

ETHOLOGY

Ethology is the science of the study of animal behaviour. This is a comparatively new science developed during the last century. It deals with the response of animals to various stimuli and factors operating in the environment.

Ethology Meaning

Ethology meaning refers to the scientific study of animal behaviour, with an emphasis on behaviour in natural environments and the idea of behaviour as an evolutionary adaptive attribute. Behaviourism also refers to the scientific and objective analysis of animal behaviour, with a focus on measured reactions to stimuli or trained behavioural responses within a laboratory environment, rather than on evolutionary adaptivity. Various naturalists have examined ethology meaning and various elements of animal behaviour across history. Charles Darwin (1809–1882) and American and German ornithologists of the late 19th and early 20th centuries, involving Oskar Heinroth (1871–1945), Charles O. Whitman, and Wallace Craig, laid the scientific foundations for ethology.

Ethology is a study that is quickly expanding. Numerous elements of animal communication, learning, culture, emotions, and sexuality which the scientific community believed it understood, have been re-examined and new findings have been made since the advent of the twenty-first century. New fields have emerged, including neuroethology.

Types of Ethology Studies:



- Sexual
- Social
- Shelter seeking
- Communicative
- Investigative
- Maternal
- Allelomimetic Eliminative
- Feeding
- Maladaptive

History

The Beginnings of Ethology

As ethology is a branch of biology, ethologists were specifically interested in the evolution of behaviour and how it may be explained in terms of natural selection. In some ways, Charles Darwin was the very first contemporary ethologist, influencing numerous ethologists with his 1872 book *The Expression of the Emotions in Man and Animals*. He continued his interest in behaviour through promoting his protégé George Romanes, who studied animal learning and intelligence using an anthropomorphic method called anecdotal cognitivism, which was not scientifically supported.

Growth of the Field

During the years leading up to World War II, ethology flourished in continental Europe thanks to the efforts of Niko Tinbergen and Konrad Lorenz. After the war, Tinbergen relocated to the University of Oxford, and ethology gained traction in the United Kingdom, thanks to the work of Robert Hinde, William Thorpe, and Patrick Bateson at the University of Cambridge's Sub-Department of Animal Behaviour. Ethology began to flourish in North America during this time period as well.

Social Ethology and Latest Developments

In 1972, the English ethologist John H. Crook distinguished comparative ethology from social ethology, arguing that the whole of the previous ethology had been comparative ethology (investigating animals as individuals), while ethologists would have to focus on the behaviour of social groups of animals and the social structure under them in the coming years. Since the publication of E. O. Wilson's book *Sociobiology: The New Synthesis* in 1975, the investigation of behaviour has become much more focused on social elements. This has also been fueled by Wilson's, Robert Trivers', and W. D. Hamilton's stronger, but far more nuanced Darwinism. Ethology has been transformed as a result of the linked development of behavioural ecology.

Learning

Associative Learning

In animal behaviour, associative learning refers to any learning process wherein a new response is linked to specific stimuli. Russian biologist Ivan Pavlov was the first to study associative learning, observing that dogs trained to link food with the banging of a bell salivated when they heard the bell.

Habituation

Habituation is a basic type of learning that can be found in a wide range of animal species. It is the act of an animal ceasing to respond to stimuli. Often, the reaction is a natural reaction. In essence, the animal learns to ignore unimportant inputs. Prairie dogs, for instance, make alarm sounds when predators arrive, driving the entire colony to scurry down burrows.

Giving warning calls every time a human goes by is time and energy-consuming when prairie dog communities are placed close to the trails utilised by people. In this setting, acclimating to people is a key adaptation.

Imprinting

Imprinting allows juveniles to distinguish between members of their own species, which is important for reproductive success. This crucial sort of education takes place during a relatively short amount of time. Lorenz noticed that young geese and chickens instantly obeyed their mothers from about the very next day after hatching, and he found that this response may be imitated via an arbitrary stimulus if the eggs have been artificially incubated and the stimulus was displayed throughout a critical period that lasted several days after hatching.

Teaching

Teaching is a noble specialised element of learning wherein the "teacher" (demonstrator) alters their behaviour in order to maximise the likelihood that the "student" (observer) achieves the desired outcome of the behaviour. Killer whales, for instance, have been seen to beach themselves in order to obtain pinniped prey. Killer whale mothers educate their young how to grab pinnipeds by dragging them onto the beach and urging them to assault the prey. This is proof of teaching since the mother killer whale is changing her behaviour to assist her children to learn to catch prey.

Mating and the Battle for Dominance

Individual reproduction has been the most significant step in the proliferation of people or genes inside a species; as a result, there seem to be elaborate mating rituals that could be rather complicated, despite the fact that they are frequently thought of as fixed action patterns.

Tinbergen's study of the stickleback's complicated mating ritual is recognised as a remarkable example.

Animals frequently battle for the freedom to reproduce and also social dominance in social life. The so-called pecking order in poultry is indeed a famous example of battling for social and sexual superiority. When a bunch of chickens live together for an extended period of time, they create a pecking order. One chicken controls the others in such groupings and can peck without becoming pecked. A second chicken, with the exception of the first, may peck everyone else, and so on. When contrasted to lower grade chickens, upper-level chickens can sometimes be differentiated by their healthier appearance.

During the establishment of the pecking order, numerous and severe battles may occur; but, once identified, the pecking order has only been broken when new members join the group, at which point the pecking order must be re-established from the beginning.

Living in Groups

Humans, like many other animals, like to stay in groups. Their social environment is heavily influenced by the size of respective groups. Social interaction is most likely a sophisticated and effective survival strategy. It's comparable to a symbiosis between members of the same species: a community is made up of a group of members from the very same species who live under well-defined rules for task assignments, food management, and reciprocal dependence.

Benefits and Costs of Group Living

Reduced predation is one benefit of existing in a group. The dilution effect may minimise the risk of predator attacks for individual victims if the number of predator assaults remains constant despite an increase in the prey group size. Moreover, as per the selfish herd theory, the fitness advantage of group life differs considerably depending on an individual's position inside the group.

According to the hypothesis, conspecifics at the centre of a group will be less vulnerable to predation, whereas those on the outskirts would be much more vulnerable. Furthermore, a predator who is perplexed by a large number of people may have a harder time identifying a single target. As a result, the zebra's stripes provide not only concealment in a tall grassy environment, but also the ability to blend in with a herd of other zebras. A prey may deliberately minimise their predation risk in groups by employing better effective defence techniques or by detecting predators early through heightened alertness.

Group Size

Social animals should, in theory, possess optimal group sizes which maximise the benefits of group existence while minimising the costs. Most natural groups, on the other hand, are persistent at slightly greater than ideal sizes. As it is often favourable for a member to enter an optimally-sized group, even if it reduces the benefit for all participants, groups might keep growing in size until it is far more profitable to stay alone than to enter an excessively large group.

- **Habituation** is a simple learned behaviour in which an animal gradually stops responding to a repeated stimulus.
- **Imprinting** is a specialised form of learning that occurs during a brief period in young animals—e.g., ducks imprinting on their mother.

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- In **classical conditioning**, a new stimulus is associated with a pre-existing response through repeated pairing of new and previously known stimuli.
- In **operant conditioning**, an animal learns to perform a behaviour more or less frequently through a reward or punishment that follows the behaviour.
- Some animals, especially primates, are capable of more complex forms of learning, such as problem-solving and the construction of mental maps.

Simple learned behaviours

Learned behaviours even though they may have innate components or underpinnings, allow an individual organism to adapt to changes in the environment. Learned behaviours are modified by previous experiences; examples of simple learned behaviours include habituation and imprinting.

Habituation

Habituation is a simple form of learning in which an animal stops responding to a stimulus, or cue, after a period of repeated exposure. This is a form of non-associative learning, meaning that the stimulus is not linked with any punishment or reward.

For example, prairie dogs typically sound an alarm call when threatened by a predator. At first, they will give this alarm call in response to hearing human steps, which indicate the presence of a large and potentially hungry animal.

However, the prairie dogs gradually become habituated to the sound of human footsteps, as they repeatedly experience the sound without anything bad happening. Eventually, they stop giving the alarm call in response to footsteps. In this example, habituation is specific to the sound of human footsteps, as the animals still respond to the sounds of potential predators.

Imprinting

Imprinting is a simple and highly specific type of learning that occurs at a particular age or life stage during the development of certain animals, such as ducks and geese. When ducklings hatch, they imprint on the first adult animal they see, typically their mother. Once a duckling has imprinted on its mother, the sight of the mother acts as a cue to trigger a suite of survival-promoting behaviours, such as following the mother around and imitating her.

How do we know this is not an innate behaviour, in which the duckling is hardwired to follow around a female duck? That is, how do we know imprinting is a learning process conditioned by experience? If newborn ducks or geese see a human before they see their mother, they will imprint on the human and follow it around just as they would follow their real mother.

An interesting case of imprinting being used for good comes from efforts to rehabilitate the endangered whooping crane by raising chicks in captivity. Biologists dress up in full whooping crane costumes while caring for the young birds, ensuring that they don't imprint on humans but rather on the bird dummies that are part of the costume. Eventually, they teach the birds to migrate using an ultralight aircraft, preparing them for release into the wild.

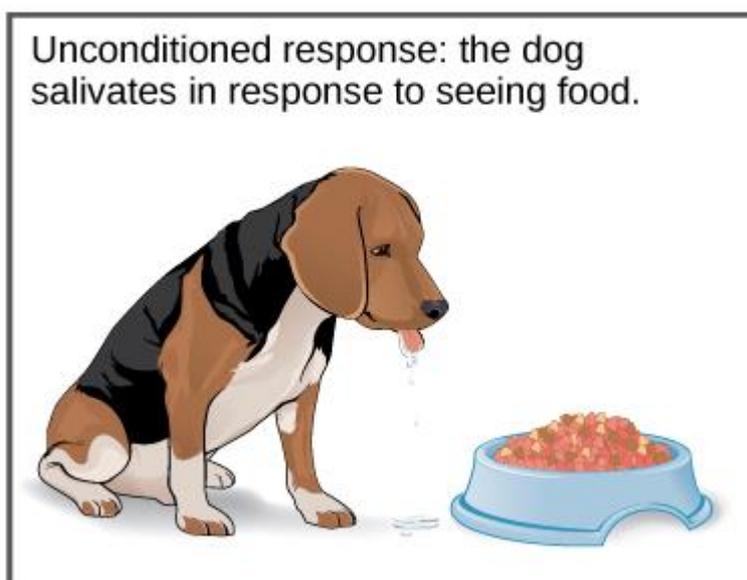
Conditioned behaviours

Conditioned behaviours are the result of associative learning, which takes two forms: classical conditioning and operant conditioning.

Classical conditioning

In classical conditioning, a response already associated with one stimulus is associated with a second stimulus to which it had no previous connection. The most famous example of classical conditioning comes from Ivan Pavlov's experiments in which dogs were conditioned to drool—a response previously associated with food—upon hearing the sound of a bell.

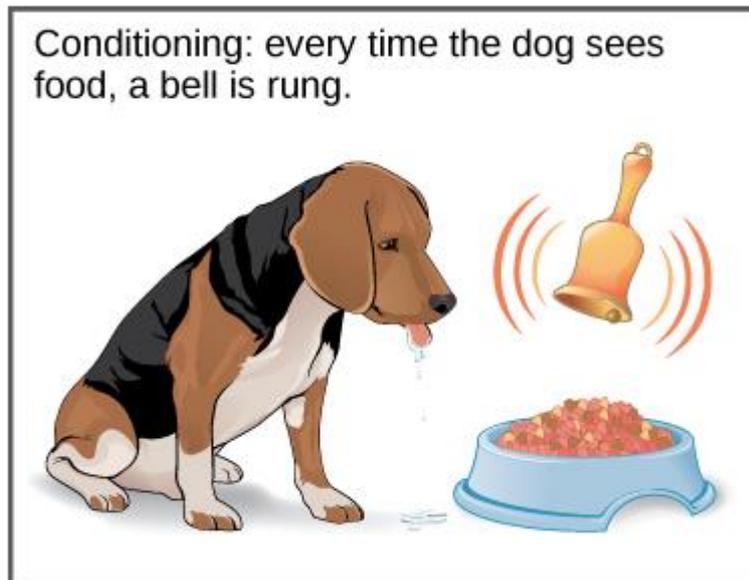
As Pavlov observed, and as you may have noticed too, dogs salivate, or drool, in response to the sight or smell of food. This is something dogs do innately, without any need for learning. In the language of classical conditioning, this existing stimulus-response pair can be broken into an unconditioned stimulus, the sight or smell of food, and an unconditioned response, drooling.



In Pavlov's experiments, every time a dog was given food, another stimulus was provided alongside the unconditioned stimulus. Specifically, a bell was

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rung at the same time the dog received food. This ringing of the bell, paired with food, is an example of a conditioning stimulus—a new stimulus delivered in parallel with the unconditioned stimulus.



Over time, the dogs learned to associate the ringing of the bell with food and to respond by drooling. Eventually, they would respond with drool when the bell was rung, even when the unconditioned stimulus, the food, was absent. This new, artificially formed stimulus-response pair consists of a conditioned stimulus, the bell ringing, and a conditioned response, drooling.

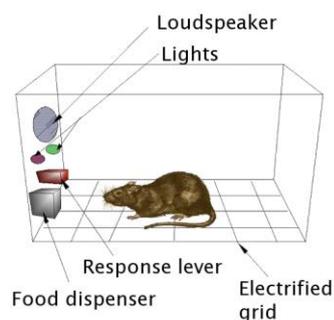


Is the unconditioned response, drooling in response to food, exactly identical to the conditioned response, drooling in response to the bell? Not necessarily. Pavlov discovered that the saliva in the conditioned dogs was actually different in composition than the saliva of unconditioned dogs.

Operant conditioning

Operant conditioning is a bit different from classical conditioning in that it does not rely on an existing stimulus–response pair. Instead, whenever an organism performs a behaviour—or an intermediate step on the way to the complete behaviour—it is given a reward or a punishment. At first, the organism may perform the behaviour—e.g., pressing a lever—purely by chance. Through reinforcement, the organism is induced to perform the behaviour more or less frequently.

One prominent early investigator of operant conditioning was the psychologist B. F. Skinner, the inventor of the Skinner box, see image below. Skinner put rats in boxes containing a lever that would dispense food when pushed by the rat. The rat would initially push the lever a few times by accident, and would then begin to associate pushing the lever with getting the food. Over time, the rat would push the lever more and more frequently in order to obtain the food.



Not all of Skinner's experiments involved pleasant treats. The bottom of the box consisted of a metal grid that could deliver an electric shock to rats as a punishment. When the rat got an electric shock each time it performed a

certain behaviour, it quickly learned to stop performing the behaviour. As these examples show, both positive and negative reinforcement can be used to shape an organism's behaviour in operant conditioning. Ouch! Poor rats!

Operant conditioning is the basis of most animal training. For instance, you might give your dog a biscuit or a "Good dog!" every time it sits, rolls over, or refrains from barking. On the other hand, cows in a field surrounded by an electrified fence will quickly learn to avoid brushing up against the fence.

As these examples illustrate, operant conditioning through reinforcement can cause animals to engage in behaviours they would not have naturally performed or to avoid behaviours that are normally part of their repertoire.

Learning and cognition

Humans, other primates, and some non-primate animals are capable of sophisticated learning that does not fit under the heading of classical or operant conditioning. Let's look at some examples of problem-solving and complex spatial learning in nonhuman animals.

Problem-solving in chimpanzees

The German scientist Wolfgang Köhler did some of the earliest studies on problem-solving in chimpanzees. He found that the chimps were capable of abstract thought and could think their way through possible solutions to a puzzle, envisioning the result of a solution even before they carried it out.

For example, in one experiment, Köhler hung a banana in the chimpanzees' cage, too high for them to reach. Several boxes were also placed randomly on the floor. Faced with this dilemma, some of the chimps—after a few false starts and some frustration—stacked the boxes one on top of the

other, climbed on top of them, and got the banana. This behaviour suggests they could visualise the result of stacking the boxes before they actually carried out the action.

Spatial learning in rats

Learning that extends beyond simple association is not limited to primates. For instance, maze-running experiments done in the 1920s—maze shown below—demonstrated that rats were capable of complex spatial learning.

In these experiments, rats were divided into three groups:

- Group I: Rats got food at the end of the maze from day one.
- Group II: Rats were placed in the maze on six consecutive days before receiving food at the end of the maze.
- Group III: Rats were placed in the maze for three consecutive days before receiving food at the end of the maze.

Not surprisingly, rats given a food reward from day one appeared to learn faster—had a more rapid drop in their number of errors while running the maze—than rats not given an initial reward. What was most striking, however, was what happened after the Group II and III rats were given food.

In both groups, the day after the food had been provided, the rats showed a sharp drop in number of errors, almost catching up to the Group I rats. This pattern suggested that the Group II and III rats had, in fact, been learning efficiently, building a mental map, in the previous days. They just didn't have much reason to demonstrate their learning until the food showed up.

These results show that rats are capable of complex spatial learning, even in the absence of a direct reward, in other words, without reinforcement. Later experiments confirmed that the rats make a representation of the

maze in their minds—a cognitive map—rather than simply learning a conditioned series of turns.

Latent Learning:

Some of the most direct evidence regarding cognitive processes comes from a series of experiments that revealed a type of cognitive learning called latent learning. In this new behaviour it is learned but it is not demonstrated until reinforcement is provided for displaying it.

In the studies, psychologists examine the behaviour of rats in a maze. In one representative experiment a group of rats was allowed to wander around the maze. Once a day for seventeen days without ever receiving any reward.

These rats made many errors and spent a relatively long time reaching the end of the maze. A second group, however, was always given food at the end of the maze. These rats learned to run quickly and directly to the food box making a few errors.

A third group of rats started out in the same situation as the unrewarded rats but only for the first ten days on the eleventh day a critical experimental manipulation was instituted from that point on the rats in this group were given food for completing the maze. The results of their manipulation were dramatic.

The previously unrewarded rats, who had earlier seemed to wander aimlessly showed reductions in summing time and declines in error rates such that their performance almost immediately matched that of a group that had received rewards from the start.

To cognitive theorists, it seemed clear that the rewarded rats had learned the layout of the maze early in their explorations; they first never displayed their talent learning until the reinforcement was offered. The rats seemed to develop cognitive maps of the maze, a mental representation of special locations and direction.

People develop cognitive maps of their surroundings based primarily on particular landmarks when they first encounter a new environment, their maps tend to rely on specific paths. As people become more familiar with an area they develop an overall concept of it which has been called an abstract cognitive map.

Observational Learning: Learning through Imitation:

Another form of cognitive learning is observational learning.

According to psychologist Albert Bandura and his colleagues, a major part of human learning consists of observational learning, which they defined as learning through observing the behaviour of another person called a model. Bandura and his colleagues demonstrated rather dramatically the ability of models to stimulate learning in what is now considered a classic experiment.

Young children saw a film of an adult wildly hitting a 5 feet tall inflatable punching toy called a bobo doll. Later the children were given an opportunity to play with the bobo doll themselves and they displayed the same kind of behaviour imitating the aggressive behaviour.

Not only negative behaviours are acquired through observational learning. In one experiment, for example, children who were afraid of dogs were exposed to a model playing with a dog. Following exposure observers were considered more likely to approach a strange dog than children who had not viewed the model.

Insight Learning:

In a typical insight situation a problem is passed, a period follows during which no progress is made and then the solution comes suddenly. A learning curve of insight learning would show no evidence of learning for a time, then suddenly learning would be almost complete.

What has been learnt can also be applied early to other similar situations. Human beings who solve a problem insightfully usually experience good feelings called an “aha” experience, “aha” we say as when we suddenly see the answer to the problems.

In insight learning, the following events occur:

1. The solution comes suddenly after a period during which various response strategies are tried.
2. There is perceptual rearrangement.
3. The solution, once got, can be generalised rather to other similar problems. These are two major characteristics of insight learning.

Insight involves a perceptual reorganisation of elements in the environment such that new relationships among objects and events are suddenly seen.

Many years ago the German psychologist Wolf Gang Kohler carried out a number of insight experiments on chimpanzees. One of the experiments he conducted was the following.

A chimpanzee was put inside the cage and outside the cage a banana was kept. Inside the cage there was a stick which was too short to reach

the food but this stick could be used to reach another longer stick outside the cage, this longer stick could be used to take in the food. In these experiments there was a period of trial and error, with little progress towards a solution.

Then Kohler reported the chimpanzee would suddenly stop what it was doing and visually survey the sticks and the food and then suddenly and smoothly and without any trial and error solve the problem by using the shorter stick to take inside the longer stick which could then be used to get the food.

In addition to the perceptual reorganisation of the environment there is often a carry over or transfer of things previously learned to onsite situations. Kohler's chimpanzee carried over what they already knew about sticks and other simple tools to the insight situation.

Transfer of Training or Learning:

Transfer of training or learning occurs when learning of one set of materials influences the learning of another set of material later. For example, driving a new car, the movements and responses in driving a new car will have similarities and differences when compared to movements and responses in driving the old car. The individual has to adapt his old habits and learn new ones.

According to Crow and Crow, transfer of learning means "the carry over of habits, thinking, feeling, working, knowledge and skills from one learning area to another learning area".

According to Bigger transfer of learning occurs when a person's learning in one situation influences his learning and performances in other situations.

Forms of Transfer:

1. Positive transfer:

When the learning in one situation facilitates the learner in another situation, we call it a positive transfer. For example, learning to ride a bicycle helps to ride a bike, etc.

2. Negative transfer:

When learning in one situation hinders the learning in a new situation it is called negative transfer. For example, some companies like to take fresh employees to avoid the process of negative learning due to earlier experience. Here earlier experience acts as a hindrance.

3. Zero transfer:

When learning in one situation does not influence the learning in another situation is said to be zero learning. For example, learning to write Kannada won't influence our learning to write in English.

4. Positive and negative:

Sometimes, previous learning may partly help as well as partly hinder the performance in a new situation. This is called positive as well as negative.

Orientation, Navigation and Homing in Animals

Orientation is the position of the animal with reference to gravity or resource. This is the position the animal maintains in order to reach the resource. Positional orientation is to maintain upright posture against

gravity for which vertebrates have membranous labyrinth and invertebrate statocyst.

Object orientation takes place when the animal tries to approach an object which may be food or water. Aquatic animals move vertically in ponds or lakes which is called strato-orientation. When the animals try to move from grassland to forests, deserts or mountains it is called zonal orientation. Animals which migrate long distances generally possess topographical or geographical orientation.

KINESIS

Kinesis is the movement of an animal in response to stimuli. It may be oriented or unoriented depending on the source of stimulus. The response may be proportional to the intensity of stimulus.

Klinokinesis is the change of direction during movement which may increase or decrease in the light of intensity. Generally the animal moves right and left alternately to compare the direction of stimulus to gain correct orientation. Animals having single receptor show alternate movements. Caterpillars and maggots looking for the sites of pupation vacillate while moving.

Orthokinesis depicts speed of locomotion which is related to the intensity of stimulus and accumulation of action specific energy in the animal. Whole body of the animal is involved. For example, burrowing animals such as Ammocoete larvae of lampreys burrows in sand away from light. Cockroaches move from brighter areas to darkness.

Different types of kinesis are termed with respect to the stimulus, e.g. hygrokinesis is with respect to humidity as in isopods; photokinesis in which stimulus is gradient of light and chemokinesis is with respect to chemical stimuli.

TAXIS

Taxis is the orientation of the animal with reference to the direction of stimulus in space. Movement can be towards or away from the stimulus and depending upon the stimulus it can be names as follows: hygrotaxis (humidity); geotaxis (gravity); chemotaxis (taste or odour); thermotaxis (temperature); anemotaxis (air current); rheotaxis (water current); phototaxis (light intensity); phonotaxis (sound waves); astro taxis (sun, moon and stars); menotaxis (angle to the stimulus); mnemotaxis (based on memory).

Klinotaxis occurs in those animals which have a single receptor, as in Euglena, which compares the intensity of stimulus by alternate lateral movements. Similarly in the maggots of Diptera the light sensitive organ is a cluster of cells above and behind the mouth and the negative response to light is compared by flexing movement of the body.

Tropotaxis is found in animals which have paired receptors as eyes in Planaria. Animals get equal inputs on both the receptors and hence it can move in a straight line towards or away from light. If one eye of an insect is painted black it makes circling movements towards the side of the painted eye.

Telotaxis is found when an animal has a choice between the positive and negative stimuli or when the animal does not have a balanced input on the two receptors. Orientation is affected by fixing the image on one side by moving the head and making a choice. Honey bee seeing two light sources flies to any one by making a choice.

Menotaxis involves maintaining a constant angle in relation to the source of stimulus. Nocturnal moths have a habit of flying by keeping the light source (usually stars and moon) at right angle to the body so that they can fly parallel to the ground. But when they do the same with artificial light that is too close, they are forced to fly in circles. Honey bees fly from their hives to the flowers by maintaining a constant angle to the sun as revealed by the wagging dance of the scout bees. The angle to the sun is remembered by foraging bees while watching the dance on the vertical surface of the comb. Foraging bees then fly towards the food source maintaining the same angle to the sun.

Mnemotaxis was first described by Kuhn (1919). This is an orientation based on memory that was studied by Niko Tinbergen (1951) with his experiment on digger wasps. Wasp circles around the nest and carries a memory map of the nest and its surroundings, which helps it to accurately orient itself and return to the nest. This is also called zonal orientation and geographical orientation which involves distance, direction and landmarks that make topography of the area and help the animal in homing to its nest.

NAVIGATION & HOMING

Migratory animals which cover long distances either to reproduce or to escape from the harsh climate must find their way accurately over oceans, deserts, forest and mountains. Fishes, birds and many invertebrates possess extraordinary capabilities to cross oceans, deserts and mountains in order to reach their destination.

Invertebrates such as crustaceans, amphipods, ants, bees and wasps possess strong homing and navigational instinct and are guided by the sun, moon, stars and topography of the area in following an accurate route. Monarch butterflies migrate thousands of kilometres from Canada

to Mexico to escape harsh winters and return back accurately to the same place.

FISH NAVIGATION

How fishes find their way in huge expanses of sea and reach their destinations which lie thousands of kilometres away has been a mystery. It is believed that they orient by the positions of stars and moon in the night sky and sun in daytime to find the direction of swimming.

They also make use of temperature gradients and ocean currents which help them in swimming and also in navigation. However, it has been experimentally proven by A.S. Hasler that salmon are guided by the odour of their parent stream during their return journey.

Odour map gets imprinted in their brains when they migrate as larvae from tributaries to the sea and they can navigate back from the sea using this odour map when they become adults. Eels can also migrate to Sargasso Sea using similar odour maps but how their larvae, leptocephali find their way back to the river mouths, crossing vast stretches of Atlantic Sea is a mystery. Probably their parents leave some kind of odour trails during their journey.

NAVIGATION IN BIRDS

Birds use a number of methods to find their way during migration. Many use celestial navigation, a method of orienting the body to the arc of the sun, to the phases of the moon, or to the pattern of stars in a particular season, which is called menotaxis. Hummingbirds and pigeons are able to determine the position of the sun even on overcast days because they can detect the ultraviolet radiation it emits.

Experiments in the planetarium on night migrant birds, such as white throated warblers and indigo buntings reveal that they orient themselves by the position of stars in the night sky.

Some birds are sensitive to coriolis force that arises by deflection of winds in the northern hemisphere by earth's rotation.

Some diurnal birds use topographical landmarks such as mountains, river valleys, and forests to orient themselves on the migration route. Some are able to detect infrasound or low-frequency sounds that are produced by ocean waves. Many birds, particularly seabirds, identify their destinations by characteristic odours.

Many birds possess instinct or some kind of internal compass or biological clock that guide them through the route of migration. Young birds follow the migration route accurately without previous training or experience by their inherent capacity to navigate.

Some birds such as oil birds of South America and Himalayan cave swift possess echolocation and can be guided by it.

The classic experiment proving the internal-clock theory was done by German Gustav Kramer during the early 1950's. He placed Starlings wanting to migrate in a cage from which they could see the sun. The birds would sit looking in the direction toward which they wanted to fly. Significantly, if the Starlings couldn't see the sun, they didn't face in any particular direction.

Also during the 1950's, the German Franz and Eleonore Sauer did a similar experiment with birds that could and could not see the night stars and arrived at similar results. Certain species can orient themselves according to the sky's major stars. In fact, an experiment with Mallard Ducks found that if the moon is so bright that important stars are hidden by glare,

released ducks can't orient themselves as well as on darker, moonless nights.

Some birds, such as pigeons, are sensitive to changes in the earth's magnetic field because of the presence of magnetite in their head and neck muscles. During the early 1970's, W.T. Keeton tied small, bar magnets on the backs of pigeons. When released at locations the birds had never seen before, the pigeons with non-magnetic bars found their ways home but those with bar magnets got confused.

In 2007 German scientists found tiny iron oxide crystals in the skin lining of the upper beak of pigeons, which might be of help to the birds to sense the earth's magnetic field and assist them to identify their geographical position.

The researchers also discovered cryptochromes, which change their chemistry in the presence of a magnetic field, in the retinas of migratory birds' eyes. The molecules might then affect light-sensing cells in the retina to create images due to the magnetic field and help the bird to navigate during flight.

Infrasound travels much farther than ordinary sound and it comes from many different natural sources, including ocean waves, surf, winds, storms, earthquakes and other geologic events. It is believed that birds can hear infrasounds that we cannot hear and hence they possess this accessory navigational capability.

Migration:

Changes of habitat periodically recurring and alternate in direction, which tend to secure optimum environmental conditions at all times.

Types of Bird Migration:

All birds do not migrate, but all species are subject to periodical movements of varying extent. The birds which live in the northern part of the hemisphere have the greatest migratory power.

Migration may be:

- (i) Latitudinal
- (ii) Longitudinal
- (iii) Altitudinal or Vertical
- (iv) Partial
- (v) Total
- (vi) Vagrant or Irregular,
- (vii) Seasonal
- (viii) Diurnal
- (ix) Nocturnal

(i) Latitudinal migration:

The latitudinal migration usually means the movement from north to south, and vice versa. Most birds live in the land masses of the northern temperate and subarctic zones where they get facilities for nesting and feeding during summer. They move towards the south during winter.

An opposite but lesser movement also occurs in the southern hemisphere when the seasons are changed. Cuckoo breeds in India and spends the summer in South-east Africa and thus covers a distance of about 7250 km.

Some tropical birds migrate during the rainy season to the outer tropics to breed and return to the central tropics in the dry season. Many marine birds also make considerable migrations. Puffinus (Great shearwater) breeds on small islands and migrates as far as Greenland in May and returns after a few months.

It covers a distance of 1300 km. Penguins migrate by swimming and cover a considerable distance of a few hundred miles. *Sterna paradisaea* (Arctic tern) breeds in the northern temperate region and migrates to the Antarctic zone along the Atlantic. It was observed that *Sterna* covers a distance of 22 500 km during migration!

(ii) Longitudinal migration:

The longitudinal migration occurs when the birds migrate from east to west and vice-versa. Starlings (*Sturnus vulgaris*), a resident of east Europe and west Asia migrate towards the Atlantic coast. California gulls, a resident and breed in Utah, migrate westward to winter in the Pacific coast.

(iii) Altitudinal migration:

The altitudinal migration occurs in mountainous regions. Many birds inhabiting the mountain peaks migrate to lowlands during winter. Golden plover (*Pluvialis*) starts from the Arctic tundra and goes up to the plains of Argentina covering a distance of 11 250 km.

Birds migrate either in flocks or in pairs. Swallows and storks migrate a distance of 9650 km from northern Europe to South Africa. Ruff breeds in

Siberia and travels to Great Britain, Africa, India and Ceylon thus travelling a distance of 9650 kilometres.

(iv) Partial migration:

All the members of a group of birds do not take part in migration. Only several members of a group take part in migration.

Blue Jays of Canada and the northern part of the United States travel southwards to blend with the sedentary populations of the Southern States of the U.S.A. Coots and spoon bills (*Platalea*) of our country may be examples of partial migration.

(v) Total migration:

When all the members of a species take part in the migration, it is called total migration.

(vi) Vagrant or irregular migration:

When some of the birds disperse to a short or long distance for safety and food, it is called vagrant or irregular migration. Herons may be the example of vagrant or irregular migration. Other examples are black stork (*Ciconia nigra*), Glossy ibis (*Plegadis falcinellus*), spotted eagle (*Aquila clanga*), and bee eater (*Merops apiaster*).

(vii) Daily migration:

Some birds make daily journeys from their nests by the influence of environmental factors such as temperature, light, and humidity also. Examples are crows, herons and starlings.

(viii) Seasonal migration:

Some birds migrate at different seasons of the year for food or breeding, called seasonal migration, e.g., cuckoos, swifts, swallows etc. They migrate from the south to the north during summer. These birds are called summer visitors. Again there are some birds like snow bunting, red wing, shore lark, grey plover etc. which migrate from north to south during winter. They are called winter visitors.

Nocturnal and Diurnal Flight:

(i) Diurnal migration:

Many larger birds like crows, robins, swallows, hawks, jays, blue birds, pelicans, cranes, geese, etc. migrate during daytime for food. These birds are called diurnal birds and generally migrate in flocks.

(ii) Nocturnal birds:

Some small-sized birds of passerine groups like sparrows, warblers, etc. migrate in darkness, called nocturnal birds. The darkness of the night gives them protection from their enemies.

Causes of Migration:

Most species of birds migrate more or less on schedule and follow the routes in a regular fashion. The actual causative factors determining the course and direction of migration are not clearly known.

The following factors may be related to the problems of migration:

i. Instinct and Gonadal changes:

It is widely accepted that the impulse to migrate in birds is possibly instinctive and the migration towards the breeding grounds is associated with gonadal changes.

ii. Scarcity of food and day length:

Other factors, viz., scarcity of food, shortening of daylight and increase of cold are believed to stimulate migration. Migration in birds depends upon two important factors— stimulus and guidance.

Scarcity of food and fall of daylight are believed to produce endocrine changes which initiate bird migration.

iii. Photoperiodism:

The increase of day length (Photoperiodism) induces bird's migration. The day length affects pituitary and pineal glands and also caused growth of gonads which secrete sex hormones that are the stimulus for migration. In India, Siberian crane, geese, swan that come from Central Asia, Himalayas, begin to return from March and onwards with the increase of day length.

iv. Seasonal variation:

The north-to-south migrations of birds take place under stimulus from the internal condition of the gonads which are affected by seasonal variation.

v. Light:

The experiments of Rowan with Juncos (summer visitor to Canada) have established that light plays an important role in the development of gonads, which has an indirect role on migration. If the gonads undergo regression, the urge for migration is not felt. So the seasonal changes in illumination appear to be a crucial factor for determining migration.

Despite all these suggestions, it is not clear how birds – through successive generations – follow the same route and reach the same spot. The instinctive behaviours like migration, breeding, moulting are phasic occurrences in the annual cycle which are possibly controlled by the endocrine system. In all migratory birds, accumulation of fat takes place for extra fuel during prolonged flight in migration.

Guiding Mechanisms in Bird Navigation:

For more than a century the celestial navigations of birds have fascinated the ornithologists. Different explanations have been advanced to explain how birds navigate. It is difficult to generalise the means of orientation and navigation in migration. The different groups of birds with different modes of existence have evolved different means of finding their way from one place to another (Pettingill, 1970).

The other reasons may be:

Fat deposition:

Migratory birds become greedy and fat is deposited in the subcutaneous region of the body. Fat deposition plays an important role in the migration of birds. Birds, those migrate a long distance, reserve enough fat which provides energy in their arduous journey and helps the birds to reach its destination, following a particular route. After fat deposition, restlessness (Zugunruhe) is seen among birds for migration.

Inherited instinct:

Birds that take part in migration or follow a more or less definite goal, evidently possess an inherited instinct. Both the direction and the goal must have been implanted in the bird's genetic code when a population can adjust to a particular location or environment.

Experienced Lead the Flock:

The theory is sometimes advanced that old and experienced birds lead the way and thereby lead the whole route and show the whole route to the younger generation. This theory may be applicable to some birds like swans, geese and cranes because they fly in flocks but not applicable in all species where old and young migrate at different times and mainly young start ahead of the adult.

Werner Ruppell of Germany, a leading experimenter on avian migration, found that Starlings of Berlin find their way back to their nesting places from about 2000 km away. A sea bird named Manx shearwater collected from the western coast of England after being flown by plane to Boston was found back in its nest in England within 12 days.

The shearwater had flown its own way about 4940 km across the unknown Atlantic Ocean! The golden plover of North America migrates from its winter home in the Hawaiian islands to its breeding place in northern Canada.

This bird lacks webbed feet and it is quite natural that it must fly for several weeks over thousands of kilometres of ocean to reach its destination. The birds have wonderful power of navigation and orientation to find their destination even in odd conditions.

Disadvantages of Bird Migration:

- i. Many young people are not able to reach their destination because they die during the course of the continuous and tiresome journey.
- ii. Sudden changes in the climate such as storms and hurricanes, strong wind, fog are the causes for the death of a sizable number of migrants.
- iii. Sometimes man-made high towers and lighthouses cause the death of migratory birds.
- iv. Men themselves are responsible for the death of the migrants. They shoot at these poor birds just for their own leisure and amusement.

Fishes migration

- In ecology, it is an animal behaviour of mass movement of animals from one place to another.
- The purposes for migration varies accordingly with the types of animals.
- Migratory behaviour of fish is a regular phenomenon. Their journey is proposed mainly for feeding and reproduction.

Types fish migration on the basis of needs:

1. **Alimentary or Feeding migration:** migration for search of feeding ground. It occurs when food resources get exhausted.
2. **Gametic or spawning migration:** it occurs during the breeding season in search for the suitable spawning ground.
3. **Climatic or seasonal migration:** migration in search for suitable climatic conditions.
4. **Osmo-regulatory migration:** migration for water and electrolytes balance from sea to fresh water and vice-versa.

5. **Juvenile migration:** it is larval migration from spawning ground to the feeding habitats of their parent

Movement of fishes during the migration

1. **Drifting movement:** It is a passive movement of fish along with water currents
2. **Dispersal movement:** It is a random locomotory movement of fish from a uniform habitat to diverse direction
3. **Swimming movement:** It is an oriented movement of fish either toward or away from the source of stimulus
4. **Denatant and Contranatant movement:** It is an active swimming movement. Denatant movement is swimming with the water current while contranatant movement is swimming against water current

Types of fish migration

The migration of some fishes is a regular journey and is truly an innate animal behaviour. Fish migration are classified into following types:

Types of fish migration

The migration of some fishes is a regular journey and is truly an innate animal behaviour. Fish migration are classified into following types:

1. Diadromous migration:

- It is the migration of fish between sea and fresh water.
- As we know, most of the fishes are restricted to either fresh water or sea water. Changes in habitat may cause osmotic imbalance in those fishes. However some fishes regularly migrate between sea and fresh water and have perfect osmotic balance, they are the true migratory fish.
- This migration is of two types-

i. Anadromous migration:

- It is the migration of marine fishes from sea to fresh water for spawning.
- Fishes spend most of their life living and feeding in the sea.
- They only migrate during breeding season to the river for spawning ground
- Eg. Salmon, Hilsa, Lamprey etc.

Salmon migrate for breeding during winter from sea to river. While migrating, some physiological changes occurs:

- stops feeding during journey
- changes colour from silver to dull reddish brown
- gonads mature

They select suitable spawning ground and make a saucer-like nest in which females lay eggs and male releases smelt over them. Juvenile larvae hatched out from the egg known as Alevins. Alevins then transform into parr and metamorphose into adults when they return to the sea.

ii. Catadromous migration:

- It is the migration of fresh water fishes from river to sea during breeding season for spawning. Eg. Eel (*Anguilla* spp)
- Both European eel (*Anguilla anguilla* or *Anguilla vulgaris*) and the American eel (*Anguilla rostrata*) migrate from the continental rivers to Sargasso Sea off Bermuda in south Atlantic for spawning, crossing the Atlantic Ocean.

ENTRI

- Before and during migration some physiological changes occur in their bodies:
 - deposit large amount of fat in their bodies which serves as reserve food during the journey
 - Colour changes from yellow to metallic silvery grey.
 - Digestive tract shrinks and stops feeding
 - Eyes get enlarged and vision sharpens. Other sensory organs also become sensitive.
 - Skin serves as a respiratory organ.
 - Gonads get matured and enlarged.

They lay eggs in suitable spawning grounds and are fertilised by males. After spawning they die. The larva hatch out and develop into young eels and finally return to the river.

2. Potamodromous migration:

It is the freshwater migration of fresh water from one habitat to another for feeding or spawning.

Eg. Carps, catfish

3. Oceanodromous migration:

It is the migration of fish within sea in search of suitable feeding and spawning ground.

eg. Clupea, Hummus, Tuna

4. Latitudinal migration:

- It is the migration of fish from north to south and vice-versa.
- It is a climatic migration.
- Eg. Swordfish migrate north in spring and south in autumn.

5. Vertical migration:

- It is a daily migration of fish from deep to the surface and vice-versa for food, protection and spawning.
- Eg. Swordfish usually move vertically downward to greater depth for food.

6. Shoreward migration:

- It is the migration of fish from water to land. However it is a temporary migration.
- Eg. Eel migrate from one pond to another pond via moist meadow grass.

Significance of fish migration

- to find suitable feeding and spawning ground
- for protection from predators
- survive from extreme climatic conditions
- increases genetic diversity
- it is an adaptational characters for survival and existences

Biological clocks

Biological clocks are organisms' natural timing devices, regulating the cycle of circadian rhythms. They're composed of specific molecules (proteins) that interact with cells throughout the body. Nearly every tissue and organ contains biological clocks. Researchers have identified similar genes in people, fruit flies, mice, plants, fungi, and several other organisms that make the clocks' molecular components.

Circadian rhythms

Circadian rhythms are physical, mental, and behavioural changes that follow a 24-hour cycle. These natural processes respond primarily to light and dark and affect most living things, including animals, plants, and microbes. Chronobiology is the study of circadian rhythms. One example of a light-related circadian rhythm is sleeping at night and being awake during the day. The Average Teen Circadian Cycle image shows the circadian rhythm cycle of a typical teen.

How do circadian rhythms affect health?

Circadian rhythms can influence important functions in our bodies, such as:

- Hormone release
- Eating habits and digestion
- Body temperature

However, most people notice the effect of circadian rhythms on their sleep patterns. The SCN controls the production of melatonin, a hormone that makes you sleepy. It receives information about incoming light from the optic nerves, which relay information from the eyes to the brain. When there is less light—for example, at night—the SCN tells the brain to make more melatonin so you get drowsy.

What factors can change circadian rhythms?

Changes in our body and environmental factors can cause our circadian rhythms and the natural light-dark cycle to be out of sync. For example:

- Mutations or changes in certain genes can affect our biological clocks.
- Jet lag or shift work causes changes in the light-dark cycle.

- Light from electronic devices at night can confuse our biological clocks.

These changes can cause sleep disorders, and may lead to other chronic health conditions, such as obesity, diabetes, depression, bipolar disorder, and seasonal affective disorder.

Circannual cycle

A circannual cycle is a biological process that occurs in living creatures over the period of approximately one year. This cycle was first discovered by Ebo Gwinner and Canadian biologist Ted Pengelley.[1] It is classified as an infradian rhythm, which is a biological process with a period longer than that of a circadian rhythm, less than one cycle per 24 hours. These processes continue even in artificial environments in which seasonal cues have been removed by scientists.[2] The term circannual is Latin, circa meaning approximately and annual relating to one year. Chronobiology is the field of biology pertaining to periodic rhythms that occur in living organisms in response to external stimuli such as photoperiod.

Cycles come from genetic evolution in animals which allows them to create regulatory cycles to improve their fitness. Evolution for these traits comes from the increased reproductive success of animals most capable of predicting the regular changes in the environment like seasonal changes and adapt capitalise on the times when success was greatest. The idea of evolved biological clocks exists not only for animals but also in plant species which exhibit cyclic behaviours without environmental cues.[3] Plentiful research has been done on the biological clocks and what behaviours they are responsible for in animals, circannual rhythms are just one example of a biological clock.

Rhythms are driven by hormone cycles and seasonal rhythms can endure for long periods of time in animals even without photoperiod signalling which comes with seasonal changes. They are a driver of annual

behaviours such as hibernation, mating and the gain or loss of weight for seasonal changes. Circannual cycles can be defined by three main aspects being that they must persist without apparent time cues, be able to be phase shifted, and should not be changed by temperature. Circannual cycles have important impacts on when animal behaviours are performed and the success of those behaviors. Circannual cycles can be defined by three main aspects being that they must persist without apparent time cues, be able to be phase shifted, and should not be changed by temperature.

The location of the physical circannual timer in organisms and how it works are almost entirely unknown.

Lunar Periodicity

A biological rhythm may be defined as lunar periodicity if the maxima and minima of the rhythmical process appear once or twice in every lunar month at the same time, that is, at the time of a certain moon-phase, or, in other words, if they follow each other periodically in distances of about 30 (precisely 29.53) or 15 (precisely 14.77) days.

Tidal

Ideas are one of the most reliable phenomena in the world. As the sun rises in the east and the stars come out at night, we are confident that the ocean waters will regularly rise and fall along our shores. The following pages describe the tremendous forces that cause the world's tides, and why it is important for us to understand how they work.

Basically, tides are very long-period waves that move through the oceans in response to the forces exerted by the moon and sun. Tides originate in the oceans and progress toward the coastlines where they appear as the regular rise and fall of the sea surface. When the highest part, or crest of

the wave reaches a particular location, high tide occurs; low tide corresponds to the lowest part of the wave, or its trough. The difference in height between the high tide and the low tide is called the tidal range.

A horizontal movement of water often accompanies the rising and falling of the tide. This is called the tidal current. The incoming tide along the coast and into the bays and estuaries is called a flood current; the outgoing tide is called an ebb current. The strongest flood and ebb currents usually occur before or near the time of the high and low tides. The weakest currents occur between the flood and ebb currents and are called "slack water" or "slack current". In the open ocean tidal currents are relatively weak. Near estuary entrances, narrow straits and inlets, the speed of tidal currents can reach up to several kilometres per hour.

Seasonality

Seasonality is a characteristic of a time series in which the data experiences regular and predictable changes that recur every calendar year. Any predictable fluctuation or pattern that recurs or repeats over a one-year period is said to be seasonal.

Seasonal effects are different from cyclical effects, as seasonal cycles are observed within one calendar year, while cyclical effects, such as boosted sales due to low unemployment rates, can span time periods shorter or longer than one calendar year.

Pheromones

Pheromones are chemical signals that have evolved for communication between members of the same species. A pheromone signal elicits a specific reaction in the receiver, for example, a stereotyped behaviour (releaser effect) or a developmental process (primer effect). Some pheromones can have both effects. All sorts of molecules, large and small,

have been found acting as pheromones, depending on whether the message is sent out on wind or water currents or placed directly on the nose or antenna of the recipient.

Most pheromones are detected by the sense of smell. However, not all smells are pheromones. Mammals, including humans, also give off a cloud of molecules that represent our unique individual "smell" or chemical profile. These differences between individuals make it possible for dogs to distinguish people by smell. People are quite good at it, too—parents can distinguish their baby from others by smell alone. Ants similarly can distinguish between members of their own colony and those from other colonies. In both mammals and insects, learning is necessary to develop this ability. The sources of the molecules that make up an animal's "individual smell" include its own secretions and also may reflect its environment, food, bacteria, immune system, and molecules picked up from other individuals in its social group.

To definitively demonstrate that a pheromone exists, one must design a repeatable experiment, a bioassay, that shows that a smell molecule (odorant) causes a particular effect on the receiver, for example inducing a behaviour. Butenandt used such a bioassay to enable his identification of the first pheromone in the silk moth: He observed that males showed excited wing fluttering in response to the smell of mature females (and extracts of their pheromone glands). The wing fluttering response gave Butenandt a bioassay to see which fractions of the extract contained the pheromone activity as he attempted the next steps of isolating the possible pheromone molecule. He and his team tested many extracts and identified the sought-after odorant when it induced the telltale fluttering behaviour. They then synthesised the molecule and showed that the synthetic molecules had the same effect as real female extracts.

These steps are basically the same ones that need to be carried out today to identify the pheromones of any organism, starting with finding a good bioassay. What has changed is that, whereas Butenandt needed 500,000

female moths to get enough material for his analysis, a team today could attempt much of the analysis using just a few individual moths. This is largely due to improvements in technology, notably gas chromatography linked to mass spectroscopy, but also because we now often know the kind of molecules we are looking for.

Moths as Pheromone Models

Because many moth species are crop pests, the pheromones of this group have been particularly well studied for their potential in biocontrol methods. Moths provide model systems to explore how animals find their way to a pheromone source to find a mate and how animals distinguish between the pheromones of different related species.

When a female moth releases her volatile sex pheromone into the night air, it is carried by the wind like an invisible smoke plume from a chimney. The wind shears it into pockets of air with pheromone separated by clean air pockets. When a pocket of air with pheromone hits the antennae of a male searching on the wing, he responds by flying upwind for a fraction of a second. If he hits another pocket of pheromone, he flies upwind again. If he doesn't hit more pheromones, he flies from side to side until he hits pheromones again. This is a neat way of effectively flying upwind towards the female despite rapidly changing wind directions. This strategy has inspired programming of robots to orient up a chemical plume, and vertebrates such as fish and albatross show similar zig-zag tracks toward an odour source.

Most female moth sex pheromones consist of a specific combination of molecules. Closely related species use the same molecules in different ratios or share many, but not all, of the molecules: The differences allow males to distinguish females of their own species from those of other species. As the male flies upwind he will only respond if the pheromone hitting his antennae contains just the right combination for his species. On

his antennae are the olfactory sensory neurons with specialised receptors. Moth males in species with multicomponent pheromones have one receptor specific for each molecule that makes up the pheromone. If all the right molecules are present, in the right ratio, then the right combination of nerve cells and their glomeruli are stimulated, sending a message to the higher brain: "Fly upwind." However, the male moths are also sensitive to distinctive molecules in the pheromone blends of related species. If a male moth detects those, he stops flying upwind to avoid wasting his time pursuing a female from another species.

The Smell of Royalty in Social Insects

Social insects have provided some of the most spectacular examples of pheromone evolution. Pheromones mediate many of the complex interplays within colonies of social insects such as bees, wasps, and ants. These include the familiar trails of ants and the honey bee alarm pheromones mentioned earlier. However, pheromones are also essential mediators of two aspects of the defining feature of social insects, the division of colony members into queens and workers. Only the queen (or a small number of queens) produces fertile eggs.

First, a pheromone "tells" the workers not to reproduce. The signal is a queen pheromone, worn like a crown only by the queen in an ant or honeybee colony. It marks her and also seems to tell the workers that because she is fertile and laying eggs, the workers do not need to do so. With colonies of up to half a million individuals, pheromones are the only practical way for the queen to send a message to all the workers in the colony.

In many species the workers' ovaries do not develop if the workers detect the queen pheromone. If the queen is removed and her pheromone is no longer detected, then the workers start to develop ovaries. This property can be used to sensitively test which molecules produced by a queen can

act in her absence. University of Leuven's Annette Van Oystaeyen and her colleagues used this bioassay to explore queen pheromones in a wide range of ants, bees, and wasps in a recent international study. They showed that in most kinds of ants, bees, and wasps the chemicals are similar to nonvolatile saturated long-chain hydrocarbons. These queen pheromones, which signal her fertility, are chemically similar to and may have evolved from sex pheromones advertising fertility in solitary ancestor species.

The second key role for pheromones in social insects is controlling which larvae become queens in the first place. This is a developmental (primer) effect of pheromones on the larvae. In the honeybee, any female larva has the genetic potential to develop into a worker or a queen, depending on what it is fed as a larva. If it is fed only royal jelly, a special food produced by nurse worker bees, the larva will develop irreversibly into a queen. The switch is triggered by the primer effects of pheromones in the royal jelly, including a protein called royalactin, recently identified by Masaki Kamakura of Toyama Prefectural University, Japan. Among the many effects of royalactin in the larva are changes in hormone release, which in turn may affect which genes are turned on and off via DNA methylation. The queen will be much larger than workers, live 20 times as long, and have functioning ovaries to lay up to a million eggs.

Primer effects also occur in mammals. Mice living together may affect each other's reproductive development via primer effects. For example, exposure to the urine of dominant adult male mice causes immature female mice to become sexually mature more quickly. However, it is not clear which molecules in the male urine are inducing this primer effect. There have also been questions about whether these effects occur in the wild, because most have only been observed in the laboratory.

Mammals Follow Their Noses

Vertebrates, including mammals, use pheromones extensively. In mammals, both small molecules and large proteins have been identified as pheromones. The range of mammals shown to use them includes elephants, goats, and pigs, but the best studied is the house mouse, building on its status as a key model species in medical research.

When we switch off the lights and go to bed, the house mouse is in its element. Like many nocturnal animals, it has large, sensitive eyes and ears. But much more important is its world of smells. A dominant male spends much of his time crisscrossing his territory, painting drops of his urine on landmarks, boasting his ownership. The volatile smells wafting from the urine marks attract females to come close to the scent mark, where they sniff up a nonvolatile protein pheromone, darcin. A message sent to the female's brain prompts her to remember the individual smell of the male who left the mark and also remember its location. She will return to the spot and mate with the territory owner, recognized by his individual smell.

All vertebrates have a main olfactory system, the nose. Frogs, salamanders, snakes, and many mammals—but not humans and other higher primates—also have a second nose, the vomeronasal olfactory system. For a while it was thought in error that vertebrate pheromones were exclusively perceived via the vomeronasal system. It is now clear that vertebrate pheromones can be detected by either or both olfactory systems, depending on the species. For example the rabbit mammary pheromone is detected by the pups' main olfactory system. There is a significant overlap even in the size of molecule that is detected by each of the two systems: In the house mouse, while protein pheromones such as darcin are likely only detected by the vomeronasal olfactory system, small molecule pheromones can be detected by either system. The two olfactory systems also have different families of receptors: A mouse pheromone with primer effects on female estrus, 2-heptanone, which is detected by both systems, must thus interact with different receptors in each system.

The main and vomeronasal olfactory systems send their information to different parts of the brain, but these inputs are brought together in the amygdala, a key centre for memory and motivation higher up in the brain. So, the two olfactory subsystems may do different things, but there is lots of integration of the inputs—both of pheromone signals and the highly individual smells that allow a mouse to recognize different individuals by smell.

Humans: The Smelly Frontier

It is highly likely that humans, like other mammals, have pheromones. However, despite the many sites on the Internet offering to sell "pheromones" to make one sexually irresistible, no human pheromones have been chemically identified to date. Sadly there is no evidence for the widely published claims that the molecules androstadienone and estratetraenol are human pheromones of any kind.

There are similar but different problems with the suggestion that women might synchronise their menstrual cycles if living in close quarters, and that this might be mediated by an unidentified pheromone. While some studies have shown the phenomenon of menstrual synchrony, many others have failed to do so. Moreover, the phenomenon has not been found in women in Mali, West Africa, who withdrew together during menstruation, a situation that would have been anticipated to facilitate the effect.

Another misuse of the term pheromone is in so-called pheromone parties, a trend started by an artist in Brooklyn in 2010. At these events, singles sniff numbered T-shirts that have been worn by others at the party to see if they like the smell and photograph themselves with the shirt in a numbered bag to facilitate meeting up later. Although these get-togethers might sound like fun, they are misnamed, because the smells on the shirts are unique to each individual, not species-wide pheromones that trigger the same behavior in every person. The idea behind these parties is based on the

surprising observation that mice preferred to mate with mice that were immunologically different from themselves in the major histocompatibility complex (MHC), a difference that can be detected by smell. When a similar experiment was tried with Swiss students sniffing T-shirts, it was discovered that women similarly found the smell of men immunologically different from themselves more attractive. However, subsequent replications of the experiment have not shown the effect consistently and, disappointingly, studies of large-scale human genome data have been equally inconclusive. Clearly, the idea of choosing a potential partner by smell has popular appeal even though the evidence is not there yet.

A human pheromone would need to be a molecule (or combination of molecules) that is characteristic not of a particular individual but of all males or all females, for example, that elicits a reliable behavioural or physiological effect on other individuals. The clearest indication that we may yet find human pheromones in relation to sex is because the smells people give off change after puberty—the sweat and sebaceous glands ramp up their secretions at that point. If we were any other kind of mammal, this change would be a prompt to investigate the smells produced by adults. The techniques for taking and analysing odour samples are now well established and have been used successfully to identify pheromones in many other mammals. The biggest challenge for work on human pheromones will be the identification of behaviours and physiological responses that will make robust bioassays. Because of our cultural complexity and diversity, influences on human behaviours are notoriously difficult to study. Whatever the future studies on humans, they will need to be guided by the essential steps for identifying a pheromone. There are no shortcuts.

It may be that the first human pheromone to be identified will not have to do with sex but instead with breastfeeding. Finding a mother's nipple just after birth is a make-or-break moment in the life of a mammal like us, and

as I mentioned earlier, other mammals such as rabbits have a pheromone that attracts newborns to the mother's nipple to suckle.

Developmental ethologist Benoist Schaal and his colleagues from Dijon, France, have found a secretion released from the areola glands around the nipple of human mothers when they produce milk that causes any baby to open its mouth, search for a nipple, and suckle. As yet, we don't know what molecules might be present—finding and identifying them would be a scientific landmark that would give us more confidence in searching for other possible human pheromones. In addition, if we could synthesize this suspected pheromone, there could be health benefits: If some mothers do not produce enough secretion, supplementing it could perhaps solve problems for nearly half of all newborn babies, who do not feed optimally during their first day, and the many mothers who struggle to breastfeed. The response of the newborn baby to secretions gives a good bioassay, because it is easily testable and infants are also the human life stage least affected by the complexities of learning and culture. I am optimistic that humans may yet join the countless other species of animal that have been shown to use pheromones.

The progress since Butenandt's identification of the silk moth pheromone molecule in 1959 has been extraordinary. The symbiosis between chemists and biologists continues to reveal pheromones in more species of more kinds of animal than ever before. Apart from the ingenuity of the new chemical techniques for analysis, I am constantly impressed by the ways that pheromones are used to study animal communication: In model animals such as the nematode *Caenorhabditis elegans*, fruit fly *Drosophila melanogaster*, many moth species, and the house mouse, researchers can study pheromones at every level—from their production through their perception and neural processing—and from every angle, from genes to development.

Putting Pheromones to Use

Entomologists have long realised that moth pheromones could be used to control pest moths, with the added advantage that natural enemies, like spiders, are left unharmed. In a technique called pheromone mating disruption, synthetic female pheromone is released in crops or orchards in sufficient quantities that male moths cannot find the real females. This technique is being used on more than 10 million hectares around the world. It's especially effective when all local farmers use it, as the apple growers of Washington State have done to combat the codling moth *Cydia pomonella*. As is often the case, farmers turned to using pheromones when the moth became resistant to pesticides.

While the use of pheromones has been well established against insect pests, they could also be used to control vertebrate pests and human diseases. For example, invading sea lampreys (*Petromyzon marinus*), a parasitic jawless fish, have devastated the fisheries of the Great Lakes in North America. Research is ongoing to see if traps baited with the lampreys' pheromones could replace the toxic chemicals currently being used. Pheromones could also be used to tackle human diseases such as those caused by parasitic nematode worms that use pheromones at crucial stages in their life cycle. One target species is the human parasitic nematode *Strongyloides stercoralis*, a cause of extensive morbidity in the developing world.

The species specificity of pheromones is one of their big advantages, because using them for pest control has fewer environmental impacts than broad-spectrum pesticides. However, the specificity is a disadvantage for commercial development, because each pest species must be studied individually to identify its pheromones. Unlike the development of broad-spectrum insecticides, the research costs are not spread over many pests. The organisations best placed to work on pheromones are universities and government research laboratories, but these are among those scientific institutions most threatened by spending

cuts in many nations. Although it is less profitable for corporations, pheromone-based pest control can be highly cost-effective compared with pesticides and has major benefits to the environment, farmers, and consumers.

Spying and Deceit

Broadcast signals can be "overheard" by unintended recipients. For example, alarm pheromones released by *Solenopsis* fire ants when fighting ants from other colonies attract unwelcome eavesdroppers: ant-decapitating flies, so named because these parasitic phorid flies lay their eggs in the heads of ants, which eventually fall off. One of these phorid fly species, *Pseudacteon tricuspis*, might be introduced into the United States as a possible biological control of invasive fire ants.

Illegal signalers make counterfeit pheromones as an aggressive form of mimicry. American bolas spider females lure male moths by mimicking the sex pheromones emitted by female moths of that species. When the male moth comes within range, the female *Mastophora hutchinsoni* spider swings her sticky "bolas" (her web reduced to a ball). If the bolas touches, moths rarely escape.

Plants can deceive, too. Instead of giving a nectar reward, many orchids dupe male bees into pollinating them by counterfeiting the pheromone of a particular bee species. For example, the European orchid, *Ophrys sphegodes*, almost perfectly mimics the multicomponent hydrocarbon female sex pheromone blend of the solitary bee, *Andrena nigroaenea*. Male bees, attracted by the counterfeit pheromone and the visual mimicry of the orchid flower, pick up a pollen pack as they attempt to mate with the flower. They later make the same mistake again and transfer the pollen to another orchid flower of the same species.