute is given to her a second season, she will not, as formerly, be content with it." [...] Blumenbach observed a bear act somewhat similarly on seeing other bears coupling, and hyenas, according to Ploss and Bartels, have been seen practicing mutual masturbation by licking each other's genitals.

In his 1999 book, *Biological exuberance*, Bruce Bagemihl PhD documents (p. 71, 209-210) that:

Autoeroticism also occurs widely among animals, both male and female. A variety of creative techniques are used, including genital stimulation using the hand or front paw (primates, Lions), foot (Vampire Bats, primates), flipper (Walruses), or tail (Savanna Baboons), sometimes accompanied by stimulation of the nipples (Rhesus Macaques, Bonobos); auto-fellating or licking, sucking and/or nuzzling by a male of his own penis (Common Chimpanzees, Savanna Bonobos, Vervet Monkeys, Squirrel Monkeys, Thinhorn Sheep, Bharal, Aovdad, Dwarf Cavies); stimulation of the penis by flipping or rubbing it against the belly or in its own sheath (White-tailed and Mule Deer, Zebras and Takhi); spontaneous ejaculations (Mountain Sheep, Warthogs, Spotted Hyenas); and stimulation of the genitals using inanimate objects (found in several primates and cetaceans).
Many birds masturbate by mounting and copulating with tufts of grass, leaves or mounds of earth, and some mammals such as primates and Dolphins also rub their genitals against the ground or other surfaces to stimulate themselves.
Autoeroticism in female mammals, as well as heterosexual and homosexual intercourse (especially in primates), often involves direct or indirect stimulation of the clitoris [...]. This organ is present in the females of all mammalian species and several other animal groups.

and that:

Apes and Monkeys use a variety of objects to masturbate with and even deliberately create implements for sexual stimulation [...] often in highly creative ways.

Petter Bøckman of the Natural History Museum at the University of Oslo commented (in respect of a 2006 exhibition on homosexuality in the animal kingdom) that:

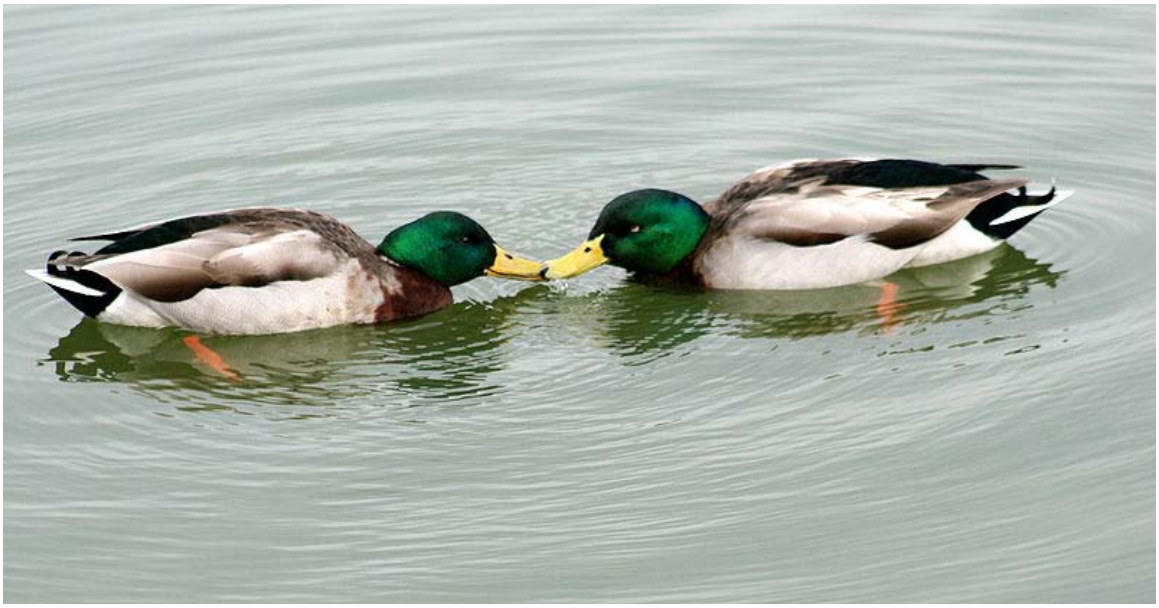
Masturbation is common in the animal kingdom ... We have a Darwinist mentality that all animals only have sex to procreate. But there are plenty of animals who will masturbate when they have nothing better to do. Masturbation has been observed among primates, deer, killer whales and penguins, and we're talking about both males and females. They rub themselves against stones and roots. Orangutans are especially inventive. They make dildos of wood and bark.

Oral sex

Animals of several species are documented as engaging in both autofellatio and oral sex. Although easily confused by lay-people, this is a separate and sexually oriented behaviour, distinct from non-sexual grooming or the investigation of scents.

Auto-fellatio or oral sex in animals is documented in goats, primates, hyaenas, bats and sheep.

Homosexual behaviour



Two male Mallards, *Anas platyrhynchos*. Mallards form male-female pairs only until the female lays eggs, at which time the male leaves the female. Mallards have rates of male-male sexual activity that are unusually high for birds, in some cases, as high as 19% of all pairs in a population.

The presence of same-sex sexual behaviour was not scientifically observed on a large scale until recent times. Homosexual behaviour does occur in the animal kingdom outside humans, especially in social species, particularly in marine birds and mammals, monkeys, and the great apes. Homosexual behaviour has been observed among 1,500 species, and in 500 of those it is well documented.

To turn the approach on its head: No species has been found in which homosexual behaviour has not been shown to exist, with the exception of species that never have sex at all, such as sea urchins and aphis. Moreover, a part of the animal kingdom is hermaphroditic, truly bisexual. For them, homosexuality is not an issue.
—

Georgetown University professor Janet Mann has specifically theorised that homosexual behaviour, at least in dolphins, is an evolutionary advantage that minimizes intraspecies aggression, especially among males.

- Male penguin couples have been documented to mate for life, build nests together, and to use a stone as a surrogate egg in nesting and brooding. In 2004, the Central Park Zoo in the United States replaced one male couple's stone with a fertilized egg, which the couple then raised as their own offspring. German and Japanese zoos have also reported homosexual behaviour among their penguins. This phenomenon has also been reported at Kelly Tarlton's Aquarium in

Auckland, New Zealand. "Humans have created the myth that sexuality can be justified only by reproduction, which by definition limits it to hetero sex," says Michael Bronski, author of The Pleasure Principle: Culture, Backlash, and the Struggle for Gay Freedom. "But here is an animal society that uses homosexuality to improve its social life."

- Mounting of one female by another is common among cattle.
- Bonobos in zoos. After studying the primates for his book *Bonobo: The Forgotten Ape*, primatologist Frans de Waal, a professor of psychology at Emory University in Atlanta, says that such expressions of intimacy are consistent with the homosexual behaviour of what he terms "the erotic champions of the world." "Same-sex, opposite-sex — bonobos just love sex play," de Waal said in an interview. "They have so much sex, it gets boring."
- Homosexual behaviour in male sheep (found in 6-10% of rams) is associated with variations in cerebral mass distribution and chemical activity. A study reported in *Endocrinology* concluded that biological and physiological factors are in effect. These findings are similar to human findings reported by Simon LeVay.

  Approximately eight percent of [male] rams exhibit sexual preferences [that is, even when given a choice] for male partners (male-oriented rams) in contrast to most rams, which prefer female partners (female-oriented rams). We identified a cell group within the medial preoptic area/anterior hypothalamus of age-matched adult sheep that was significantly larger in adult rams than in ewes...

- Male bighorn sheep are divisible into two kinds: the typical males among whom homosexual behaviour, including intercourse, is common and "effeminate sheep", or "behavioural transvestites", which are not known to engage in homosexual behaviour.

Cross species sex

While it is commonly believed that animal sexuality is instinctive and thus somewhat mechanistic, research regularly records that many animals are sexual opportunists, partaking in sexual relations with individuals of visibly distinct species. This is more visible in domesticated species and animals in captivity, as domestication commonly selects for increased breeding rate (and so an accelerated breeding cycle has commonly arisen in domesticated species over the centuries), and also because these species are more easily observed by humans. Nevertheless, animals have been observed in the wild to attempt sexual activity with other species or indeed inanimate objects. Attempts by wild moose to obtain sex from domestic horses are apparently well known by wildlife specialists.

In the wild, where observation is harder, genetic studies have shown a "large number" of inter-species hybrids, and other investigations describe productive and non-productive inter-species mating as a "natural occurrence". Recent genetic evidence strongly suggesting this has occurred even within the history of the human species, and that early humans often had sexual activity with other primate species, is considered below.

Hybrid offspring can result from two organisms of distinct but closely related parent species, although the resulting offspring is not always fertile. According to the definition of a species, if two organisms *cannot or will not* mate and produce a fertile offspring, they are different species. The mule, for example (a horse/donkey cross) is normally sterile, whilst the liger (lion/tiger cross) has fertile females and sterile males. Novosibirsk zoo director Rostislav Shilo says on the liger (born in its zoo); "It's just that the lion and the tiger live in neighboring caves in the Novosibirsk zoo, and got used to each other. It's practically impossible in the wild".

Due to the difficulties of observation, interspecies sex of this kind between two top-level predators, occurring in the wild, was only conclusively documented with the finding of a grizzly-polar bear hybrid in April 2006. Again, as with lions and tigers, the two species would normally not share enough common territory to provide adequate opportunity for much cross-species sexual activity.

Animal sexual advances on, and attempted interactions with, humans and other species, have been documented by ethologists such as Kohler, Gerald Durrell and Desmond Morris, as well as authoritative researchers such as Birute Galdikas who studied orangutans in Borneo. Philosopher and animal welfare activist Peter Singer reports:

While walking through the camp with Galdikas, my informant was suddenly seized by a large male orangutan, his intentions made obvious by his erect penis. Fighting off so powerful an animal was not an option, but Galdikas called to her companion not to be concerned, because the orangutan would not harm her, and adding, as further reassurance, that 'they have a very small penis' ... though the orangutan lost interest before penetration took place.

Prostitution

In some penguin species, the females, even when in a committed relationship, will exchange sexual favours with strange males for the pebbles they need to build their nests. Prostitution was also observed among chimpanzees, who trade food for sex.

Sexual fetishes

Although not often reported, animals, or primates at the least, are able to sexualize inanimate objects similar to the way human beings sexualize the objects of their sexual fetishes. Not only will an animal that has a habitual object for masturbation sometimes appear to sexualize that object, primates have generalized further to sexualize *kinds of objects* for which no instinctual or prior sexual connection exists.

Thus Gabriel, a chimpanzee at the Southwest National Primate Research Center, is said to have a shoe fetish (or possibly a leather fetish) according to caretaker Bert Barrera, and it is reported that:

A male chimpanzee raised in captivity developed a bit of a shoe fetish, masturbating obsessively by rubbing his caretaker's leather boot.

The sexualization of objects or locations is also well recognized in the breeding world. So for example, stallions may often 'drop' (become sexually aroused) upon visiting a location where they have been allowed to have sex before, or upon seeing a stimulus previously associated with sexual activity such as an artificial vagina.

In this case however, the primary structure is Pavlovian conditioning, and the fetishistic association is due to a conditioned response (or association) formed with a distinctive 'reward'. Human fetishism can also be traced back to similar or near-identical conditioning: likewise based upon the Pavlovian association between an erotic sensation or anticipation, and objects which become mentally associated with that activity.

Sexual imagery viewing

A study by Platt, Khera and Deaner at Duke University North Carolina (reported in *Current Biology* and online here), showed that male monkeys will give up privileges (in this case, juice, which is highly valued), to be allowed to see a female monkey's hindquarters.

Deaner and his team reported that monkeys would take a juice cut to look at powerful males' faces or the perineum of a female, but to persuade the monkeys to stare at subordinate males, the researchers had to bribe them with larger drinks. "Virtually all [male] monkeys will give up juice to see female hindquarters ... they really value the images."

The researchers stress that in monkey society, such behaviours have great social utility and we should therefore not simply reach the conclusion that "monkeys enjoy pornographic pictures". There is no evidence at this point that viewable pictures or movies of sexual activity are valued for their sexual enjoyment, although as noted above (Masturbation), there are reports that watching sex in real life may have such an effect. The subject of animals and sexual imagery is not yet well researched.

Problems with encouraging pandas to mate in captivity have been very common. However, showing young male pandas "panda pornography" is widely credited with a recent population boom among pandas in zoos.

Coercive sex

Controversial interpretations and implications aside, sex in a forceful or apparently coercive context has also been documented in a variety of species. A notable example is bottlenose dolphins, where at times, a pod of bachelor males will 'corner' a female. Furthermore, in a zoo where it is common practice to put newly captured dolphins in with dolphins who are established in their enclosures, other species of dolphin are never put in together with bottlenoses because the bottlenose dolphins frequently torment and rape

them. The behaviour is also common in some arachnids (spiders), notably those whose females eat the males during sex if not tricked with food and/or tied down with threads, and in some herbivorous herd species or species where males and females are very different in size, where the male dominates sexually by sheer force and size.

Some species of birds appear to combine sexual intercourse with apparent violent assault; these include ducks, geese, and white-fronted bee-eaters. According to Emlen and Wrege (1986) forced copulations occur in this socially nesting species, and females must avoid the unwelcome attention of males as they emerge from their nest burrows or they are forced to the ground and mated with. Apparently, such attacks are made preferentially on females who are laying and who may thus mother their offspring as a result.

In 2007, research suggested that in the *Acilius* genus of water beetles (also known as "diving beetles"), an "evolutionary arms race" between the genders means that there is no courtship system for these beetles. "It's a system of rape. But the females don't take things quietly. They evolve counter-weapons." Cited mating behaviours include males suffocating females underwater till exhausted, and allowing only occasional access to the surface to breathe for up to six hours (to prevent them breeding with other males), and females which have a variety of body shapings (to prevent males from gaining a grip). Foreplay is "limited to the female desperately trying to dislodge the male by swimming frantically around."

Charles Siebert reports in his New York Times article *Elephant Crackup?* that:

Since the early 1990's, for example, young male elephants in Pilanesberg National Park and the Hluhluwe-Umfolozi Game Reserve in South Africa have been raping and killing rhinoceroses; this abnormal behaviour, according to a 2001 study in the journal Pachyderm, has been reported in ''a number of reserves'' in the region.
—

Sex between adults and juveniles

It has also been recorded that certain species of mole will impregnate newborns of their own species. It is not clear if this is forceful or not. Similarly, the male stoat (Mustela erminea) will mate with infant females of their species. This apparently is a natural part of their reproductive biology - there is a delayed gestation period, so these females give birth the following year when they are fully grown.

A male spotted hyena which attempted to mate with a female which succeeded in driving it off, eventually turned to its ten-month-old cub, repeatedly mounting it and ejaculating on it. The cub sometimes ignored this and sometimes struggled 'slightly as if in play'. The mother did not intervene.

Infants and children in Bonobo societies are often involved in sexual behaviour.

Sexual cannibalism

Sexual cannibalism, which has been documented in arachnids, insects and amphipods, is a phenomenon in which a female organism kills and consumes the male before, during, or after copulation. Although it does confer some known advantages to reproduction, whether or not the male is complicit has not been scientifically determined.

Necrophilia

Necrophilia in animals is where a living animal engages in a sexual act with a dead animal. In one of the most well-known examples, Kees Moeliker of the Rotterdam Natural History Museum, Netherlands observed sexual activities outside his office between a live duck and a dead one. Two male mallards which Moeliker believed were engaged in rape flight, a common motif in duck sexual behaviour, collided with his window. "When one died the other one just went for it and didn't get any negative feedback—well, didn't get any feedback," according to Moeliker, who described the event as "homosexual necrophilia." The case was reported scientifically in Deinsea 8-2001, along with photos., and earned Moeliker an Ig Nobel Prize in biology, awarded for research that cannot or should not be reproduced.

Additionally, male cane toads have been documented (in Cane Toads: An Unnatural History) engaging in copulation with dead toads and inanimate objects.

Notes on specific species

Bonobos

The Bonobo, which has a matriarchal society, is a fully bisexual species — both males and females engage in sexual behaviour with the same and the opposite sex, with females being particularly noted for engaging in sexual behaviour with each other and at up to 75% of sexual activity being nonreproductive. Primatologist Frans de Waal believes that Bonobos use sexual activity to resolve conflict between individuals. Sexual activity occurs between almost all ages and sexes of Bonobo societies.

Birds

Some black swans of Australia form sexually active male-male mated pairs and steal nests, or form temporary threesomes with females to obtain eggs, driving away the female after she lays the eggs. More of their cygnets survive to adulthood than those of different-sex pairs possibly due to their superior ability to defend large portions of land.

In early February 2004 the *New York Times* reported that a male pair of chinstrap penguins named Roy and Silo in the Central Park Zoo in New York City were partnered and had successfully hatched a female chick from an egg. Other penguins in New York have also been reported to be forming same-sex pairs.

Zoos in Japan and Germany have also documented male penguin couples. The couples have been shown to build nests together and use a stone to replace an egg in the nest. Researchers at Rikkyo University in Tokyo, found twenty such pairs at sixteen major aquariums and zoos in Japan. Bremerhaven Zoo in Germany attempted to break up the male couples by importing female penguins from Sweden and separating the male couples; they were unsuccessful. The zoo director stated the relationships were too strong between the couples.

Recently, a mated pair of swans in Boston were found to both be female. They too had attempted to raise eggs together.

Studies have shown that ten to fifteen percent of female western gulls in some populations in the wild prefer other females.

As many as 19% of Mallard pairs in a given population have been observed to consist of male-male homosexuals.

Lizards

Whip-tailed lizard females have the ability to reproduce through parthenogenesis and as such males are rare and sexual breeding non-standard. Females engage in sexual behaviour to stimulate ovulation, with their behaviour following their hormonal cycles; during low levels of estrogen, these (female) lizards engage in "masculine" sexual roles. Those animals with currently high estrogen levels assume "feminine" sexual roles.

Lizards that perform the courtship ritual have greater fecundity than those kept in isolation due to an increase in hormones triggered by the sexual behaviours. So, even though asexual whiptail lizards populations lack males, sexual stimuli still increase reproductive success.

From an evolutionary standpoint these females are passing their full genetic code to all of their offspring rather than the 50% of genes that would be passed in sexual reproduction. Certain species of gecko also reproduce by parthenogenesis.

Flatworm

Penis fencing is a mating behaviour engaged in by certain species of flatworm, such as *Pseudobiceros bedfordi*. Species which engage in the practice are hermaphroditic, possessing both eggs and sperm-producing testes.

The species "fence" using two-headed dagger-like penises which are pointed, and white in color. One organism inseminates the other. The sperm is absorbed through pores in the skin, causing fertilization.

Sheep

An October 2003, study by Dr. Charles E. Roselli et al. (Oregon Health & Science University) states that homosexuality in male sheep (found in eight percent of rams) is associated with a region in the rams' brains which the authors call the "ovine Sexually Dimorphic Nucleus" (oSDN) which is half the size of the corresponding region in other male sheep.

However, some view this study to be flawed in that the determination of homosexuality within the sheep, (sample population of twenty-seven for the study), was to have animals who were unable to mount female ewes placed in a cage with two stanchioned males and two unstanchioned females (that is, the males could not move or struggle while the females could). Given the aggressive nature of the sheep copulation, the uneven treatment of males and females, many see this as simply evidence that the sheep in question were unable to be aggressive enough to mount females. Some say that the results were situational sexuality, unlike the bonds seen in human homosexuality.

The scientists found that, "The oSDN in rams that preferred females was significantly larger and contained more neurons than in male-oriented rams and ewes. In addition, the oSDN of the female-oriented rams expressed higher levels of aromatase, a substance that converts testosterone to estradiol, an estrogen hormone believed to facilitate typical male sexual behaviours. Aromatase expression was no different between male-oriented rams and ewes."

"The dense cluster of neurons that comprise the oSDN express cytochrome P450 aromatase. Aromatase mRNA levels in the oSDN were significantly greater in female-oriented rams than in ewes, whereas male-oriented rams exhibited intermediate levels of expression." These results suggest that "...naturally occurring variations in sexual partner preferences may be related to differences in brain anatomy and its capacity for estrogen synthesis." As noted previously, given the potential unagressiveness of the male population in question, the differing aromatase levels may also have been evidence of aggression levels, not sexuality. The results of this study have not been confirmed by others.

Spotted Hyena

The female Spotted Hyena has a unique urinary-genital system, closely resembling the penis of the male, called a pseudo-penis. The family structure is matriarchal and dominance relationships with strong sexual elements are routinely observed between related females.

They are notable for using visible sexual arousal as a sign of *submission* and not *dominance*, in males as well as females (females have a sizable erectile clitoris), to the extent that biologist Robert Sapolsky speculates that in order to facilitate this, their sympathetic and parasympathetic nervous systems may be partially reversed in respect to their reproductive organs.

Bottlenose Dolphins

Bottlenose Dolphin males have been observed working in pairs to follow and/or restrict the movement of a female for weeks at a time, waiting for her to become sexually receptive. The same pairs have also been observed engaging in intense sexual play with each other.

Janet Mann, a professor of biology and psychology at Georgetown University, argues that the common same-sex behaviour among male dolphin calves is about bond formation and benefits the species evolutionarily. They cite studies that have shown the dolphins later in life are bisexual and the male bonds forged from homosexuality work for protection as well as locating females with which to reproduce.

In 1991 an English man was prosecuted for allegedly having sexual contact with a dolphin. The man was found not guilty after it was revealed at trial that the dolphin was known to tow bathers through the water by hooking its large penis around them.

Seahorses

Seahorses, long upheld as monogamous and mating for life, are identified as "promiscuous, flighty, and more than a little bit gay" according to research published in 2007.

Scientists at 15 aquariums studied 90 seahorses of 3 species. Of 3168 sexual encounters, 37% were same sex acts. Flirting was common (up to 25 potential partners a day of both genders); only one species (the British Spiny Seahorse) included faithful representatives, and for these 5 of 17 were faithful, 12 were not. Bisexuality was widespread and considered "both a great surprise and a shock", with big bellied seahorses of both genders not showing partner preference. 1986 contacts were male-female, 836 were female-female and 346 were male-male.

Lions

Male lions often lead their social groups jointly with one or more of their brothers. To ensure loyalty, the male co-leaders will "strengthen the bonds" by often having sex with each other.

Horses

Anecdotal evidence suggest that some horses have environment or appearance preferences when selecting mates. There is also anecdotal evidence of limited bisexual behaviour in some stallions, although there is (as of 2008) no conclusive scientific confirmation. The anecdotal evidence claims this is most likely to occur in a single isolated group, with no access to mares.

Humboldt penguins

In 2009 at a zoo in Bremerhaven, Germany, two male adult humboldt penguins adopted an egg that had been abandoned by its biological parents. After the egg hatched, the two penguins raised, protected, cared for, and fed the chick in the same manner that heterosexual penguins raise their own biological offspring.

Other evidence of interspecies sexual activity

Looking back in history, current research into human evolution tends to confirm that in some cases, interspecies sexual activity may have been responsible for the evolution of entire new species. Analysis of human and animal genes in 2006 provides strong evidence that after humans had diverged from other apes, interspecies mating nonetheless occurred regularly enough to change certain genes in the new gene pool:

A new comparison of the human and chimp genomes suggests that after the two lineages separated, they may have begun interbreeding. [...] A principal finding is that the X chromosomes of humans and chimps appear to have diverged about 1.2 million years more recently than the other chromosomes.

The research suggests that:

There were in fact two splits between the human and chimp lineages, with the first being followed by interbreeding between the two populations and then a second split. The suggestion of a hybridization has startled paleoanthropologists, who nonetheless are "treating the new genetic data seriously."

The *Washington Post* comments, "If this theory proves correct, it will mean modern people are descended from something akin to chimp-human hybrids."

A 1932 exploitation film, *The Sex Life of a Gorilla,* was based on supposed reports of primitive cults in Africa routinely having sexual relations with gorillas.

Role in discussion of human sexuality

Information about animal sexuality frequently arises as a persuasive device in arguments regarding human sexuality. Originally, the lack of documented animal sexual behaviour deviant from heterosexual sexual monogamy was used to argue that the dominant heterosexual monogamy of most modern human societies is more natural and acceptable. Likewise, the lack of documented sex between animals for the purpose of pleasure was used to promote the moral standard of reserving sex primarily for procreation. Proponents of alternate sexuality attribute this early lack of documented evidence to an observer bias in researchers, who, they argue, tended to interpret sexual behaviour inconsistent with their values as other behaviour.

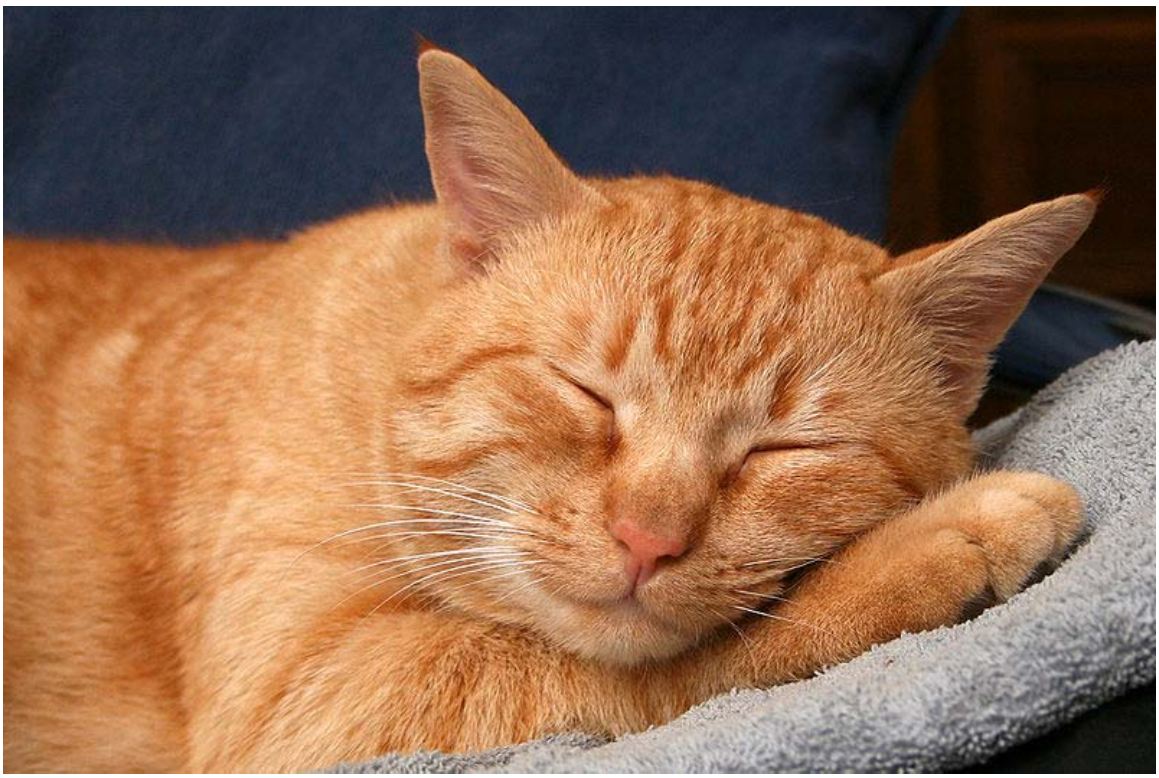
With increasing published evidence of different types of sexual behaviour between animals, arguments for heterosexual monogamy in human society have moved towards characterizing these behaviours as resulting from differences between humans and animals, and in particular on ambiguity in motivation and subjective experience in animals, which is difficult to study. Arguments identifying human and animal behaviour are characterized as anthropomorphism, and in some cases an opposite observer bias is attributed to researchers. Supporters of alternate sexuality embrace the new research as confirmation of the naturalness of alternate sexual behaviour and evidence of its long-term feasibility and utility.

In both cases, any argument that claims that something is good or right because it is natural, or that something is bad or wrong because it is unnatural or artificial is know as the appeal to nature fallacy.

Chapter- 8

Sleep (Non-Human)

Sleep in non-human animals refers to how the behavioral and physiological state of sleep, mainly characterized by reversible unconsciousness, non-responsiveness to external stimuli, and motor passivity, appears in different categories of animals.



A sleeping cat. The upright ears and the body position suggest the cat is experiencing NREM sleep. In REM sleep, the ears would have been tucked in and the skeletal muscles would have been relaxed due to the functional paralysis signifying REM sleep.

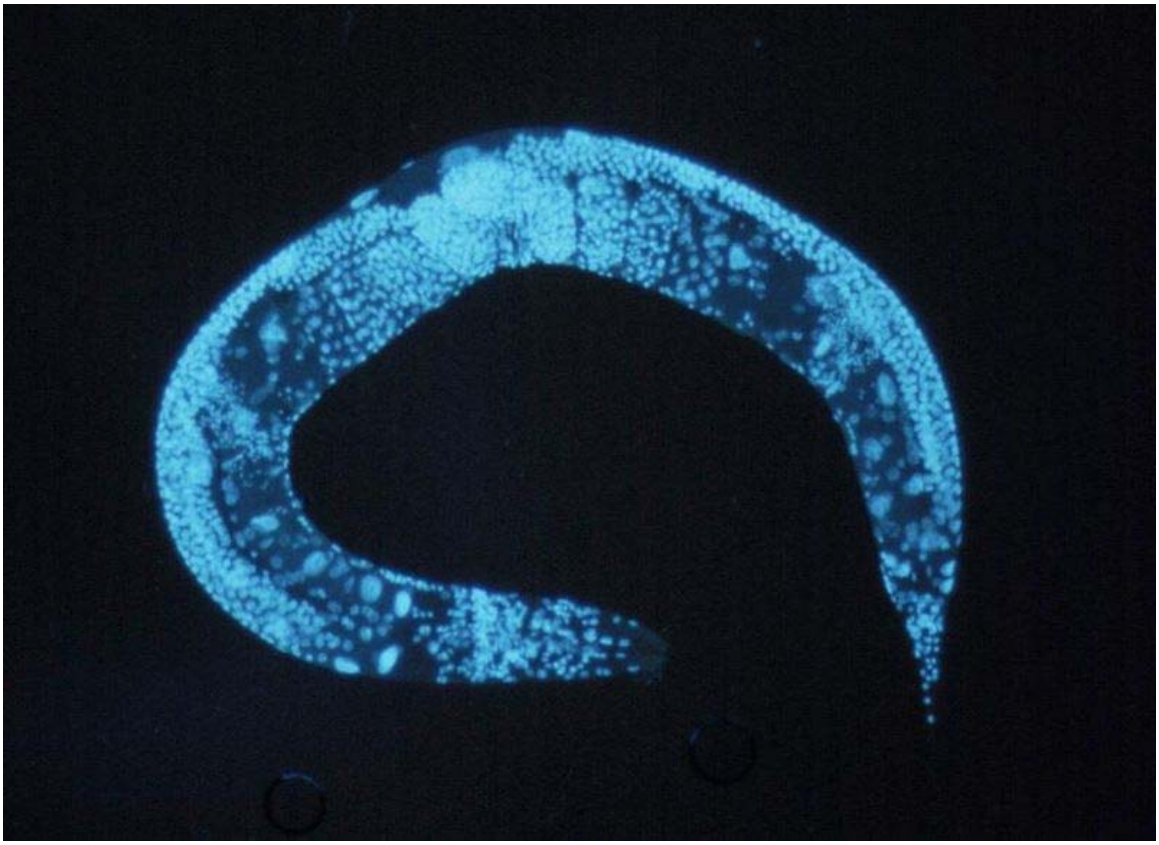
Rats kept from sleeping die within a couple of weeks, but the exact function of sleep is still unknown.

Definition

Sleep can follow a physiological or behavioral definition. In the physiological sense, sleep is a state characterized by reversible unconsciousness, special brainwave patterns, sporadic eye movement, loss of muscle tone (possibly with some exceptions; see below regarding the sleep of birds and of aquatic mammals), and a compensatory increase following deprivation of the state. In the behavioral sense, sleep is characterized by non-responsiveness to external stimuli, the adoption of a typical posture, and the occupation of a sheltered site, all of which is usually repeated on a 24-hour basis. The physiological definition applies well to birds and mammals, but in other animals (whose brain is not as complex), the behavioral definition is more often used. In very simple animals, behavioral definitions of sleep are the only ones possible, and even then the behavioral repertoire of the animal may not be extensive enough to allow distinction between sleep and wakefulness.

Sleep in different species

Sleep in invertebrates



Caenorhabditis elegans is the most primitive organism in which sleep-like states have been observed.

Sleep as a phenomenon appears to have very old evolutionary roots. The nematode *C. elegans* is the most primitive organism in which sleep-like states have been observed. Here, a *lethargus* phase occurs in short periods preceding each moult, a fact which may indicate that sleep primitively is connected to developmental processes. Raizen *et al.*'s results furthermore suggest that sleep is necessary for changes in the neural system.

The electrophysiological study of sleep in small invertebrates is complicated. However, even such simple animals as fruit flies appear to sleep, and systematic disturbance of that state leads to cognitive disabilities. There are several methods of measuring cognitive functions in fruit flies. A common method is to let the flies choose whether they want to fly through a tunnel that leads to a light source, or through a dark tunnel. Normally, flies are attracted to light. But if sugar is placed in the end of the dark tunnel, and something the flies dislike is placed in the end of the light tunnel, the flies will eventually learn to fly towards darkness rather than light. Flies deprived of sleep require a longer time to learn this and also forget it more quickly. If an arthropod is experimentally kept awake longer than it is used to, then its coming rest period will be prolonged. In cockroaches that rest period is characterized by the antennae being folded down and by a decreased sensitivity to external stimuli. Sleep has been described in crayfish, too, characterized by passivity and increased thresholds for sensory stimuli as well as changes in the EEG pattern, markedly differing from the patterns found in crayfish when they are awake.

Sleep in fish and reptiles

Sleep in fish is not extensively studied. Some species that always live in shoals or that swim continuously (because of a need for ram ventilation of the gills, for example) are suspected never to sleep. There is also doubt about certain blind species that live in caves. Other fishes seem to sleep, however. For example, zebrafish, tilapia, tench, brown bullhead, and swell shark become motionless and unresponsive at night (or by day, in the case of the swell shark); Spanish hogfish and blue-headed wrasse can even be lifted by hand all the way to the surface without evoking a response. A 1961 observational study of approximately 200 species in European public aquaria reported many cases of apparent sleep. On the other hand, sleep patterns are easily disrupted and may even disappear during periods of migration, spawning, and parental care.

Sleeping African Dwarf Fischers chameleon: *Kinyongia tavetanum*, previously known as *Bradypodion tavetanum*.

A Komodo dragon sleeping

Reptiles have been subjected to electrophysiological studies of sleep. That is to say that electrical activity in the brain has been registered when the animals have been asleep. However, the EEG pattern in reptilian sleep differs from what is seen in mammals and other higher animals. In reptiles, sleep time increases following sleep deprivation, and stronger stimuli are needed to awaken the animals when they have been deprived of sleep as compared to when they have slept normally. This suggests that the sleep which follows deprivation is compensatorily deeper.

Sleep in birds

A sleeping Cockatiel

There are significant similarities between sleep in birds and sleep in mammals, which is one of the reasons for the idea that sleep in higher animals with its division into REM and NREM sleep has evolved together with warm-bloodedness. Birds compensate for sleep loss in a manner similar to mammals, by deeper or more intense SWS (slow-wave sleep).

Birds have both REM and NREM sleep, and the EEG patterns of both have similarities to those of mammals. Different birds sleep different amounts, but the associations seen in mammals between sleep and variables such as body mass, brain mass, relative brain mass, basal metabolism and other factors (see below) are not found in birds. The only clear explanatory factor for the variations in sleep amounts for birds of different species is that birds who sleep in environments where they are exposed to predators have less deep sleep than birds sleeping in more protected environments.

A flamingo with at least one cerebral hemisphere awake

A peculiarity that birds share with aquatic mammals, and possibly also with certain species of lizards (opinions differ about that last point), is the ability for unihemispheric sleep. That is the ability to sleep with one cerebral hemisphere at a time, while the other hemisphere is awake. When only one hemisphere is sleeping, only the contralateral eye will be shut; that is, when the right hemisphere is asleep the left eye will be shut, and vice versa. The distribution of sleep between the two hemispheres and the amount of unihemispheric sleep are determined both by which part of the brain has been the most active during the previous period of wake—that part will sleep the deepest—and it is also determined by the risk of attacks from predators. Ducks near the perimeter of the flock are likely to be the ones that first will detect predator attacks. These ducks have significantly more unihemispheric sleep than those who sleep in the middle of the flock, and they react to threatening stimuli seen by the open eye.

Opinions partly differ about sleep in migratory birds. The controversy is mainly about whether they can sleep while flying or not. Theoretically, certain types of sleep could be possible while flying, but technical difficulties preclude the recording of brain activity in birds while they are flying.

Sleep in mammals

Flying foxes, asleep

Sleep duration

Different animals sleep different amounts. Some animals, such as bats, sleep 18–20 hours per day, while others, including giraffes, sleep only 3–4 hours per day. There can be big differences even between closely related animals. There can also be differences between laboratory and field studies: for example, researchers in 1983 reported that captive sloths slept nearly 16 hours a day, but in 2008, when miniature neurophysiological recorders were developed that could be affixed to wild animals, sloths in nature were found to sleep only 9.6 hours a day.

Sleeping polar bears

As for birds, the main rule for mammals (with certain exceptions, see below) is that they have two essentially different stages of sleep: REM and NREM sleep (see above). An animal's feeding habits are associated with its sleep length. The daily need for sleep is highest in carnivores, lower in omnivores and lowest in herbivores. Humans do not sleep unusually much or unusually little compared to other animals, but we sleep less than many other omnivores. Many herbivores, like Ruminantia (such as cattle), spend much of their wake time in a state of drowsiness, which perhaps could partly explain their relatively low need for sleep. In herbivores, a direct correlation is apparent between body mass and sleep length; big animals sleep more than smaller ones. This correlation is thought to explain about 25% of the difference in sleep amount between different animals. Also, the length of a particular sleep cycle is associated with the size of the animal; on average, bigger animals will have sleep cycles of longer durations than smaller animals. Sleep amount is also coupled to factors like basal metabolism, brain mass and relative brain mass.

Mammals born with well-developed regulatory systems, such as the horse and giraffe, tend to have less REM sleep than the species which are less developed at birth, such as cats and rats. This appears to echo the greater need for REM sleep among newborns than among adults in most mammal species.

Sleep in monotremes

Since monotremes, egg-laying mammals, are considered to represent one of the evolutionarily oldest groups of mammals, they have been subject to special interest in the study of mammalian sleep. As early studies of these animals could not find clear evidence for REM sleep, it was initially assumed that such sleep did not exist in monotremes but developed after the monotremes left the rest of the mammals and became a separate, distinct group. However, EEG registrations of the brain stem in monotremes show a firing pattern that is quite similar to the patterns seen in REM sleep in higher mammals. In fact, the largest amount of REM sleep known in any animal is found in the platypus.

Sleep in aquatic mammals

Northern Sea Lion pup with adult female and male, the largest of the eared seals. Habitat: the northern Pacific

Among others, seals and whales belong to the aquatic mammals. Seals are grouped in earless seals and eared seals, which have solved the problem of sleeping in water differently. Eared seals, like whales, show unihemispheric sleep. The sleeping half of the brain does not awaken when they surface to breathe. When one half of a seal's brain shows slow-wave sleep, the flippers and whiskers on its opposite side are immobile.

While in the water, these seals have almost no REM sleep and may go a week or two without it. As soon as they move onto land they switch to bilateral REM sleep and NREM sleep comparable to land mammals, surprising researchers with their lack of "recovery sleep" after missing so much REM.

Cape Fur Seal, asleep in a zoo

Earless seals sleep bihemispherically like most mammals, under water, hanging at the water surface or on land. They hold their breath while sleeping under water, and wake up regularly to surface and breathe. They can also hang with their nostrils above water and in that position have REM sleep, but they do not have REM sleep underwater.

REM sleep has been observed in the pilot whale, a species of dolphin. Whales do not seem to have REM sleep, nor do they seem to have any problems because of this. One reason REM sleep might be difficult in marine settings is the fact that REM sleep causes muscular atony; that is to say, a functional paralysis of skeletal muscles that can be difficult to combine with the need to breathe regularly.

Unihemispheric sleep

Unihemispheric sleep refers to sleeping with only a single cerebral hemisphere. The phenomenon has been observed in birds and aquatic mammals, as well as in several

reptilian species (the latter being disputed: many reptiles behave in a way which could be construed as unihemispheric sleeping, but EEG studies have given contradictory results). Reasons for the development of unihemispheric sleep are likely that it enables the sleeping animal to receive stimuli, threats, for instance, from its environment, and that it enables the animal to fly or periodically surface to breathe when immersed in water. Only NREM sleep exists unihemispherically, and there seems to exist a continuum in unihemispheric sleep regarding the differences in the hemispheres: in animals exhibiting unihemispheric sleep, conditions range from one hemisphere being in deep sleep with the other hemisphere being awake to one hemisphere sleeping lightly with the other hemisphere being awake. If one hemisphere is selectively deprived of sleep in an animal exhibiting unihemispheric sleep (one hemisphere is allowed to sleep freely but the other is awoken whenever it falls asleep), the amount of deep sleep will selectively increase in the hemisphere that was deprived of sleep when both hemispheres are allowed to sleep freely.

The neurobiological background for unihemispheric sleep is still unclear. In experiments on cats, where the connection between the left and the right halves of the brain stem is severed, the brain hemispheres show a desynchronized EEG where the two hemispheres can sleep independently of each other. In these cats, the state where one hemisphere slept NREM and the other was awake, as well as one hemisphere sleeping NREM with the other state sleeping REM were observed. Interestingly, the cats were never seen to sleep REM sleep with one hemisphere while the other hemisphere was awake. This is in accordance with the fact that REM sleep, as far as is currently known, does not occur unihemispherically.

Sleep in hibernating animals

Animals that hibernate are in a state of torpor, differing from sleep. Hibernation markedly reduces the need for sleep, but does not remove it. Hibernating animals end their hibernation a couple of times during the winter so that they can sleep.

Chapter- 9

Collective Animal Behavior

Sort sol. Starling flock at sunset in Denmark

Collective animal behavior describes the coordinated behavior of large groups of similar animals and the emergent properties of these groups. Facets of this topic include the costs and benefits of group membership, the transfer of information across the group, the group decision-making process, and group locomotion and synchronization. Studying the principles of collective animal behavior has relevance to human engineering problems through the philosophy of biomimetics. For instance, determining the rules by which an individual animal navigates relative to its neighbors in a group can lead to advances in

the deployment and control of groups of swimming or flying micro-robots such as UAVs (Unmanned Aerial Vehicles).

Examples

Examples of collective animal behavior include:

- Flocking birds
- Herding ungulates
- Shoaling and schooling fish
- Swarming Antarctic krill
- Pods of dolphins
- Marching locusts
- Nest building ants

Proposed functions

Many functions of animal aggregations have been proposed. These proposed functions may be grouped into the four following categories: social and genetic, anti-predator, enhanced foraging, and increased locomotion efficiency.

Social interaction

Support for the social and genetic function of aggregations, especially those formed by fish, can be seen in several aspects of their behavior. For instance, experiments have shown that individual fish removed from a school will have a higher respiratory rate than those found in the school. This effect has been attributed to stress, and the effect of being with conspecifics therefore appears to be a calming one and a powerful social motivation for remaining in an aggregation. Herring, for instance, will become very agitated if they are isolated from conspecifics. Fish schools have also been proposed to serve a reproductive function since they provide increased access to potential mates.

Protection from predators

School of goldband fusiliers

Several anti-predator functions of animal aggregations have been proposed. One potential method by which fish schools or bird flocks may thwart predators is the 'predator confusion effect' proposed and demonstrated by Milinksi and Heller (1978). This theory is based on the idea that it becomes difficult for predators to pick out individual prey from groups because the many moving targets create a sensory overload of the predator's visual channel.

A second potential anti-predator effect of animal aggregations is the 'many eyes' hypothesis. This theory states that as the size of the group increases, the task of scanning the environment for predators can be spread out over many individuals. Not only does this mass collaboration presumably provide a higher level of vigilance, it could also allow more time for individual feeding.

A third hypothesis for an anti-predatory effect of animal aggregation is the 'encounter dilution' effect. Hamilton, for instance, proposed that the aggregation of animals was due to a "selfish" avoidance of a predator and was thus a form of cover-seeking. Another formulation of the theory was given by Turner and Pitcher and was viewed as a combination of detection and attack probabilities. In the detection component of the theory, it was suggested that potential prey might benefit by living together since a

predator is less likely to chance upon a single group than a scattered distribution. In the attack component, it was thought that an attacking predator is less likely to eat a particular animal when a greater number of individuals are present. In sum, an individual has an advantage if it is in the larger of two groups, assuming that the probability of detection and attack does not increase disproportionately with the size of the group.

Enhanced foraging

A third proposed benefit of animal groups is that of enhanced foraging. This ability was demonstrated by Pitcher and others in their study of foraging behavior in shoaling cyprinids. In this study, the time it took for groups of minnows and goldfish to find a patch of food was quantified. The number of fishes in the groups was varied, and a statistically significant decrease in the amount of time necessary for larger groups to find food was established. Further support for an enhanced foraging capability of schools is seen in the structure of schools of predatory fish. Partridge and others analyzed the school structure of Atlantic bluefin tuna from aerial photographs and found that the school assumed a parabolic shape, a fact that was suggestive of cooperative hunting in this species (Partridge et al., 1983).

Increased locomotion efficiency

This theory states that groups of animals moving in a fluid environment may save energy when swimming or flying together, much in the way that bicyclists may draft one another in a peloton. Geese flying in a Vee formation are also thought to save energy by flying in the updraft of the wingtip vortex generated by the previous animal in the formation. Ducklings have also been shown to save energy by swimming in a line. Increased efficiencies in swimming in groups have also been proposed for schools of fish and Antarctic krill.

Group structure

The structure of large animal groups has been difficult to study because of the large number of animals involved. The experimental approach is therefore often complemented by mathematical modeling of animal aggregations.

Experimental approach

Experiments investigating the structure of animal aggregations seek to determine the 3D position of each animal within a volume at each point in time. It is important to know the internal structure of the group because that structure can be related to the proposed motivations for animal grouping. This capability requires the use of multiple cameras trained on the same volume in space, a technique known as stereophotogrammetry. When hundreds or thousands of animals occupy the study volume, it becomes difficult to identify each one. In addition, animals may block one another in the camera views, a problem known as occlusion. Once the location of each animal at each point in time is known, various parameters describing the animal group can be extracted.

These parameters include:

Density: The density of an animal aggregation is the number of animals divided by the volume (or area) occupied by the aggregation. Density may not be a constant throughout the group. For instance, starling flocks have been shown to maintain higher densities on the edges than in the middle of the flock, a feature that is presumably related to defense from predators.

Polarity: The group polarity describes if the group animals are all pointing in the same direction or not. In order to determine this parameter, the average orientation of all animals in the group is determined. For each animal, the angular difference between its orientation and the group orientation is then found. The group polarity is then the average of these differences (Viscido 2004).

Nearest Neighbor Distance: The nearest neighbor distance (NND) describes the distance between the centroid of one animal (the focal animal) and the centroid of the animal nearest to the focal animal. This parameter can be found for each animal in an aggregation and then averaged. Care must be taken to account for the animals located at the edge of an animal aggregation. These animals have no neighbor in one direction.

Nearest Neighbor Position: In a polar coordinate system, the nearest neighbor position describes the angle and distance of the nearest neighbor to a focal animal.

Packing Fraction: Packing fraction is a parameter borrowed from physics to define the organization (or state i.e. solid, liquid, or gas) of 3D animal groups. It is an alternative measure to density. In this parameter, the aggregation is idealized as an ensemble of solid spheres, with each animal at the center of a sphere. The packing fraction is defined as the ratio of the total volume occupied by all individual spheres divided by the global volume of the aggregation (Cavagna 2008). Values range from zero to one, where a small packing fraction represents a dilute system like a gas. Cavagna found that the packing fraction for groups of starlings was 0.012.

Integrated Conditional Density: This parameter measures the density at various length scales and therefore describes the homogeneity of density throughout an animal group.

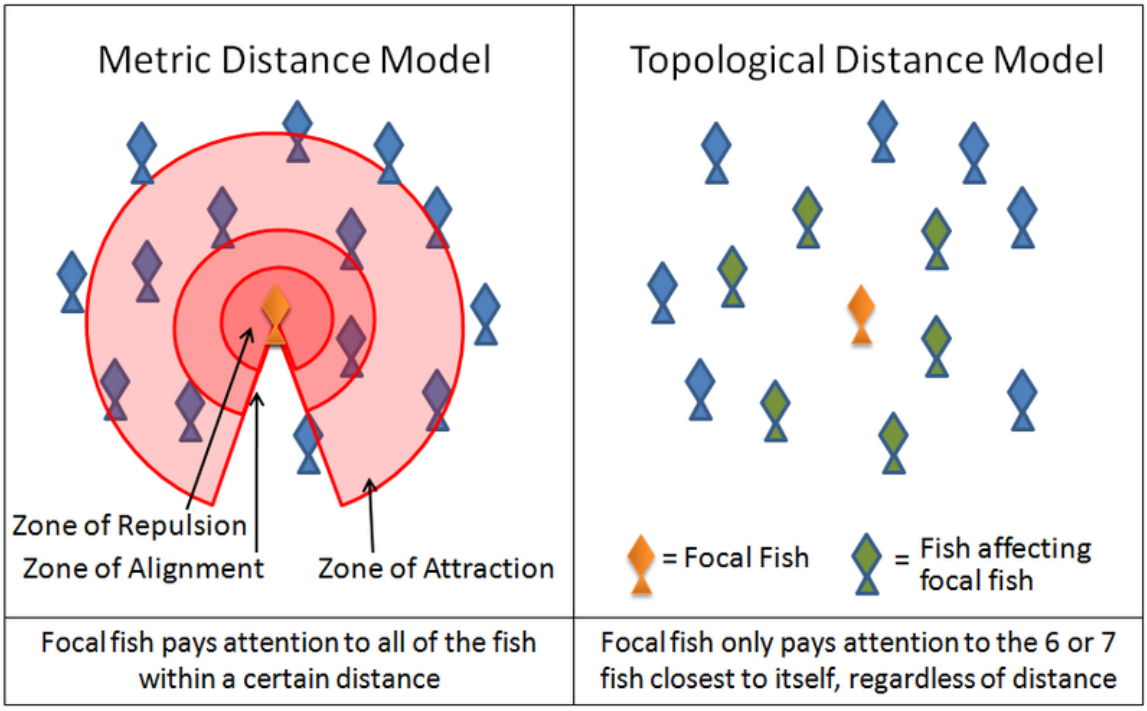
Pair Distribution Function: This parameter is usually used in physics to characterize the degree of spatial order in a system of particles. It also describes the density, but this measures describes the density at a distance away from a given point. Cavagna et al. found that flocks of starlings exhibited more structure than a gas but less than a liquid.

Modeling approach

The simplest mathematical models of animal aggregations generally instruct the individual animals to follow three rules:

1. Move in the same direction as your neighbor

2. Remain close to your neighbors
3. Avoid collisions with your neighbors



A diagram illustrating the difference between 'metric distance' and 'topological distance' in reference to fish schools

An example of such a simulation is the Boids program created by Craig Reynolds in 1986. Another is the Self Propelled Particle model. Many current models use variations on these rules. For instance, many models implement these three rules through layered zones around each animal. In the zone of repulsion very close to the animal, the focal animal will seek to distance itself from its neighbors in order to avoid a collision. In the slightly further away zone of alignment, a focal animal will seek to align its direction of motion with its neighbors. In the outmost zone of attraction, which extends as far away from the focal animal as it is able to sense, the focal animal will seeks to move towards a neighbor. The shape of these zones will necessarily be affected by the sensory capabilities of the animal. For example, the visual field of a bird does not extend behind its body. Fish, on the other hand, rely on both vision and on hydrodynamic signals relayed through its lateral line. Antarctic krill rely on vision and on hydrodynamic signals relayed through its antennae.

Recent studies of starling flocks have shown, however, 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 rule rather than a metric rule. It remains to be seen whether the same rule can be applied to other animals.

Collective decision making

Aggregations of animals are faced with decisions which they must make if they are to remain together. For a school of fish, an example of a typical decision might be which direction to swim when confronted by a predator. Social insects such as ants and bees must collectively decide where to build a new nest. A herd of elephants must decide when and where to migrate. How are these decisions made? Do stronger or more experienced 'leaders' exert more influence than other group members, or does the group make a decision by consensus? The answer probably depends on the species. While the role of a leading matriarch in an elephant herd is well known, studies have shown that some animal species use a consensus approach in their collective decision-making process.

A recent investigation showed that small groups of fish used consensus decision-making when deciding which fish model to follow. The fish did this by a simple quorum rule such that individuals watched the decisions of others before making their own decisions. This technique generally resulted in the 'correct' decision but occasionally cascaded into the 'incorrect' decision. In addition, as the group size increased, the fish made more accurate decisions in following the more attractive fish model. Consensus decision-making, a form of collective intelligence, thus effectively uses information from multiple sources to generally reach the correct conclusion.

Chapter- 10

Cat Behavior

Cat eating grass

Cat behavior generally refers to the behaviors and habits of domestic cats, including body language and communication. Cat behavior may vary among breeds and individual cats. Many common behaviors include hunting techniques and reactions to certain events as well as interactions with humans and other animals, such as dogs. Communication can vary greatly depending on a cat's temperament. In a family with multiple cats, social position can also affect behavior patterns with others. A cat's eating patterns can also vary depending on the owner's choice of food or eating times/quantities. In the case of a family having two or more cats, one cat may become dominant over the other cats.

Body language

Cats rely strongly on body language to communicate.

- Disgust — The lifting or constant shaking of a paw or paws. The more times the paw is shaken, the stronger the cat's feeling; this can sometimes be a four paw affair with each paw being lifted and shaken in turn. This behavior is possibly related to the identical action displayed after stepping into water. Displeasure at a situation can be shown by moving the ears back and rapidly swishing the tail.

- Agitation or Aggression — the swishing or sweeping of the tail in a wide swath, in mid-air or against a person. Tail flicking indicates inner conflict, while wide tail swishing shows external conflict. Further irritation may result in the cat moving or leaving the room and even physical aggression.

- Contentedness — Kneading with the paws on a person or, for example, a favorite blanket or sleeping spot. Young kittens knead their mother's nipples to stimulate the feeding reflex so that her milk flows. Cats may knead for a short or extended period of time; the extended period is sometimes interpreted by people as a sign of discomfort or restlessness, but it is more likely that the cat is happy. Most cats will demonstrate this for about ten minutes at the longest, although some have been known to knead and suckle on their favorite human's shirt or ear lobe over the course of an entire night. Researchers at Oxford University have demonstrated that cats derive immense pleasure from kneading, similar to the relaxing sensation for humans from snacking on favorite foods or being massaged.

- Relaxation — sprawling on the side or back and, possibly, rolling about; this may be seen, for example, when a person enters the room or stirs from their seat. Sometimes they roll over onto their back and shake their paws in the air. This behavior shows complete relaxation. The cat may display this at the same time as the person's movement.

- Affection — a pressing of the face or top of the head against a person's body (head rubbing, nuzzling), leaving a scent to mark the cat's territory; or rubbing in quick succession. Cats may also blink slowly as an expression of affection or security. Many cats also use a question mark-shaped tail to show desire to greet someone they are fond of. They will also stretch to show they are content with

their surroundings. Cats may also lick their owner or another person to show affection.

- Submission — Upon being approached, it will fall down on its side, indicating it is not seeking attention and is unwilling to put up a fight.

- Interest and Rejection — The position of the ears communicates the degree of desire to engage with the situation around them. Ears up and moved slightly forward shows real interest in what is going on, while ears moved backward shows distaste and desire to not engage with the situation. Cats show disapproval by moving their ears back, an equivalent of a human frown. They also crouch and turn their back to the situation to indicate disinterest or unhappiness. A cat will either move a little or give a faint "meow" if it does not want to be picked up.

- Desire for Attention — To solicit attention (for food or affection) from humans, cats will rub their bodies against the human's legs with back arched and tail raised. Less often, a cat may reach out and touch a human with its forepaw to get attention.

Scent rubbing and spraying

This behavior is used primarily to claim ownership of something, although unlike male cats, female cats do not usually spray. Some spayed females may spray to mimic males, but do not have enough scent to mark. Once male cats are neutered the *scent rubbing* or *spraying* will, in most cases, decrease or stop. Some male cats continue to spray if not neutered early enough.

Courting

Cats, compared to many other mammals, have a unique courting style. The first step in courtship is the female coming into season, or "heat". Male cats will be able to smell a female cat in heat miles away and will therefore seek her out. Males will fight mercilessly for the right to be the first to mate with the female. After the dominant male has left, the less dominant males will then each mate with the female in turn. It is therefore possible that even if a male cat loses first breeding rights, he can still be the father. This is also the reason that a litter of kittens can have two or sometimes even three fathers.

Vocal calls

- Purring — Purring is often a sign of contentment. Some cats purr when they are in extreme pain, or in labor, simply to try to calm themselves down. Purring therefore can be a sign of pleasure or pain; usually it is the former. Scientists have not yet been able to discover how purring works, but it is suspected that it is caused by minute vibrations in the voice box.
- Greeting — A particular sort of vocalization, such as a low meow or chirp, possibly with simultaneous purring.

- Distress — Mewing is a plea for help or attention often made by kittens. There are two basic types of this call, one more loud and frantic, the other more high-pitched. In older cats it is more of a panicky repeated meow.
- Attention — Often simple meows and mews in both older cats and young kittens. A commanding meow is a command for attention, food, or to be let out.
- Protest — Whining meows.
- Frustration — A strong sigh or exhaled snort.
- Happy — A meow that starts low then goes up and comes back down.
- Watching/Interest — Cats will often "chatter" or "chirrup" on seeing something of interest. This is sometimes attributed to mimicking birdsong to attract prey or draw others' attention to it, but often birds are not present.

Panting

Unlike dogs, panting is an uncommon occurrence in cats. However, some cats can pant after brisk play or in times of stress, such as a car ride. Most commonly cats will pant in response to environmental changes, such as anxiety, fear, excitement, or heat. However, if panting is excessive or the cat appears in distress, it becomes important to identify the underlying cause, as panting may be a symptom of a more serious condition, such as a nasal blockage, heartworm disease, head trauma, or drug poisoning. In particular, the cat's owner should look for signs of immediate distress such as coughing, difficulty breathing (dyspnea), or blue color to the mucus membranes (cyanosis). Other problems, such as fatigue, weight loss, poor appetite, excessive drinking, vomiting, or diarrhea, may also be present. If the panting appears to be in response to normal events such as exercise, excitement, heat or fear, the owner should remove the stimulation and continue to observe his or her pet. If panting continues, the owner should consult a veterinarian. Pregnant cats often pant when going into labor.

Righting reflex

The righting reflex is the ability for cats to land on their feet with little or no injury. They can do this more easily than other animals due to their flexible spine and lack of a collar bone. Cats also use vision and/or their vestibular apparatus to help tell which way to turn. They then can stretch themselves out and relax their muscles. Cats do not always land unharmed. They can break bones or die from excessive falls.

Food eating patterns

Cat eating frog

Cats are obligate carnivores, and can survive without vegetation. Felines in the wild will usually hunt smaller mammals regularly throughout the day to keep themselves nourished. Domestic cats, however, are used to a relaxed lifestyle and, therefore, will eat even smaller amounts, but more regularly. Many cats will find and chew small quantities of long grass but this is not for its nutritional value, it is a purely mechanical function. The eating of grass triggers a regurgitation reflex to help expel indigestible matter, like hairballs and the bones of prey.

Food covering

Cats scratch at the ground around food to cover it, for three reasons. First, it makes the food less visible to others, reducing its chances of being taken. Second, it keeps insects off the food. Third, it slows the food's drying out by excluding sun and air circulation.

Too much covering will tend to make food mold; not enough covering will dry out food. Thus the covering behavior varies according to the condition of the food, with food sometimes being well covered, sometimes lightly covered, and sometimes completely uncovered.

Socialization

Cats can be sociable. Here, two cats are sleeping together, probably to keep warm.

A Persian kitten play fighting with its owner. When separated from mother and siblings, a kitten would engage in active play fighting with humans. Play fighting may involve playful biting, but the bite is generally not serious.

Kittens are naturally scared of people at first, but if handled and well cared for in the first 16 weeks, they will develop trust in the humans who care for them. To decrease the odds of a cat being unsocial or hostile towards humans, kittens should be socialized at an early age.

It is a challenge to socialize an adult feral cat. Socialized adult feral cats tend to trust only those people they have learned over time can be trusted, and can be very fearful around strangers.

Cats can be extremely friendly companions. The strength of the cat-human bond is mainly correlated with how much consideration is given to the cat's feelings by his human companion. The formula for a successful relationship thus has much in common with human to human relationships.

Some people regard cats as sneaky, shy, or aloof animals. Cats have an inherent distrust for predator species such as humans, and often seek to minimize any contact with people they do not perceive as trustworthy. Feline shyness and aggression around people with cat social skills is often a result of lack of socialization, abuse or neglect. Cats relate to

humans differently than more social animals, enjoying some time on their own each day as well as time with humans.

Cats have a strong 'escape' instinct. Attempts to corner, capture or herd a cat can thus provoke powerful fear-based escape behavior. Socialization greatly reduces the number of humans that a cat will respond to in this way. Socialization is a process of learning that many humans can be trusted.

There is a widespread belief that relationships between dogs and cats are problematic. However, both species can develop amicable relationships by reading each others' body language correctly. The animals can better read each others' language when they first encountered each other at a young age, due to the fact that they are learning to communicate simultaneously. The order of adoption may also cause significant differences in their relationship. Sometimes the dog may be simply looking to play with the cat while the cat may take the approach a lot more seriously and lash out with its sharp claws causing painful injury. Such an incident may cause an irreversible animosity between the cat and dog.

Chapter- 11

Dog Behavior

Dogs roughhousing

Dog behavior refers to the collection of behaviors by the domestic dog, *Canis lupus familiaris*, and is believed to be influenced by genetic, social, situational and environmental causes. The domestic dog is a subspecies of the grey wolf, and shares many of its behavioral characteristics. Although there are important and distinct

differences between dogs and wolves, contemporary views of dog behavior are heavily influenced by research on wild wolves.

Social behavior

The social unit of dogs is the pack. From research on wolf packs that are formed in captivity, the pack has traditionally been thought of as a tightly knit group composed of individuals that have earned a ranking in a linear hierarchy, and in which there is intense loyalty within the group. It is believed that dogs were able to be domesticated by and succeed in contact with human society because of their social nature. According to this traditional belief, dogs generalize their social instincts to include humans, in essence "joining the pack" of their owner/handler. However, much of this traditional view is based on findings from grey wolf packs that are formed of unrelated animals in captivity, and thus may not apply to natural wolf packs, natural dog packs, or dogs incorporated into a human household. Research in packs formed in the wild indicates that wolves form a family group, including a breeding pair and their offspring. In these familial packs, the terms "dominance," and "submission" are less useful than "parent," and "offspring," and bring with them a number of misconceptions. While the majority of research to date indicates that domestic dogs conform to a hierarchy around an Alpha-Beta-Omega structure, domestic dogs, like their wild wolf counterparts, also interact in complex hierarchical ways.

The existence and nature of personality traits in dogs have been studied (15329 dogs of 164 different breeds) and five consistent and stable "narrow traits" identified, described as playfulness, curiosity/fearlessness, chase-proneness, sociability and aggressiveness. A further higher order axis for shyness–boldness was also identified.

Applicable research on grey wolves

Dr. David Mech of the University of Minnesota, who has studied wolves in their natural habitat, claims that much of what is widely believed about wolf packs is mistaken. From observations of wolf packs on Ellesmere Island over more than a decade, he claims that natural wolf packs are not at all similar to those formed in captivity by unrelated wolves. He attributes many of the misconceptions about wolf packs to generalizations from these unnatural packs in captivity, and equates this to erroneous inferences we might draw from generalizing human behavior from studying refugee camps.

Dr. Mech argues that the natural wolf pack is typically a family, with a breeding pair of adult wolves and their offspring. In such cases, the terms "alpha" and "dominant" are less appropriate than "parent." Of course, the parent wolves are both "alpha" and "dominant" (by definition), but he argues that these terms are misleading because they imply that a pack of wolves typically include multiple families and that the members assume a place in a linear hierarchy. A wolf pack should not be seen as a tribe of individuals who have an established place in a hierarchy until a younger dog usurps the role. Rather, a wolf pack should be seen as a family unit, with young wolves of age dispersing into new territories of their own, to find other wolves and begin their own family units.

Mech also states that dominance is rare in wild wolves, and does not arise from sexual competition. Because young wolves usually disperse before age two, and almost always before age 3, there is little sexual tension within a pack. Instead of "dominance" and "submission", he uses the terms "assertiveness" and "passiveness" to reflect the role of the wolf in the pack. Dominant breeding pairs led the pack most of the time (71%), and initiated most new behaviors (70%). Leadership behavior in subordinate pack members tended to be followed by dispersion.

Dominance and submission

Properly socialized dogs can interact with unfamiliar dogs of any size and shape and understand how to communicate.

It is believed by some that dogs establish a dominance hierarchy through aggressive play and roughhousing along a continuum of dominance and submission, although the concept of social hierarchies in dogs is unproven and controversial. It is important for successful socialization that puppies participate with their littermates in learning to relate to other dogs. Dogs learn to successfully relate to other dogs by keeping the peace, rather than by constantly fighting to reestablish this hierarchy.

Dominance behavior

Although dogs are commonly characterized in terms of their dominance (e.g., "Fido is the alpha."), there is some controversy as to whether dominance is a stable personality trait.

In wild wolf packs, displays of dominance have been observed to include "licking up," which involves essentially begging for food; "pinning," in which the dominant dog appears to threaten another, which shows submission by rolling over; "standing over;" territorial marking; and more passive expressions of body language, including holding the

tail and ears erect, looking directly at other dogs, circling and sniffing other dogs, growling if the other dog moves.

Submissive displays mirror dominant displays and include adopting a posture that is physically lower than other dogs, such as crouching, rolling over on the back and exposing the abdomen, lowering the tail (sometimes to the point of tucking it between the legs), flattening of the ears, averting the gaze, nervously licking or swallowing, dribbling of urine, and freezing or fleeing when other dogs are encountered.

In wolves, recent research has indicated that dominant behaviors have been misinterpreted as personality traits that determine the inidividual's place in a linear hierarchy in the pack. In contrast, Mech (see recent research, below) argues that packs are family units, and that the "alpha" of a pack does not change through struggles for dominance. Rather, he argues that the family unit serves to raise the young, which then disperse to pair up with other dispersed wolves to form a breeding pair, and a pack of their own. This model undermines the popular conception of dominance in wolf social behavior.

Research on canine familiaris has also questioned whether dominance is a personality trait. Svartberg and colleagues (2002) gathered behavioral data from 15,000 dogs of 164 breeds in attempt to identify major personality traits. In an approach similar to those used in humans, the authors performed a factor analysis of their data, and identified five major traits: "Playfulness," "Curiosity/Fearlessness," "Chase-proneness," "Sociability," "Aggressiveness." A similar analysis by Goddard and Beilharz (1985) revealed two major factors in social behavior: "Confidence," and "Aggression-dominance."

These studies suggest that dominance, per se, may not be a personality trait. Rather, underlying personality traits such as aggressiveness, confidence and curiosity may affect the prevalence of dog behaviors that are viewed as dominant.

Human attachment

A Pomeranian as a recipient of human interaction during Christmas

Research has shown that there are individual differences in the interactions between dogs and their human masters that have significant effects on dog behavior. For instance, Topal and colleagues (1997) have shown that the type of relationship between dog and master, characterized as either *companionship* or *working relationship*, significantly affected the dog's performance on a cognitive problem-solving task. They speculate that companion dogs have a more dependent relationship with their owners, and look to them to solve problems. In contrast, working dogs are more independent.

Behavior when isolated

Dogs value the companionship of the others in their "pack" and are sometimes distressed if they are separated from it. Typical reactions when a dog is separated from the pack are barking, howling, digging, and chewing. These activities may distress humans when they need to leave dogs alone for a period of time. However, this behavior, called *separation anxiety*, can be overcome with training, or at least decreased to the point where it becomes manageable. If young puppies are habituated to periods alone from an early age, this can normally be prevented entirely. Dogs are also crepuscular, meaning their natural period of peak activity is dawn and dusk, and may be content to rest during the day and night. Some owners struggling to deal with this problem resort to debarking, a controversial practice considered cruel by animal advocates and outlawed in many countries.

Dog play

From a young age, dogs engage in play with one another. Dog play is made up primarily of mock fights. It is believed that this behavior, which is most common in puppies, is training for important behaviors later in life. Research on puppy play has shown that puppies do not engage equally in both dominant and submissive roles in fights; rather, puppies will tend to start play fights with weaker puppies they believe they can dominate. Additionally, puppies will intervene in play engaged by other pairs. In these situations, the puppies overwhelmingly aid the dominant dog. Puppies do not show reciprocity in interventions, suggesting that they prefer to be dominant in a fight, and are being opportunistic in the short-term. In the long-term, intervention may aid the puppies in learning coordination.

A common behavior among domesticated dogs is chasing their own tails. Researchers are not completely certain why dogs chase their own tail, however some research studies found a link between tail chasing and high cholesterol. A study found that when dogs experience an increase in activity of hormones tied to the "fight or flight" response caused dogs to chase their tails more often.

Classification of dog behaviours

Behavior Type	Ears	Eyes	Mouth & Teeth	Body	Tail	Vocalization
Aggressive	Forward or back, close to head.	Narrow or staring challengingly.	Lips open, drawn back to expose teeth bared in a snarl. Possible jaw snapping.	Tense. Upright. Hackles on neck up. Completely Dominant position.	Straight out from body. Fluffed up.	Snarl. Growl. Loud bark.
Alert	Perked-up. Turning to catch sounds.	Open normally or wide.	Mouth closed or slightly open with teeth covered.	Normal. Possibly standing on tiptoe. Slightly	Up. Possibly wagging.	None. Low whine or alarm bark.

				Dominant position.		
Anxious	Partially back.	Slightly narrowed.	Mouth closed, or slightly open in a "grin."	Tense. Slightly lowered in a Submissive position.	Partially lowered.	Low whine or moaning-type bark.
Before Chasing	Perked-up, forward-pointing.	Wide open. Very alert.	Mouth slightly open. Excited panting.	Tense. Crouched low in a predatory position. Legs bent, poised to run.	Extended straight out from body.	None.
Curious, eager, excited	Perked-up, forward-pointing.	Wide open.	Mouth open, teeth covered. Possible panting.	Normal stance. Possible wiggling, standing on tiptoe, or pacing.	Up. Wagging.	Excited short barking, whining.
Dominant	Up straight or forward.	Wide open, staring.	Mouth closed or slightly open.	Very tall posture. Hackles may be up.	Stiffened and fluffed. Up or straight out from body.	Low, assertive growl or grunt.
Fearful	Laid back flat and low on head.	Narrowed, averted. Possibly rolled back in head, whites showing.	Lips drawn back to expose teeth.	Tense. Crouched low in submissive position. Shivering, trembling. Possible secretion from anal scent glands.	Down between legs.	Low, worried yelp, whine, or growl.
Before flight	Back.	Wide open. Possibly rolled back with whites showing.	Slightly opened mouth. Possible drooling.	Tense. Shivering. Low, poised to run.	Low or between legs.	None. Possible yelp or whine.
Friendly	Perked-up.	Wide open. Alert look.	Relaxed, possibly slightly open, "smiling" mouth.	Normal posture. Still, or possible wiggling of whole rear end.	Up or out from body. Wagging.	Whimpering, yapping, or short, high bark.
Guarding	Perked-up. Forward.	Wide open, alert.	Mouth slightly open, teeth bared. Snapping or gnashing of teeth.	Tense. Rigid. Hackles up. Standing very tall in an aggressive or dominant stance.	Rigid. Held straight out from body. Sometimes fluffed.	Loud alert bark. Growl. Snarl.

Happy/Playful	Perked-up and forward, or relaxed.	Wide open. Sparkly/merry-looking.	Mouth relaxed and slightly open, teeth covered. Excited panting.	Relaxed, or front end lowered, rear end up in the air, wiggling in a play-bow. Excited bouncing and jumping up and down. Circling around and running forward and back in an invitation to play.	Wagging vigorously.	Excited barking. Soft play-growling.
Predatory	Alert. Held forward or backward to catch sounds.	Wide open. Staring, focusing.	Mouth closed.	Rigid. Low to ground, ready to spring forward. Quietly sniffing the air.	Straight and low.	None.
Subordinate/Submissive	Down, flattened against head.	Narrowed to slits or wide open, whites showing.	Lips pulled way back from teeth in a "grin". Nuzzling or licking other animal or person on face.	Lowered to ground, front paw raised. Lying on back, belly up. Possible urine leaking/dribbling. Possible emptying of anal scent glands.	Down, between legs.	None, or low, worried whining. Possible yelping/whimpering in fear.

Chapter- 12

Horse Behavior

Free-roaming mustangs (Utah, 2005)

Horse behavior is best understood from the perspective that horses are prey animals with a well-developed fight-or-flight instinct. Their first response to a threat is to flee, although they are known to stand their ground and defend themselves or their offspring in cases where flight is untenable, such as when a foal would be threatened.

Nonetheless, because their physiology is also suited to a number of work- and entertainment-related tasks, humans domesticated horses thousands of years ago, and they have served humans ever since. Through selective breeding, some breeds of horses have been bred to be quite docile, particularly certain large draft horses. On the other hand, most light horse riding breeds were developed for speed, agility, alertness and endurance; building on natural qualities that extended from their wild ancestors.

The instincts of horses can be used to human advantage to create a bond between human and horse. These techniques vary, but are part of the art of horse training.

Horses as herd animals

Horses are highly social herd animals that prefer to live in a group. Like all creatures, equine social behavior developed to help the species survive.

There also is a linear dominance hierarchy in any herd. They will establish a "pecking order" for the purpose of determining which herd member directs the behavior of others, eats and drinks first, and so on. This behavior pattern also applies to their interrelationship with humans. A horse that respects the human as a "herd member" who is higher in the social order will behave in a more appropriate manner towards all humans than a horse that has been allowed to engage in dominant behavior over humans.

Horses are able to form companionship attachments not only to their own species, but with other animals, including humans. In fact, many domesticated horses will become anxious, flighty and hard to manage if they are isolated. Horses kept in near-complete isolation, particularly in a closed stable where they cannot see other animals may require a stable companion such as a cat, goat or even a small pony or donkey to provide company and reduce stress.

When anxiety over separation occurs while a horse is being handled by a human, the horse is described as "herd-bound". However, through proper training, horses learn to be comfortable away from other horses, often because they learn to trust a human handler, essentially ranking humans as a dominant member of a "herd."

Herd behavior in the wild

Feral and wild horse herds are usually made up of several separate small bands who share a given territory. Bands are organized on a "harem model" in that they usually consist of one adult male and a group of females. Each band is led by a mare who is dominant in the hierarchy, called the "dominant mare," the "lead mare" or the "boss mare." The band contains additional mares, their foals, and immature horses of both sexes. There is usually a single "herd" or "lead" stallion, though occasionally a few less-dominant males may remain on the fringes of the group.

Bands are usually on the small side, as few as three to five animals, but sometimes over a dozen. The makeup of bands shifts over time as young animals are driven out of the band they were born into and join other bands, or as young stallions challenge older males for dominance. However, in a given closed ecosystem such as the isolated refuges in which most wild horses live today, to maintain genetic diversity the minimum size for a sustainable wild horse or burro population is 150-200 animals.

Hierarchical structure

Survival dictates that the herd members ultimately cooperate and stick together. As with many animals that live in large groups, establishment of a stable hierarchical system or "pecking order" is important to smooth group functioning. This is often, but not always, a completely linear system. Situations arise where horse A may be dominant over horse B who is dominant over horse C, yet in certain circumstances horse C could be dominant over horse A in competition for a particular resource. Dominance depends on a variety of factors, including an individual's need for a particular resource at a given time. It is therefore variable throughout the lifetime of the herd or individual animal. Some horses may be dominant over all resources and some may indeed be submissive over all resources.

Contention for dominance can be risky since one well-placed kick to a leg could cripple another horse to such an extent that it would be defenseless, exposed, and possibly unable to get to food or water. Therefore, once this system of dominance and submission is generally established aggressive behaviour is minimal between herd members, though higher-ranked animals often will assume a role of exercising control and moderating aggressive behavior in the herd.

In times of stress, whether from predators or extreme weather, the center of the herd is the safest because it offers the most protection from the elements and is further away from predators than any other part. Because of this, "punishment" of misbehaving members is sometimes delivered in the form of expulsion from the herd—temporarily or sometimes permanently.

Most young horses in the wild are allowed to stay with the herd until sometime in their yearling or 2-year old year, when they reach full sexual maturity. Studies of wild herds have shown that the herd stallion will usually drive out both young colts and fillies. Experts who study wild horses theorize that this may be an instinct that prevents inbreeding, so that the herd stallion does not mate with his own female offspring. The fillies usually join another band in fairly short order, and the colts driven out from various herds usually join together for safety in small "bachelor" groups until those who are able establish dominance over an older stallion in another herd.

Role of the lead mare

Contrary to traditional portrayals of the herd stallion as the "ruler" of a "harem" of females, the actual leader of a wild or feral herd is the alpha or dominant mare, commonly known as the "boss mare" or "lead mare." She is usually one of the more mature animals, responsible for the overall safety of the herd, familiar with the terrain and resources available. She takes the lead when the herd travels, determines the best route, when to move from one place to another, and claims the right to drink first from watering holes and stake out the best location for grazing.

Role of the stallion

A stallion exhibiting the characteristics of a Flehmen response

The edge of the herd is the domain of the herd stallion, who must fight off both predators and other males. When the herd travels, the stallion brings up the rear, watching for predators and driving straggling herd members on, keeping the group together. During mating season, stallions tend to act more aggressively, in order to keep the mares from straying off. However, most of the time, the stallion is fairly relaxed, spending much of his time "guarding" the herd not by herding the mares around, but by scent-marking manure piles and urination spots in order to make clear his position as herd stallion.

By living on the periphery of the herd, exposed to weather, predators, and challenges from other stallions, the herd stallion endures a somewhat vulnerable existence. He is exposed to more risks than any other herd member and can be replaced by a stronger successor at any time. Interestingly, a herd stallion will occasionally tolerate one young stallion to live at the edge of the herd, possibly as a sort of designated successor, even though the young horse will eventually gain mastery over the older stallion and claim the herd.

Ratio of stallions and mares

Biologically, and depending on the physical environment available to a herd in the wild, there is only a need for one stallion for every 10 to 20 mares, though most bands are smaller than this. Domesticated stallions, with careful human management, often "cover" more mares in a year than is possible in the wild. Traditionally, Thoroughbred stud farms limited stallions to breeding between 40 and 60 mares a year. Today, by carefully breeding mares only when at the peak of their Estrous cycle, a few thoroughbred stallions have "covered" over 200 mares per year. With use of technologies such as artificial insemination one stallion could sire thousands of offspring annually, though in actual practice, economic considerations usually limit the number of foals produced.

Domesticated stallion behavior

Some horse breeders keep horses in semi-natural conditions, allowing a single stallion to run with a group of mares. This is referred to as "pasture breeding." Young stallions who are not of breeding age live in a separate "bachelor herd." While this has advantages of less intensive labor for human caretakers, and full time turnout may be psychologically healthy for the horses, pasture breeding presents a risk of injury to valuable breeding stock, both stallions and mares, particularly when unfamiliar animals are added to the herd. It also raises questions of when or if a mare is bred, and may also raise questions as to parentage of ensuing foals. Thus, keeping stallions in a natural herd is not particularly common, especially on breeding farms standing multiple stallions to outside mares. It is more often seen on farms with closed herds; only one or a few stallions with a stable mare herd and few, if any, outside mares.

More often, mature domesticated stallions are commonly kept by themselves in a stable or small paddock with a strong, high fence that prevents escape. When stallions are stabled in such a way that they can both see each other and touch nose to nose, such as through bars or a grill, they will often challenge one another and sometimes attempt to fight. For this reason, stallions are often kept from sight and touch of other stallions, due to risk of injury and disruption to the rest of the stable, even if several are kept in the same barn. If they have access to paddocks, there often is a corridor between the paddocks so the stallions cannot touch one another, and in some cases, stallions are let out for exercise at different times of day so they do not see or hear one another.

To avoid stable vices associated with isolation, some stallions, though not all, do well when stabled with a non-horse companion, such as a gelded donkey or a goat. (The Godolphin Arabian was said to be particularly fond of a barn cat). While many domesticated stallions become too aggressive to tolerate the close presence of any other male horse without fighting, some tolerate a gelding as a companion, particularly one that has a very calm, unflappable temperament. One example of this was the racehorse Seabiscuit, who lived with a gelding companion named "Pumpkin." Other stallions may tolerate the close presence of an immature and thus less dominant stallion.

While stallions and mares often compete together at horse shows and in horse races, stallions generally must be kept away from close contact with mares, both to avoid unintentional or unplanned matings, but also to minimize their instincts to fight one another for dominance when in the presence of mares. When horses are lined up for placing at shows, handlers keep stallions at least a horse's length from any other animal and do not allow their horses to touch noses with any other animals. Stallions can be taught to ignore any mares or other stallions that are in close proximity while they are working.

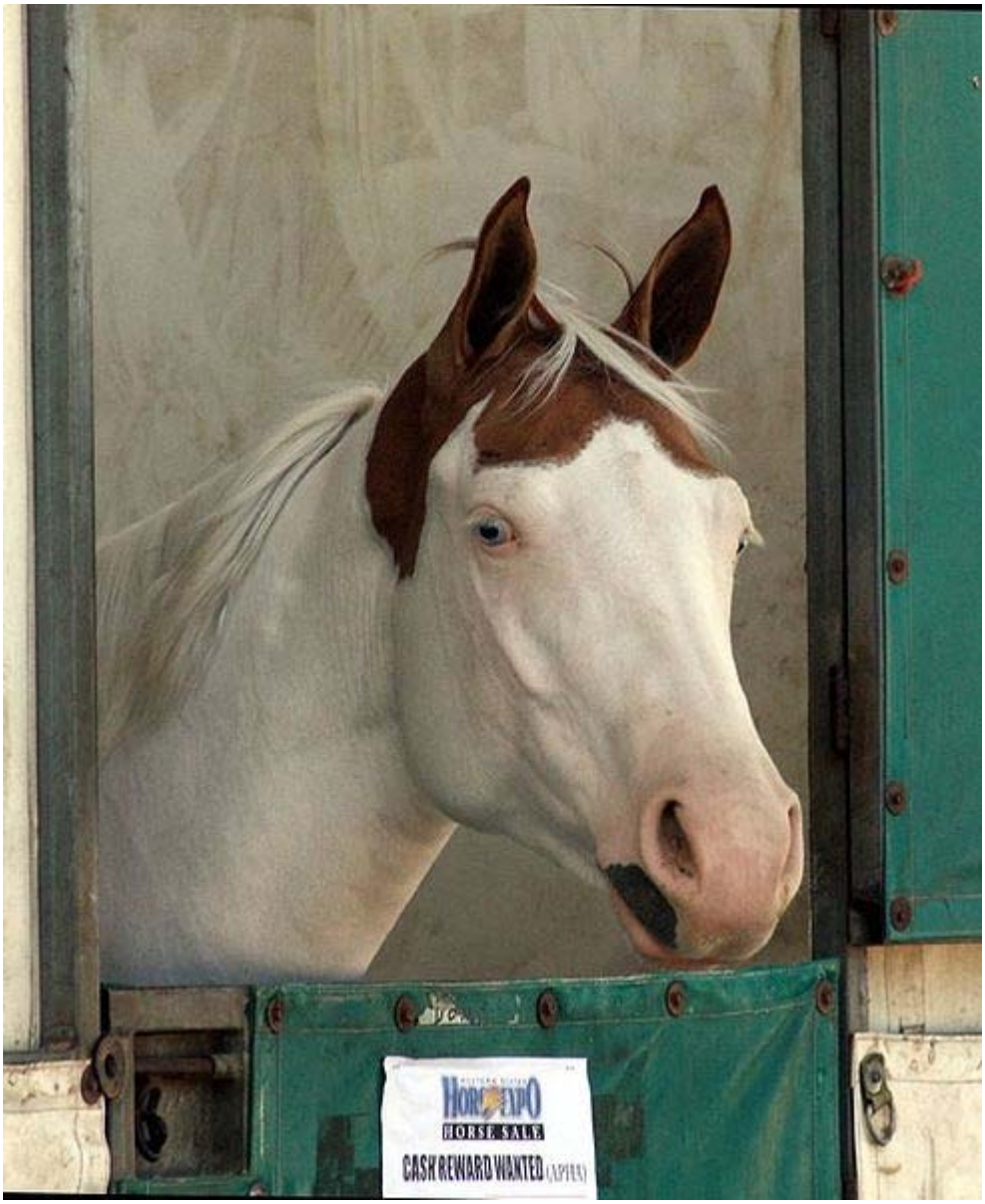
However, stallions do live peacefully in bachelor herds in the wild and in natural management settings. Domesticated stallions are still herd animals, and some farms feel that carefully managed social contact benefits stallions. Well-tempered stallions who will be kept together for a long period of time may be stabled in closer proximity, though this method of stabling is generally used only by experienced stable managers. An example of this are the stallions of the Spanish Riding School, who travel, train and are stabled close together. In these settings more dominant animals are kept apart by stabling a young or less dominant stallion in the stall between them. Sometimes a stallion raised in isolation from other horses cannot be stabled in this fashion at all due to aggressive behavior.

Dominance in domesticated herds

Because domestication of the horse usually requires stallions to be isolated from other horses, either mares or geldings may become dominant in a domestic herd. Usually dominance in these cases is a matter of age and, to some extent, temperament. It is common for older animals to be dominant, though old and weak animals may lose their rank in the herd. There are also studies suggesting that a foal will "inherit" or perhaps imprint dominance behavior from its dam, and at maturity seek to obtain the same rank in a later herd that its mother held when the horse was young.

In recent studies of domesticated horses, new evidence indicates that horses appear to benefit from a strong female presence in the herd. Groupings of all geldings, or herds where a gelding is dominant over the rest of the herd (for example, if the mares in the herd are quite young or of low status), may be more anxious as a group and less relaxed than those where a mare is dominant.

Communication



Forward ear position indicating alertness and pleasant attitude

One ear forward and one ear back, corresponding to where horse is looking with each eye, usually indicating divided attention

Relaxed ear position of a bored or resting horse. Lower lip is loose, also indicating relaxation. The sclera of this horse's eye shows a bit of white, but it is not rolled back in fear or anger.

Tense laid back ear position indicating unhappiness. Mouth and lips are also tense, which may indicate an urge to bite.

Ears pulled back flat against the head with teeth bared and white of the eye showing, indicating anger. Usually a presage of aggressive behavior, such as biting or kicking.

Horses communicate in various ways, including vocalizations such as nickering, squealing or whinnying; touch, through mutual grooming or nuzzling; smell; and body language. Body language is probably the predominant means of communication. Horses use a combination of ear position, neck and head height, movement, and foot stomping or tail swishing to communicate. Discipline is maintained in a horse herd first through body language and gestures, then, if needed, through physical contact such as biting, kicking, nudging, or other means of forcing a misbehaving herd member to move. In most cases, the animal that successfully causes another to move is dominant, whether it uses only body language or adds physical reinforcement.

Horses can interpret the body language of other creatures, including humans, who they view as predators. If socialized to human contact, horses usually respond to humans as a non-threatening predator. Humans do not always understand this, however, and may behave in a way, particularly if using aggressive discipline, that resembles an attacking predator and triggers the horse's fight-or-flight response. On the other hand, some humans exhibit fear of a horse, and a horse may interpret this behavior as human submission to the authority of the horse, placing the human in a subordinate role in the horse's mind. This may lead the horse to behave in a more dominant and aggressive fashion. Human handlers are more successful if they learn to properly interpret a horse's body language and temper their own responses accordingly. Some methods of horse training explicitly instruct horse handlers to behave in ways that the horse will interpret as the behavior of a trusted leader in a herd and thus more willingly comply with

commands from a human handler. Other methods encourage operant conditioning to teach the horse to respond in a desired way to human body language, but also teach handlers to recognize the meaning of horse body language.

Horses are not particularly vocal, but do have four basic vocalizations: the neigh or whinny, the nicker, the squeal and the snort. They may also make sighing, grunting or groaning noises at times.

Ear position is often one of the most obvious behaviors that humans notice when interpreting horse body language. In general, a horse will direct the pinna of an ear toward the source of input it is also looking at. Horses have a narrow range of binocular vision, and thus a horse with both ears forward is generally concentrating on something in front of it. Similarly, when a horse turns both ears forward, the degree of tension in the horse's pinna suggests if the animal is calmly attentive to its surroundings or tensely observing a potential danger. However, because horses have strong monocular vision, it is possible for a horse to position one ear forward and one ear back, indicative of similar divided visual attention. This behavior is often observed in horses while working with humans, where they need to simultaneously focus attention on both their handler and their surroundings. A horse may turn the pinna back when also seeing something coming up behind it.

Due to the nature of a horse's vision, head position may indicate where the animal is focusing attention. To focus on a distant object, a horse will raise its head. To focus on an object close by, and especially on the ground, the horse will lower its nose and carry its head in a near-vertical position. Eyes rolled to the point that the white of the eye is visible often indicates fear or anger.

Ear position, head height, and body language may change to reflect emotional status as well. For example, the clearest signal a horse sends is when both ears are flattened tightly back against the head, sometimes with eyes rolled so that the white of the eye shows, often indicative of pain or anger, frequently foreshadowing aggressive behavior that will soon follow. Sometimes ears laid back, especially when accompanied by a strongly swishing tail or stomping or pawing with the feet are signals used by the horse to express discomfort, irritation, impatience, or anxiety. However, horses with ears slightly turned back but in a loose position, may be drowsing, bored, fatigued, or simply relaxed. When a horse raises its head and neck, the animal is alert and often tense. A lowered head and neck may be a sign of relaxation, but depending on other behaviors may also indicate fatigue or illness.

Tail motion may also be a form of communication. Slight tail swishing is often a tool to dislodge biting insects or other skin irritants. However, aggressive tail-swishing may indicate either irritation, pain or anger. The tail tucked tightly against the body may indicate discomfort due to cold or, in some cases, pain. The horse may demonstrate tension or excitement by raising its tail, but also by flaring its nostrils, snorting, and intently focusing its eyes and ears on the source of concern.

The horse does not use its mouth to communicate to the degree that it uses its ears and tail, but a few mouth gestures have meaning beyond that of eating, grooming, or biting at an irritation. Bared teeth, as noted above, are an expression of anger and an imminent attempt to bite. Horses, particularly foals, sometimes indicate appeasement of a more aggressive herd member by extending their necks and clacking their teeth. Horses making a chewing motion with no food in the mouth do so as a soothing mechanism, possibly linked to a release of tension, though some horse trainers view it as an expression of submission. Horses will sometimes extend their upper lip when scratched in a particularly good spot, and if their mouth touches something at the time, their lip and teeth may move in a mutual grooming gesture. A very relaxed or sleeping horse may have a loose lower lip and chin that may extend further out than the upper lip. The curled lip flehmen response, noted above, most often is seen in stallions, but is usually a response to the smell of another horse's urine, and may be exhibited by horses of any sex. Horses also have assorted mouth motions that are a response to a bit or the rider's hands, some indicating relaxation and acceptance, others indicating tension or resistance.

Horses and humans

Horses are creatures of habit and have excellent memories, which make consistent training extremely important to the horse. Untrained young horses, even with top bloodlines, can be bought for relatively little money compared to those with training. Once a horse is started under saddle and demonstrates that it is trainable, ridable and has some athletic talent for its work, the price easily triples.

Humans are usually viewed by wild horses as potential predators. However, horses are also innately curious and may investigate any creature that is interesting but not threatening.

Horse-human interaction

Any domesticated horse with some experience of humans usually views people as generally harmless objects of curiosity worth at least minor notice, especially if they know that humans may bring food or treats. Rarely will any domestic horse become truly vicious unless it has been spoiled or abused by humans, though many stallions have a great deal of naturally aggressive, dominant behavior that requires that they be managed only by knowledgeable handlers. However, any horse is a large animal that retains some wild instincts, so can react unpredictably by running, biting, striking, or kicking. Thus humans must always be alert around horses because they can accidentally harm people.

The ability of humans to work in cooperation with the horse is based on both the natural curiosity of the horse and the strong social bonds that horses have with each other. Horses do not like to be separated from their herd, because to be alone is to be exposed to predators on all sides. Also, in a herd, less dominant horses tend to gravitate toward the most mature and confident members. Therefore, many horse training principles are based upon having the horse accept a human as the dominant herd member. Ideally this is not done by force, but by the horse developing trust in the ability of the human and confidence that the human will be a responsible "herd leader."

Horses are also adapted to covering large amounts of territory and must have a certain boldness to do so. A horse that is afraid more than necessary will expend energy needlessly and then may not be able to escape when a threat is real. Thus, horses have an ability to check out the unusual and not immediately flee from something that is merely different.

Humans turning a horse loose so that it can run

This willingness to consider new things can also be used by a human trainer to adapt the horse's behavior to an extraordinary range of activities that are well outside the range of instinctive horse behavior, including acts considered naturally dangerous by the average horse such as bullfighting, jumping off cliffs, diving into water, jumping through a ring of fire, or walking into a modern television studio, complete with enclosed space, bright lights, and tremendous noise.

People who train horses first have to educate them that some normal herd behavior is inappropriate around humans. For example, biting and "shadow boxing" (rearing, striking) that is common play among young horses, colts in particular, could be injurious or fatal to people. Other instinctive traits, such as running away when frightened, bucking off anything that lands on a horse's back (like a mountain lion or other predator), or never entering a small enclosed area, also have to be overcome before the horse is useful to humans.

Even when trained, most horses will still test boundaries, at least mildly, and some horses with dominant personalities will openly challenge a weak or inexperienced handler. For example, if handled with incompetence or abuse, a horse may ignore its training and

attempt to nip, bite, kick, refuse to be led, or try other ways to challenge human dominance. Without consistent handling, some horses, especially young ones, will revert to their untrained ways. However, due to their good memory, horses with solid training from trustworthy handlers often retain what they have learned, even after a gap of many years.

Sleep patterns

A draft horse sleeping while standing up

Horses are able to sleep both standing up and lying down. They are able to doze and enter light sleep while standing, an adaptation from life as a prey animal in the wild. Lying down makes an animal more vulnerable to predators. Horses are able to sleep standing up because a "stay apparatus" in their legs allows them to relax their muscles and doze without collapsing. In the front legs, their equine forelimb anatomy automatically engages the stay apparatus when their muscles relax. The horse engages the stay apparatus in the hind legs by shifting its hip position to lock the patella in place. At the stifle joint, a "hook" structure situated on the inside bottom end of the femur cups the patella and the medial patella ligament, preventing the leg from bending.

Unlike humans, horses do not need a solid, unbroken period of sleep time. They obtain needed sleep by means of many short periods of rest. This is to be expected of a prey animal, one that needs to be ready on a moment's notice to flee from predators. Horses

may spend anywhere from four to fifteen hours a day in standing rest, and from a few minutes to several hours lying down. However, not all this time is the horse actually asleep; total sleep time in a day may range from several minutes to a couple of hours. Horses require approximately two and a half hours of sleep, on average, in a 24-hour period. Most of this sleep occurs in many short intervals of about 15 minutes each.

Horses need to lie down occasionally, and prefer soft ground for a nap.

Horses must lie down to reach REM sleep. They only have to lie down for an hour or two every few days to meet their minimum REM sleep requirements. However, if a horse is never allowed to lie down, after several days it will become sleep-deprived, and in rare cases may suddenly collapse as it involuntarily slips into REM sleep while still standing. This condition differs from narcolepsy, though horses may also suffer from that disorder.

Horses sleep better when in groups because some animals will sleep while others stand guard to watch for predators. A horse kept entirely alone may not sleep well because its instincts are to keep a constant eye out for danger.

Eating patterns

Horses have a strong grazing instinct, preferring to spend most hours of the day eating forage. Horses and other Equids evolved as grazing animals, adapted to eating small amounts of the same kind of food all day long. In the wild, the horse adapted to eating prairie grasses in semi-arid regions and traveling significant distances each day in order to obtain adequate nutrition. Thus, they are "trickle eaters," meaning they have to have an almost constant supply of food to keep their digestive system working properly. Horses

can become anxious or stressed if there are long periods of time between meals. When stabled, they do best when they are fed on a regular schedule; they are creatures of habit and easily upset by changes in routine. When horses are in a herd, their behavior is hierarchical; the higher-ranked animals in the herd eat and drink first. Low-status animals, who eat last, may not get enough food, and if there is little available feed, higher-ranking horses may keep lower-ranking ones from eating at all.

Psychological disorders

When confined with insufficient companionship, exercise or stimulation, horses may develop stable vices, an assortment of bad habits, mostly psychological in origin, that include wood chewing, wall kicking, "weaving" (rocking back and forth) and other problems.

Chapter- 13

Tinbergen's Four Questions

Tinbergen's four questions, named after Nikolaas Tinbergen, are categories of explanations of animal behavior.

When asked about the purpose of sight in humans and animals, even elementary school children can answer that animals have vision to help them find food and avoid danger (adaptation). Biologists have three additional explanations: sight is caused by a particular series of evolutionary steps (phylogeny), the mechanics of the eye (causation), and even the process of an individual's development (ontogeny). Although these answers may be very different, they are consistent with each other. This idea was hashed out in the 1960s when Tinbergen delineated the **four questions** based on Aristotle's four types of causes. This schema constitutes a basic framework of the overlapping behavioral fields of ethology, behavioral ecology, sociobiology, evolutionary psychology, and comparative psychology.

Four categories of questions and explanations

The first two categories pertain to the evolution of the species and the second two pertain to the individual.

Evolutionary (ultimate) explanations

1 Function (adaptation)

Darwin's theory of evolution by natural selection is the only scientific explanation for why an animal's behavior is usually well adapted for survival and reproduction in its environment. The literature conceptualizes the relationship between function and evolution in two ways. On the one hand, function and evolution are often presented as separate and distinct explanations of behavior. On the other hand, the definition of adaptation, a central concept in evolution, is a trait that is functional to the reproductive success of the organism and that is the result of natural selection; that is, function and evolution are inseparable. Given this, it is best to conceptualize function as an evolutionary explanation. The term "function" is preferable to "adaptation", because it is

understandable to students prior to an explanation of evolution. Many examples are well-known. For instance, birds fly south in the winter to find food and warmth, and mammalian mothers nurture their young, thereby having more surviving offspring.

Ultimate function corresponds to Aristotle's final cause.

2 Phylogeny (evolution)

“Phylogeny” captures all evolutionary explanations other than function/adaptation. There are several reasons why natural selection may fail to achieve optimal design (Mayr 2001:140–143; Buss et al. 1998). One entails random processes such as mutation and environmental events acting on small populations. Another entails the constraints resulting from early evolutionary development. As many characteristics are retained over the course of phylogeny, each organism harbors characteristics of various (phylogenetic) ages. This applies equally to anatomy and behavior. Reconstructing the phylogeny of a species often makes it possible to understand the "uniqueness" of recent characteristics: Earlier phylogenetic stages and (pre-) conditions which persist often also determine the form of more modern characteristics. For instance, the vertebrate eye (including the human eye) has a blind spot, whereas octopus eyes do not. In those two lineages, the eye was originally constructed one way or the other. Once the vertebrate eye was constructed, there were no intermediate forms that were both adaptive and would have enabled it to evolve without a blind spot.

Proximate explanations

3 Causation (*proximate* mechanisms or *proximate* cause effect relations)

Here are several prominent classes of proximate mechanisms:

- Brain: For example, Broca’s area, a small section of the human brain, has a critical role in linguistic capability (The Language Instinct).
- Hormones are chemicals used to communicate among cells of an individual organism. Testosterone, for instance, stimulates aggressive behavior in a number of species.
- Pheromones are chemicals used to communicate among members of the same species. Some species (e.g., dogs and some moths) use pheromones to attract mates.

Proximate mechanisms correspond to Aristotle's material cause.

In examining living organisms biologists are confronted with diverse levels of complexity (e.g. the chemical level, the physiological level, the psychological level, the social level). Subject of investigation are **functional relations between cause and effect** within and between the levels. Within the scope of (behavioral) physiology they examine, inter alia, hormonal and neuronal aspects such as the influence of social and ecological conditions on the release of certain transmitters and hormones, and the effects of such

releases on behavior. In mammals, stress during birth has a tokolytic (contraction-suppressing) effect. Findings regarding the basic levels are a (proximate) prerequisite for understanding superior levels. However, awareness of the chemical messengers of nerve cells (transmitters) is not enough to understand the superior levels of neuroanatomic circuit diagrams or behavior: "The whole is more than the mere sum of its parts." – All levels must be considered as being equally important (cf. "Laws about the Levels of Complexity" of Nicolai Hartmann).

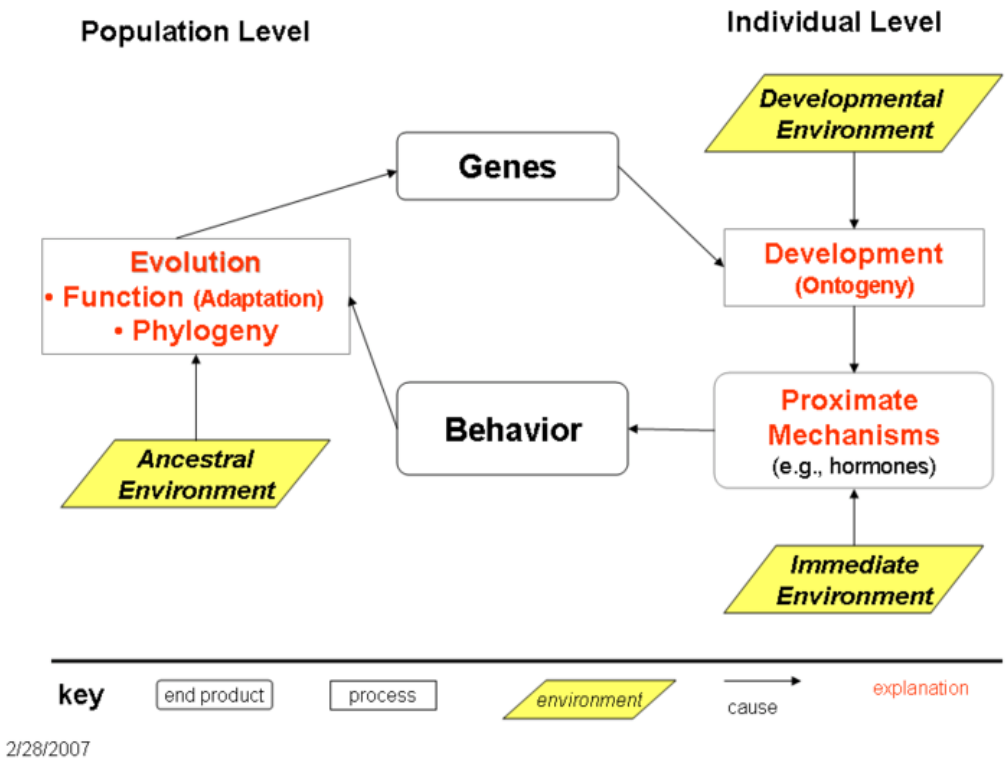
4 Development (ontogeny)

In the latter half of the twentieth century, social scientists debated whether human behavior was the product of nature (genes) or nurture (environment in the developmental period, including culture). The consensus among biologists now is that behavior is the product of gene-environment interaction, in which the whole can be more than the sum of the parts, that is, the genetic and environmental components. By way of contrast, tallness may simply be the sum of "tall genes" and an environment rich in food.

An example of interaction (as distinct from the sum of the components) involves familiarity from childhood. In a number of species, individuals prefer to associate with familiar individuals but prefer to mate with unfamiliar ones (Alcock 2001:85–89, Incest taboo, Incest). By inference, genes affecting living together interact with the environment differently from genes affecting mating behavior. A homely example of interaction involves plants: Some plants grow toward the light (phototropism) and some away from gravity (gravitropism). Such species react differently to the same environment because of different genes.

Many forms of developmental learning have a critical period, for instance, for imprinting among geese and language acquisition among humans. In such cases, genes determine the timing of the environmental impact.

A related concept is labeled "biased learning" (Alcock 2001:101–103) and "prepared learning" (Wilson, 1998:86–87). For instance, after eating food that subsequently made them sick, rats are predisposed to associate that food with smell, not sound (Alcock 2001:101–103). Many primate species learn to fear snakes with little experience (Wilson, 1998:86–87).



Explanations of Animal Behavior: Causal Relationships; Adopted from Tinbergen (1963)

Causal relationships

The figure shows the causal relationships among the categories of explanations. The left-hand side represents the evolutionary explanations at the species level; the right-hand side represents the proximate explanations at the individual level. In the middle are those processes' end products—genes (i.e., genome) and behavior, both of which can be analyzed at both levels.

Evolution, which is determined by both function and phylogeny, results in the genes of a population. The genes of an individual interact with its developmental environment, resulting in mechanisms, such as a nervous system. A mechanism (which is also an end-product in its own right) interacts with the individual's immediate environment, resulting in its behavior. Here we return to the population level. Over many generations, the success of the species' behavior in its ancestral environment (or more technically, the **e**nvironment of **e**volutionary **a**daptedness [EEA]) may result in evolution as measured by a change in its genes.

In sum, there are two processes—one at the population level and one at the individual level—which are influenced by environments in three time periods.

Examples

Returning to the initial issue of why we see, here are explanations by the four categories:

- Ultimate (functional): To find food and avoid danger.
- Phylogeny: The vertebrate eye initially developed with a blind spot, but the lack of adaptive intermediate forms prevented the loss of the blind spot.
- Development: Neurons need the stimulation of light to wire the eye to the brain (Moore, 2001:98–99).
- Proximate (mechanistic): The lens of the eye focuses light on the retina visual system.

The Westermarck effect is the lack of sexual interest in one's siblings (Wilson, 1998:189–196):

- Ultimate (functional): To discourage inbreeding, which decreases the number of viable offspring.
- Phylogeny: Found in a number of mammalian species, suggesting initial evolution tens of millions of years ago.
- Development: Results from familiarity with another individual early in life, especially in the first 30 months for humans. The effect is manifested in nonrelatives raised together, for instance, in the Israeli kibbutz system..
- Proximate (mechanistic): Little is known about the neuromechanism.

Use of the four-question schema as "periodic table"

The four-question schema is used as the central organizing device in some texts but not others. For instance, it is used in one of the most widely used animal behavior texts (Alcock, 2001) but not in one of the most widely used evolutionary psychology texts (Buss, 2004:12). An advantage of the schema is that it highlights gaps in knowledge, analogous to the role played by the periodic table of elements in the early years of chemistry:

The **"periodic table of life sciences"** becomes clear, when the following levels are graphed against the questions: the bio-molecule, cell, organ, individual and group level.

1. ***Causation*** **2.** ***Ontogeny*** **3. Adaptation 4. Phylogeny**

a. **Molecule**

b. **Cell**

c. **Organ**

d. ***Individual***

e. ***Family***

f. ***Group***

g. ***Society***

This "bio-psycho-social" table is a framework of reference, which demonstrates the associations between all non-human biological (levels a–f), as well as all anthropological and human sciences (levels a–g). Especially in anthropological and human sciences it helps to structure interdisciplinary discussions, teaching and research (i.e. "Fundamental Theory of Anthropology":). In the Table the questions and planes in *italics* are also the subject of the humanities. In this "**periodic table of human sciences**", all anthropological disciplines (paragraph C in the table of the pdf-file below), their questions and results can be intertwined and allocated with each other. This “bio-psycho-social” orientation framework is the basis for the development of an interdisciplinary consensus: It is the starting point for a systematical order for anthropological and human sciences, and also the basis for a consistent networking and structuring of their results. In terms of epistemology: Since the answers to the reference planes and to all four central questions must fit together without contradictions, misconceptions can thus be revealed by inconsistencies. The periodic table can help in estimating how much interdisciplinarity is implemented in specific scientific approaches.