

Animal Communication

Few have supposed that living species other than *Homo sapiens* possess methods of communication that shed much light on issues that arise from the study of human language and linguistics. Methods of communication used by animals have however received attention from those interested in describing and accounting for animal behaviour itself. That there often remain implicit analogies with human exchange of information is indicated by the difficulties of defining which sorts of animal behaviour should be counted as communicative and which not.

1. *Definition of Animal Communication*

It is not difficult to select examples of behaviours which obviously qualify as some sort of communication — such as warning cries, or the release of chemical attractants. There is little agreement, however, on a formal definition to cover less obvious cases. The widest includes any method by which one animal (or cell) demonstrably influences the behaviour of another (Wilson, 1975). This is straightforward enough, but it is usual to qualify it in ways related to intuitive notions of functional specialization. The natural world is sustained by one animal eating another: an act of this kind undoubtedly alters the behaviour of both, but is certainly not primarily communicative. Predation can easily be excluded, and for most purposes it is convenient only to consider interactions between members of the same species, although symbiotic relations between different species, and deception of predators by prey, may involve interesting specializations. A narrow definition would focus attention on behaviours which it is reasonable to suppose have been selected because of the benefits to both the sender and the receiver of the transient messages thus conveyed. Mechanisms which appear to have evolved particularly to serve communicative and therefore social functions, such as vocalization and the release of chemicals, and clearly of most interest. but the benefits which they bring are not always easy to determine, and when they are the distinction between transient and sustained signals is not always supported. It is arguable that any frequent social interaction between conspecifics will come to involve communication, but many would wish to exclude such apparently trivial examples as the avoidance of collisions. As an alternative to defining communication, it may be sufficient to discuss uncontentious examples, and to examine their functions.

2. *Functions of Animal communication*

The over-riding explanatory principle for animal behaviour is that of the theory of evolution, most often expressed not just in terms of the advantage of the individual, but by reference to the individual's genes. Behaviours under genetic control persist only if they optimise transmission of the individual's genes to the next generation. The initial presumption is that of selfishness, and this does not suggest that communicative mechanisms which provide mutual benefit should be at a premium. Communicative activities, if specialized, must entail costs of time, energy and computational effort to both sender and receiver: if both are selfish why do they not confine themselves to securing individual comfort and well

being? General theories of social behaviour supply two kinds of qualification. The first is kin-selection. In genetic terms selfishness can encompass parental care, and indeed more extreme forms of self-sacrifice in return for the survival of sufficient numbers of close relatives. Observations of interactions between parents and young form a substantial part of the discipline of ethology — the approach to the study of animal behaviour which has supplied some of the conceptual framework for analyses of communication. The second qualification is "reciprocal altruism", which can be mathematically justified, but is suggested partly because of observations of elaborate social interactions not otherwise readily explicable. The most selfish individual should co-operate with others if its own benefits are increased as a result, which can happen if favours are returned, or if collective activities benefit all co-operators more than cheaters or individualists.

The direct relevance of these corollaries of evolutionary theory to the analysis of animal communication is that they both require some kind of individual and group *recognition*. If parental care is to be justified by kin-selection it ought to be directed at the correct offspring: in relatively solitary species a minor constraint, but a major one in those breeding in colonies or flocks. Where group behaviour is co-operative, recognition of particular individual conspecifics is implied by the rules of reciprocal altruism, while where groups are formed as less complex aggregations, presumptively on "safety in numbers" grounds, there needs to be at least a sensitivity to whom else to aggregate with.

2.1 *Recognition.*

A first function for communication is therefore recognition of species: more detailed social interactions for a variety of purposes need to be with conspecifics. Species recognition may be in many cases built in to sensory systems, but in some birds and mammals infants may acquire it from interactions with their parents, this process being known as *imprinting*. Acquired recognition is more obvious when local group membership is a factor in the details of communication, as for example with local dialects of vocalization (some song-birds) or local variations in group odour (some rodents). Within communities of social insects caste distinctions are typical, and within small groups of birds and mammals there is usually recognition of group members in terms of size, age and gender, and often also, as in the peck-orders of chickens and in other dominance hierarchies, recognition of each individual by any of the others. Generally it is assumed that animal communicative behaviours are genetically determined, and common to all members of the same species. Paradoxically however, it can be demonstrated in higher vertebrates, if not in insects, that one of the functions of the innate mechanisms is to enable individuals to acquire information which is peculiar to their own circumstances of life, which can include recognition of the identity of unique individuals, and membership of local groups. Even recognition of species membership may be learned, as with imprinting.

2.2 *Courtship and mate selection*

Even the most solitary species must engage in the social interactions required for sexual reproduction (parthenogenesis is extremely rare). Evolutionary theorists from Darwin himself onwards have deduced that mate choice is likely to produce via sexual selection effects not predictable from the more humdrum

necessities of day-to-day survival. Hence the antlers of the stag and the tail-feathers of the male peacock, and the behaviours that accompany these. Dispersed species must communicate at a distance to bring males and females into proximity. Especially where several similar species co-exist in the same geographical area (not unusual for insects) fine distinctions between species-specific signals need to be made. Some species differences may be very straightforward, as with the different frequencies of calls made by species of cricket which differ in size. In other cases there appears to be more specialization in the evolution of particular signals, as in the patterning of acoustic messages in some other species of crickets, and more notably in bird song. The flashing of different species of firefly is also distinguished by temporal patterning. A further source of differentiation of species (and individual) recognition in mate selection lies in sequential "handshaking" between members of a pair. Male fireflies typically discriminate females of their own species by the precise time-delay between their own signal and the female's flash in response. Detailed sequential ordering of male-female interactions is common in courtship involving visual recognition, with an example being found in the ethologist Tinbergen's classic studies of the "zig-zag dance" during which a male stickleback leads a female back to his nest for spawning.

The degree of social interaction involved in mate selection varies from a single act of spawning to much more protracted shared parental activities, which are common in birds, where a male and female often pair permanently, or for several seasons, in some species remaining together throughout the year, but in others separating outside the breeding period. Among mammals similar "pair-bonding" occurs in for instance beavers, when dam construction and/or maintenance is shared, in wolves and other canids, in which food is brought to pregnant or nursing females and young, and gibbons, where the functional reasons for the pairing are less obvious. Clearly methods of individual recognition, and signals for shared activities (e.g. turn-taking in incubation) are necessary in these cases. Sometimes the pair engage in elaborate gestural "ceremonies" during courtship, as in Great Crested Grebes, and these may contribute to both species and individual recognition via the visual modality. Individual recognition by smell is fairly standard in terrestrial mammals, but the use of all the sensory modalities available to any species is to be expected. Striking examples of vocal communication occur in species which use "duetting" or antiphonal singing between mated pairs. In East African shrikes, which forage together in dense foliage, each pair develops some idiosyncratic patterns among the several heard in antiphonal singing, while other patterns represent geographically localized dialects. Of seven species of pair-bonding lesser apes (gibbons and the Siamang) all but one have antiphonal singing between pairs (the other has lengthy all male and all female chorusing between adjacent groups). In two of these six species the male and female contributions never overlap. In the other four they do: in one species the male produces similar sounds to the female but at a lower pitch; but with the rest the male makes limited additions to a more complex female song.

2.3 *Aggression and Threat*

In deer and peacocks and many other species there is competition among males for access to females, along with male self-advertisement. Much but not all bird song is in this category. Aggression is of course also found in relation to

disputes over territory and food. It is communicative in the specialized sense in so far as the interaction in the form of assertive calls and snarls, or gestural displays and postures, as alternatives or additions to direct physical struggle, which is usually the case. In highly social species including wolves and many monkeys aggressive displays may be finely tuned according to the status of the interacting individuals in the group structure, and gestures of submission and appeasement from subordinates may be as important as those of threat from the more dominant. In these instances communication is usually over short distances, and indeed may include tactile sensation. Threat between neighbouring groups or between dispersed individuals usually involves greater distances and is well-served by loud vocalization, or territorial scent marking. It has been shown that bird song (even from a loudspeaker) deters other males from entering the vicinity of its location. The roars of the howler monkey can be heard a kilometre away, and may reasonably be assumed to have a territorial function. The elaborate chest-beating display of the male gorilla, which includes hooting, the shaking of branches and the slapping of the ground, is often directed at a neighbouring troop but is also probably related to the maintenance of dominance relations with closer observers.

2.4 *Alarm and Distress*

A more benign form of social signalling is anything which serves as a warning to others of danger from predators. There is an explanation for pure and simple social aggregation from the benefits to any single individual in terms of predator avoidance. But a selfish individual, on detecting danger, might seem best advised in the short term to make a disguised retreat, and indeed to maximize rather than reduce the disadvantage to its conspecific competitors. In groups with a high degree of consanguinity warning to others, or indeed self-sacrificial defence of them, would be explicable in terms of kin-selection, and this is obviously the case for the social insects (which have single breeding queens for each community, and sterile workers; and, except for termites, have complicated increases in consanguinity because all males come from unfertilized eggs). Lesser degrees of consanguinity may contribute to the prevalence of alarm signals in small groups, particularly in monkeys and apes, where longevity, long-term group coherence and mutual dependence may foster reciprocal altruism. It has been suggested that in other cases giving an alarm call may in fact directly benefit the transmitting individual. That acoustic warnings (as opposed to alarms which elicit defensive aggression by the group) have evolved so as to be difficult to localize indicates that they are not without risk. However, it may to the advantage of an alerted individual to elicit collective evasive action — for instance, an individual bird in a ground feeding flock would probably be unwise to fly off on its own if it sights a hawk. Alternatively, signals given in reaction to predator proximity which are ostensibly altruistic may not be what they seem: it is now believed that the leaping ("stotting") of gazelles when fleeing advertises the vigour and alertness of the fleeing individual to the predator, rather than the presence of the predator to alternative prey. For whatever reason, apparently communicative reactions to predator presence are common, and are sometimes utilized by species other than that of the transmitter. They may differ in the same transmitting species, according to circumstances, including predator type. Mobbing calls in birds differ from other alerting or warning calls, in particular by being easy to localize, and the different cries made by vervet monkeys in response sightings of leopards, hawks, or

pythons cause others to run to trees, to look up, or to look down, respectively. It is believed that infants learn the individual meanings of these calls, and experimental evidence suggests that fear of both natural and artificial objects is induced in both primates and birds if the young observe adults making alarm reactions to their presence.

Vocal or chemical signals elicited by fear or pain may function as warning messages, but as a special case, infant distress signals clearly function to elicit parental assistance. In experiments mother rats, cats, and hens react to the vocalization of a misplaced infant by taking steps to retrieve it (the specificity of the response in hens having been demonstrated by the fact that they ignore offspring visible distressed but acoustically isolated under a glass bell). Much less common than signs of distress in infants are "satisfaction messages" but the familiar purring of domestic cats, and similar sounds produced by only the young of wild carnivores, are sometimes given this description. As these sounds are accompanied by vibrations it is thought they may function to confirm bodily contact.

2.5 *Signals related to feeding*

The most celebrated example of animal communication is the system by which foraging honey bees convey to their fellows information about the location of recently used food sources (see SPECIALIZED ARTICLE: in related bee species, and many species of ant, individuals lay olfactory trails to known food sources which are subsequently used by other colony members). But this kind of specific communication of the location of distant food sources is known only in the social insects. The most general form of communication in this category is simply the visual observation by one animal of another feeding, which has behavioural effects which are readily obvious in seagulls and other flocking birds. There is rarely any suggestion that the feeding animal emits signals with a specialized communicative role. However among social primates "food finding calls" have been identified, such as the low grunting of the chimpanzee when it discovers highly preferred food such as bananas or palm fruit. Food sharing occurs within chimpanzee groups and the rarity of food-finding signals is undoubtedly related to the fact that feeding is usually competitive. In chimpanzees and baboons there is occasional hunting of the young of other species by males, with its products being shared with females and infants, among whom there is the intuitively understandable begging gesture of holding out the hand, palm upwards. In wolves and other canids meat sharing is routine in family groups, the reactions of the young, such as licking the muzzle of the returning parent, often being required to elicit regurgitation.

A similar pattern is very common in birds, and the interactions between parental feeding and the begging responses of nestlings was an early focus of attention for ethologists. A gaping response, with vocalization, occurs in the nestlings of many species, and the probability of being fed is related to the vigour of the begging. In gulls, nestlings peck at the parental beak to elicit regurgitation, and the precise visual features of the parent's head and beak which act best as stimuli for these pecks have been studied by the use of models. In fowl, where the young feed themselves from birth, there are usually special calls used by both parents to attract the young to food, and these are sometimes also included in courtship feeding of females by males.

2.6 *Co-ordination of group behaviours*

Flocking, herding and schooling require that individual animals influence one another, but these kinds of co-ordination may occur without the emission of specialized signals, as long as individuals are sensitive to the movements of others. Thus social facilitation is sometimes distinguished from co-ordination via known communicative mechanisms. However, in most social species, especially of birds and mammals, many more communicative behaviours are observed than can be accounted for in terms of the specific functions of mate selection, alarm calls and so on listed above. There are of course other functional categories, such as group migration and co-operative hunting, which have not been listed. Another area is juvenile play, in carnivores and primates, which is recognizable from specialized gestures, cries and facial expressions, and which is assumed to have some functions which are related to socialization. But there are also more general categories of behaviour which may serve vaguer functions such as social cohesion and affiliation. Thus species are said to use, for instance, "greeting displays" and "bonding messages" (vocal chorusing being an example of the latter). As the last point in this section on functions of communication therefore, one should note that although functionality is an underlying assumption it is by no means the rule that the functions of any agreed instance of animal communication can be readily identified.

3. *Channels of communication*

Channels of communication map on to the available sensory modalities, usually taste, smell, touch, vision and hearing. (These cover everything except the production and detection of electrical fields, which is peculiar to a few species of fish.) There are issues surrounding the advantages and disadvantages of each modality. The following factors vary: the cost in time and energy of coding and decoding signals, especially in relation to the effect on other concurrent activities; the distance signals need to carry; the ease with which the location of the transmission can be fixed; and the capacity of the channel in terms of the rate at which information can be transmitted.

3.1 *The chemical channel*

The substances used as signals are known as pheromones. These are secreted as liquid and transmitted as liquids or gases. Pheromones may be smelt as gases at great distances, but can also operate locally. The distinction between taste and smell is not always clear-cut, especially in insects, although olfaction is obviously the main route for chemical detection of signals in land mammals. An important aspect of pheromones in both mammals and insects is their deposit as trails or markers — in this case the individual which transmits the signal can be distant from the receiver in both space and time. However, the airborne dispersal of chemical attractants provides an efficient mechanism for bringing together dispersed individuals of opposite sex, and the precise compounds used are known for many species. The female silkworm moth secretes one termed *bombykol*: males are sensitive to just a few molecules of this substance and may be attracted from distances of several kilometres. In higher concentrations, for moths and

some other insects, full male sexual behaviour is elicited towards any object strongly marked with the scent.

Chemical transmission of information is in some ways primitive, as it can operate at the cellular level, and it has similarities to the internal communication between bodily organs via hormones. However, the complexity of chemical communication reaches its peak in the social insects and mammals. Over 100 species of mammal are known to have anal glands for adding distinctive pheromones to faeces, and many mammals possess a number of specialized scent glands. A deer, for example, can transmit scents from glands on the legs and head through the air, can also mark trees and twigs from the same glands, and has other glands on the feet for leaving scent trails on the ground. For the most part transmission of signals by this sort of scent marking is not cognitively demanding, though interpretation on reception may sometimes be less straightforward. Some insect pheromones disperse very rapidly, but typically chemical signals have the advantage of being long lasting, and the corresponding limitation of carrying a relatively low rate of information transmission, by comparison with acoustic and visual signals. Chemical communication is nevertheless responsible for complex social organization: the societies of ants, bees and termites are ordered very largely by pheromones, and scent in mammals is used for several kinds of social identification. Although the initial reception of chemical signals may be regarded as less psychologically demanding than the decoding of auditory or visual cues, it may be noted that tracking the location of a distant source of pheromones presents problems, even for insects, whose solution requires at the very least a combined sensitivity to concentration gradients and wind direction.

There appears to be no evidence for the use of olfaction for social communication in birds, although olfactory cues may be involved to some extent in avian homing and migration. Although whales are mammals, they make minimal use of chemical communication (see section 3.4). Old-world monkeys and apes rely less on olfaction than most other terrestrial mammals: pheromones certainly influence sexual behaviour in some species, but there is a marked lack of specialized glands and scent-marking behaviours in higher primates. However, although in modern human societies the possible functional roles of natural social odours are culturally inhibited, humans, like other primates, still possess apocrine sweat glands. These are not important for cooling purposes (as they are in non-primates: in primates the epicrine glands serve for thermoregulation) but are responsible for body odours typically judged as unpleasant. The apocrine glands only become active at puberty, are highly responsive to stress and excitement, and are larger in males – suggesting that they originally had some social and therefore communicative functions.

3.2 *The tactile channel*

The limitation on communication by touch is clearly that of distance. It is nevertheless widely and perhaps inevitably part of close-contact social and emotional interactions between animals. Hugging, kissing, caressing and biting may take specialized forms in sexual contexts, and elicit specialized reactions: indeed in many mammals other than primates ovulation and/or the hormonal changes associated with pregnancy are induced by the tactile consequences of copulation. Physical contact is also an important element of the social relationship between offspring and parent in most mammals.

A particular case of tactile stimulation associated with a less obvious social process occurs in mutual grooming. This might be thought to be a purely utilitarian example of reciprocal altruism, and indeed this may be its functional origin, but the grooming or preening of one animal by another is often interpreted as a ritualized form of conciliation or social bonding. Monkeys and apes spend a surprising amount of time meticulously picking parasites and dirt from each other's hair, and, as attention is frequently (but not always) concentrated on parts of the body which the recipient would have difficulty reaching, this must in part be a matter of co-operative cleaning. However, the timing of grooming bouts, and their distribution between individuals placed in dominance hierarchies and other social sub-groupings, suggest that the motivation for grooming is inversely related to aggression. (It is difficult to determine the extent to which the sensation of touch is important in this, since the postures and gestures involved in soliciting and proffering grooming are more readily observable).

Apart from its prevalence in primates, social grooming between adults is extensive in rodents and occurs intensively in several bird species. Its social function in carnivores may be indicated by the propensity of domestic dogs and cats for licking the hands and faces of their owners.

3.3 *The visual channel*

The emission of light in dark environments by fireflies, other invertebrates and deep sea fish provides a clear example of an activity which is specialized for communicative purposes, but overwhelmingly the use of the visual channel means recognition by sight in daylight. There is here an unmistakeable ecological constraint on choice of channel: visual communication is useful only when animals can easily see each other, which is normally by day, with uninterrupted sight-lines. The acoustic and olfactory channels do not have this limitation. And although people can (in daylight) often identify each other by appearance and gesture at distances from which it is impractical to converse, the visual channel in most species operates best at short distances, by comparison with chemical and acoustic cues.

Visual specializations for social communication are nevertheless common. Most obvious is the evolution of distinctive features or markings as aids to species, gender, and individual identification. Visual appearance might of course be *used* for species identification without features having evolved for that purpose (an elephant is large, and has a trunk, for other reasons) but many species have colouring or bodily appurtenances such as crests which are specialized for communicative functions. These may be permanently fixed, or variable according to age or season, and the relative permanence, at little or no cost in time and energy to the transmitting individual, provides an advantage for the visual channel. However there is sometimes more interest in transient communicative acts, construed as the sending of signals, precisely because these involve a greater behavioural investment on the part of the sender. There is no shortage of examples within the visual channel. Behaviours thus categorized are often termed *displays*. In fish, reptiles and cephalopods (octopus and squid) they may include rapid changes in skin colour or marking. In mammals, particularly carnivores and primates, visual displays include changes in facial expression, although these are often accompanied by vocalization. In social lizards changes in the appearance of the head by extensions and colourings of dewlaps, crests and frills are normal. But

any part of the body may take part in visual displays. Lizards have back arching, tail lashing, head bobbing and circular forelimb waving for aggressive and submissive gestures. Posture, gait, and gestures via movements of the extremities can be identified as social signals in a wide range of vertebrate and invertebrate species which have the ecological and perceptual opportunities for the detection of visual messages.

3.4 *The acoustic channel*

Clearly, acoustic forms of animal communication have greater superficial similarity to human speech than chemical or visual signals. Apart from this, this acoustic channel shares with olfaction the virtues of broadcast transmission over considerable distances, and availability in the dark or when lines of sight are interrupted. It is arguable that in many species (songbirds, crickets) hearing as a sense must be specialized for the purpose of social communication, as opposed to food seeking and predator avoidance. In others, by contrast, (bats and dolphins) the acoustic sense is utilized as the major avenue for prey detection — by echo-location. This is sometimes considered to be "solipsistic communication", but falls outside the present social perspective. Many other predators (cats, owls) have highly developed hearing which is used for detecting sounds produced by prey. The *production* of sounds for the purposes of echo-location would be one kind of exception to the general rule that distinctive animal noises will have evolved because of their advantage in within-species communication. Another category of exception is the noise of locomotion, and in particular the flight sounds of insects, which are the inevitable consequences of wing-movements. These sounds are not usually detectable by flying conspecifics, although the male mosquito has a sense organ on its antennae tuned precisely to the distinctive drone of the female and insensitive to the higher pitched flight sounds of other males. This is an example of an entire perceptual mechanism being specialized for social communication: another is in a species of tree frog in which males produce a bi-phasic call of a low-frequency "co" followed by a high-frequency "qui"; the inner ears of the males being tuned to the "co", which serves as a territorial signal maintaining their dispersal, while the inner ears of the females are tune to the "qui", as a sexual attractant. In higher vertebrates the peripheral hearing apparatus is, as far as is known, exclusively general purpose, but there are often ways in which the central nervous system is clearly able to selectively process sounds with species-specific characteristics (e.g. newly hatched ducks being sensitive to the parental calls of their particular species).

Vocalizations in higher vertebrates, and many courtship noises produced by fish and insects, are quite obviously specialized ways of sending social signals. In animals communicative sound production is frequently very effortful: insects such as crickets produce a large amount of noise in relation to their size, and a cicada may need to increase its resting metabolic rate by a factor of 20 in order to sing; some small frogs which increase their metabolic rate while calling by a factor of 5 have been estimated to expend more than 80% of their total calorific intake on this activity during a 6-month breeding season. This may be contrasted with the use of chemical signals, where, since the recipient can be sensitive to just a molecule or two and air-borne transmission is free, minute amounts of pheromone are sufficient to produce dramatic effects. This raises the question of

why the auditory channel should ever be preferred to the chemical for broadcast transmission.

The presumed advantages of the acoustic channel are in its high carrying capacity for rapid serial transmission, and in the possibilities for swift and accurate source localization which, though not perhaps as direct as those for visual signals, are in general much more favourable than those for dispersed chemicals. Some of the complexities which may be carried by the acoustic channel are apparent even in the courtship calls of male frogs, particularly in sub-tropical species which breed opportunistically after heavy rains. In many of these species males gather together to make simple sounds in choruses, and often several different species occupy the same areas. Auditory discrimination of species-characteristic signals is therefore required of females. Aggregations of males could be fortuitous if breeding sites are limited, but there is evidence that the groupings are systematic, the assumption being that the greater volume or longer duration of a chorus means that dispersed individuals would be at a disadvantage. This assumption is supported by the finding of highly organized sub-groups within choruses. There are species in which individuals within a chorus alternate calls within duos, trios, and quartets, at precise intervals. There are leading individuals in the sub-groups, and leading sub-groups within choruses. Thus chorusing is actively synchronised, rather than being the result of the accidental contiguity of individuals. The balance of advantage to individuals which supports this collectively organized form of communication is clearly very complicated to determine, but this is typical of most animal social behaviour.

Frogs are modern amphibians, and their vocalization has evolved in the context of nocturnal and time-limited (after rains) breeding. Higher vertebrates, that is birds and mammals, both evolved from reptiles, which as a class post-dates amphibians. Existing species of reptile are not generally very vocal. However, the neural organization of the auditory pathways in the reptilian brain is surprisingly similar to that of higher vertebrates, and the absence of acoustic communication in many reptiles is therefore likely to be due to ecological factors which favour visual or olfactory methods of communication when any is required. A limited range of vocalization occurs during the courtship and mating of several species of tortoises and turtles. Use of the acoustic channel as extensive as that of frogs appears to be confined to the geckos, a large family of lizards distinguished by nocturnality. Not all geckos are equally nocturnal, or equally vocal, but the family differs from other reptiles in having an external auditory meatus, and in many species the cochlea is highly developed. Vocalization in geckos is characterized as chirruping, or multiple chirruping, but very little is known about its behavioural functions. Most species are communal and territorial, and some vocalization probably functions as an assertion display for territorial defence. Loud continuous chirruping during a "dusk chorus" is heard in the gecko *Ptenopus garrulus garrulus*, when individuals emerge from their burrows.

Thus in amphibians and reptiles acoustic communication seems to be clearly correlated with nocturnality, but this correlation does not hold for other taxonomic groups. Among insects diurnal sound production occurs in grasshoppers and cicada, and the most elaborate use of the acoustic channel is of course in birds, almost all of which are diurnal, but which are usually too small to be easily visible at a distance. Owls and nightingales vocalize at night, and the most intensive singing in song-birds takes place at dawn and dusk. But enough

avian (and mammalian) vocalization takes place during the hours of daylight to dispose of the notion that nocturnality is the only factor favouring the use of the acoustic channel. There may however be some trade-off between visual and auditory communication depending on the ease of visibility. In most birds vision and hearing are both well developed, while olfaction is of lesser importance. It has been suggested that male courtship singing is less elaborate in more highly coloured species, and there may also be a negative correlation between size and complexity of vocalization: the song birds (*Oscines*) which have very detailed control of the sound producing organ (the syrinx) are relatively small, while larger and therefore more conspicuous birds tend to produce a narrower range of sounds, storks being almost mute, and the cries of geese and cranes being notable for volume rather than variety. Whatever the underlying reason for it, the extensive use of vocalization in birds raises a number of theoretical issues, in particular the interplay between inherited and species-specific control of sound-production and the development of individual variation by within-species learning and cross-species mimicry (see below).

The original mammals were nocturnal, and as a vertebrate class mammals are notable for extensive reliance on olfaction. Apart from primates, mammals have little or no colour vision, and no retinal fovea for high visual acuity, and therefore have little opportunity to use colour signals and some limitation on very detailed visual display or markings. As a very rough generalization, reptile communication is olfactory and visual, with little use of vocalization except in nocturnal lizards, birds have highly developed use of both visual and acoustic channels, and mammals use all four channels with the emphasis, if any, on the chemical. This is clearly an over-simplification, and primates (monkeys and apes) are in this context closer to birds than other mammals, since they share with them foveal colour vision, and a reduced reliance on social odours. Colour is in fact of little importance in primate social signalling, apart from one or two species of monkey (and perhaps human blushing). But social primates such as rhesus and vervet monkeys, chimpanzees and gibbons have a wide range of vocalizations, as well as making considerable use of the visual channel for gestural and postural displays, and for facial expression (see SPECIALIZED ARTICLE).

Whales and dolphins (small toothed whales) are even clearer exceptions to the rule that mammals make extensive use of chemical communication, since baleen whales (e.g. the Humpback, Sei and Rorqual) are considered to have very little sense of smell, and toothed whales (Sperm, Killer and all dolphins) none at all, since they have reduced or entirely lacking olfactory bulbs (and there is no evidence to suggest that their sense of taste functions to detect water-borne chemicals). In addition to lacking an acute sense of smell, many cetacean species have poor vision, as they feed in deep water, or under ice, or are nocturnal (the Gangetic river dolphin is nocturnal and almost blind). Therefore most whales must rely heavily on audition for any form of distant social communication. The picture is complicated because many toothed cetaceans also emit sounds for the purpose of echo-location of prey, but since most species are highly social, it is usually assumed that sound production and reception also play a part in communication. Detailed evidence of the precise functions of particular sounds is sparse for species other than the bottlenosed dolphin. Here a distinction can be drawn between pure tone whistles or squeals, which serve for individual

identification and other social purposes, and pulsed clicks which are primarily for echo-location. However, many different categories of pulsed sounds have been identified, whose behavioural function is unclear. An extremely wide range of sounds other than clicks or whistles have been recorded in other species, such as the baleen humpback, whose song carries vast distances, and the odontocete Beluga, or "sea canary." (See SPECIALIZED ARTICLE)

4. *Theoretical Issues in Animal communication*

The description of animal communication given so far has inevitably encompassed some underlying theoretical assumptions about its behavioural functions, and the relative advantages of the various sensory channels. There are however some additional points to be made.

4.1 *Evolutionary development*

Several theoretical ideas about the evolution of communicative mechanisms go back to Darwin's *The Expression of the Emotions in Man and Animals* (1872). In this work he put forward three general principles which are reflected to some extent in more recent analyses of the topic. His first principle was that of "serviceable associated habits", which may be construed as the notion that actions which initially evolved for other reasons may come to be selected for more specialized communicative purposes. One of Darwin's examples was the laying back of the ears in cats as part of the facial expression of fear. This, together with narrowing of the eyes, he supposed had initially a purely protective function. In this case it is not clear how supposed original and later communicative functions can be separated but modern ethologists employ the similar concept of *ritualization* on the basis of many other examples. For instance, behaviours which form part of courtship, such as mutual feeding in birds, are often similar to those which occur in other contexts — in this case parental feeding of the young. The concept of ritualization implies that already present behavioural units may become incorporated into communicative displays, and then exaggerated or otherwise altered. It is not of course necessary to suppose that all forms of communication are ritualized versions of other behaviours — it would be difficult for instance to account for elaborate vocalization in this way. The same caveat applies to Darwin's principle of "the direct action of the nervous system". His example here was trembling, which occurs in both people and animals under conditions of fear or excitement. The argument is that trembling movements are a side-effect of arousal and muscle tension rather than the transmission of a specialized signal. In general, it is necessary to separate the interests of the senders and receivers of possible messages.

4.2 *Discrete and graded signals*

The remaining one of Darwin's three principles is that of "antithesis". A dog's tail indicates happiness when aloft but sadness when lowered between its legs: in general opposed emotions are expressed by opposite movements. This no doubt simplifies both the production and interpretation of messages. It also incorporates the possibility that a continuously varying signal can convey a range of information: there is good reason to believe that intermediate positions of a

dog's tail convey intermediate emotional states, and there are many other examples, particularly in facial expression, and gestures which convey an individual's mood. By contrast, signals are regarded as "discrete" if their production is unvarying and stereotyped, *or* if reactions to them occur in an all-or-nothing manner. Those for group and species recognition may be in this category, such as contact calls in birds and the flashing of fireflies. Receptive reactions to discrete versus graded signals may be compared to the distinction between categorical and continuous perception of human speech, although whether or not variable signals are actually elicited a wide range of responses is not always tested. Another terminological variation is to refer to "analog" or "digital" signals. It is usually assumed that most species will use a mixture of discrete and graded signals, even within the same modality. Discrete signalling, and/or on/off responding to signals is presumed to have advantages over long distances, or where for some other reason variations in the graded aspects of the received signal may not reflect the targeted aspect of message content. (In speech, graded aspects such as tone and accent represent mood and identity, while linguistic information is received discretely). Graded signalling, if it is reliable, has clear benefits in terms of economy of information exchange, and is expected to be found in close range, within-group communication. An example of different kinds of signalling within the same modality is the song of the European Robin. Songs consist of about 4 phrases, selected out of a repertoire of several hundred for each bird. All the phrases within each song are different, and all songs in a consecutive run are different. Variability and elaboration are clearly at a premium, and presumably have value in impressing other males or attracting females. However, from experiments using the play-back of artificially assembled robin phrases, and electronically generated artificial phrases, it is apparent that an important factor in *species*-recognition is the discrete rule that phrases within a song alternate between high and low pitch – if all phrases are different, and they alternate in pitch, lack of verisimilitude in the phrases themselves is largely ignored. This contrasts with other species such as Bonelli's warbler, which has a much simpler song based on the repetition of a single element, and in which subtle analog changes to the real song element significantly reduces the responsiveness of listening birds of the same species.

4.3 *Communication and ecology*

The analysis of animal communication is directed at discovering its functions, broadly characterised earlier in this article. Variations in modalities used, and in mapping relationships between signals produced and responses elicited by them, should in theory be explicable in terms of the details of the environmental circumstances a given species is adapted to, even though this is only supported by case-by-case examination. The physical environment clearly limits choices of modality in the example of the absence of visual communication in nocturnal species, and more detailed inspection reveals correspondences between, for instance, the precise characteristics of vocalizations and those most appropriate for optimal dispersion in given geographical conditions. The social environment of a species and individuals within it is no less important. For instance in the example of Bonelli's warbler, above, the fact that transposing its song upwards in pitch slightly severely reduced responses to it, while transformation downwards had little effect, is almost certainly because this species often co-exists with another which has a similar but higher-pitched song.

More general comparisons suggest that both song-birds and forest primates which need to communicate acoustically over relatively short distances, with comparatively little "noise" from other similar species, have a larger species repertoire of calls with greater amounts of individual variation, than those in which group or species members are more widely dispersed, with greater likelihood of between-species confusions.

4.4 *Inherited constraints and universals*

The assumption that animal communication systems have evolved to fit particular species circumstances leads, other things being equal, to the expectation that both the structure of the motor and sensory organs employed for these purposes, and the behaviour-controlling functions of the nervous systems that control them, will be innately determined. Biologists are not surprised by species-specific universals. There are however exceptions to this expectation, at least in birds and mammals. The main category is that individuals in social groups learn to recognise each other by sight, sound and smell. Learning to produce communicative signals as opposed to perceptual learning is less widespread, but is a significant factor in bird-song. Vocal learning of one sort or another is pervasive in birds and ubiquitous, though not universal, in song birds, for reasons which remain obscure, but which may include, in varying species: i) evolutionary factors which favour the establishment of local dialects; ii) benefits to the individual of increased variability of vocal production, either because of distinctiveness for recognition or where degree of elaboration of song influences female mate choice and/or impresses other males. An important distinction within avian vocal learning is that between within-species imitation (and creative elaborations within a specific species pattern), and vocal mimicry, where birds such as the Mockingbird or Starling adopt recognizable parts of other species' calls. For within-species imitation, conformity to a standard form may reflect in some cases social proximity in early learning (hand reared parents may transmit human sounds learned by imitation to their offspring) but experimental evidence for others has led to the concept of an "auditory template", which enables the young to identify their own species' song as what should be modelled and elaborated. Inter-species mimicry, on the other hand, demonstrates, (in approximately 15% of all species), a part of the language learning device in birds which is more genuinely a *tabula rasa*. Its existence remains an evolutionary puzzle, since it occurs in a wide range of habitats and families, although it is more common in non-migratory insectivorous species. However, not surprisingly, the only common factor is that it occurs in birds that are dependent on vocal learning for their own species' calls, and mimicry may be an extreme case of the usefulness of variability, as well as serving special cases such as the mimicry of host by parasite species, and the recording of local or migratory histories.

4.5 *The evolution of human language.*

Little has been learned about the evolution of human language from the study of animal communication. Marginally more useful comparisons may be made possible however, if human language is no longer either a) held to be entirely culturally determined, or, b), assumed to be substantially and crucially innate, but for reasons that are fortuitous and non-Darwinian. The case has

recently been made that innate capacities underlying human language must have evolved by Darwinian processes (Pinker and Bloom 1990), and accepting this implies that there may be points of commonality between the evolutionary biology of human language and animal communication systems, even though there are striking differences in the nature of the end-products.

Viewed from the stand-point of natural history, human language remains unique in its syntactic and propositional character, and the degree to which it supports cultural transmission and change. It is also unusual in that its functional importance is not matched by noticeable evolution of the structure of the peripheral sensory and motor mechanisms which support it, possibly because it is an extreme case of a system for a large and highly variable repertoire of low-energy signals transmitted within groups of individuals at close quarters, rather than one for broadcasting a fixed set of messages reliably at long distances. It is not remarkable in having both innate and acquired aspects, but far exceeds any other natural system in the degree to which sociocultural factors are superficially predominant. Despite features which are arguably unique products of evolutionary processes, and many others which clearly post-date biological changes (for example historical language development, and in particular all aspects of language that are dependent on its *written* forms) human language continues to serve some of the same functions as animal communication systems — identification of the individual, recognition of gender and group, and the other social functions of greeting, affiliation, assertion and attachment.

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See also: (e.g. – to be added by Subject Editor) COMMUNICATION IN INSECTS; THE DANCE-LANGUAGE OF HONEY BEES; BIRD-SONG; COMMUNICATION IN DOLPHINS AND WHALES; NATURAL COMMUNICATION IN PRIMATES; ARTIFICIAL TRAINING EXPERIMENTS WITH CHIMPANZEES, ETC.

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