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E. RITUALIZATION OF ANIMAL ACTIVITIES IN RELATION TO PHYLOGENY, SPECIATION AND ECOLOGY

Reduction of ambiguity through ritualization

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Zoologists studying the social communication of animals have used the word 'ritualization' broadly speaking to describe changes in the signalling system during the course of evolution which have come about to make the signals more effective in evoking appropriate behaviour in a partner. (Critiques of different uses of the term in animal studies may be found in Blest (1961) and Wickler (1961).) Usually such signals operate within a species but some symbiotic relationships between different species also involve signals for which the word may reasonably be used (Baerends 1950). The chief emphasis in discussions of ritualization has been laid on evolutionary changes in form such as exaggerated amplitude of movement, alterations in frequency, increased regularity of rhythm, stereotyping of orientation, etc., besides the acquisition of morphological characters such as colours, sound-producing structures, to enhance the effectiveness of the signals. For signals to work the responding partner must of course be suitably tuned to them, but relatively little is known how well signal and responsiveness are matched (Marler 1961). Moreover, some ritualized signals may work, at least partly, through their general attention-catching properties rather than as the result of specifically evolved responsiveness, e.g. the red spot on the beak of an adult Herring Gull (*Larus argentatus*) makes the young peck at it for food partly through its mere contrast with the yellow beak (Tinbergen & Perdeck 1951). In addition, learning may play some role in the tuning of responsiveness to signals in natural situations, as can be seen in the development of inter-specific responses of species which consort (Bergman 1957). In spite of these uncertainties there is no doubt that with the evolution of much ritualized behaviour changes in responsiveness of the recipient have also evolved.

Ritualization has not merely produced signals which are conspicuous but, more important, it has lessened their ambiguity and made them more distinguishable from signals carrying a different message. Two examples may be cited to show what happens when this ambiguity arises. In her pre-copulatory invitation posture the female Shag (*Phalacrocorax aristotelis*) tilts her body forward, raises her tail and then bows her head abruptly forwards to nibble at the nest material (Snow 1963, fig. 1*g*). In response to the display the male often mounts her. When preparing to defecate a Shag tilts its body and raises its tail in much the same way, though tending to orientate with the tail outwards from the nest. These preliminaries by a female occasionally provoke her mate to mount, though mating is not consummated and when the male dismounts or is thrown off, the female completes her defecation (personal observation). Such mistakes are not serious and the ambiguity of the female's posture has presumably not been worth eliminating.

The second example of the ambiguity of signals concerns Honey-bees performing the dance which conveys to their fellows the distance and direction of food they have located. Distance is coded in some measure of the number of dances per unit time, probably the mean duration of the central run (von Frisch & Jander 1957) or perhaps a sound closely correlated with this (Wenner 1962). Schweiger (1958) showed that there were distinct differences in individual coding: for food at a particular distance some bees danced more slowly than others. There was also a surprisingly large scatter. One third of the dances of a particular stock of bees indicating food at 200 m were more than 90 m out according to the 'average' coding. (These observations were only made under standard wind conditions as changes in wind are known to affect the dance code.) One source of individual variation was found to be age; with food at 200 m there was a smooth decline in dance rate from the first day of foraging to the 24th, and this decrease was such that the code of old bees indicated that the food was about 150 m farther away than the young ones. Schweiger also showed that errors in dancing led to the foragers recruited by the dance making errors in searching for the food. Fast dancers made the recruits search for food at a shorter distance. That differences in dance rates affect the searching distance of recruits had been found earlier by Boch (1957) studying different races of Honey-bees, which differ slightly in their coding of dance rate and distance. If bees of two races were mixed in a hive, each would correctly code and decode the dances of her own race, but would make mistakes when decoding the dances of the other. It is not surprising that differences exist in the coding pattern of different races of bees since, except under experimental conditions, they will seldom decode each other's dances, but the variation within members of a single hive is a more serious defect. It should be remembered, however, that the importance of visual and olfactory cues given off by flowers increases the 'target area' of the natural food.

When considering animal signalling systems it would seem natural to try and make use of the formal analyses of communication channels developed in information theory (e.g. Shannon & Weaver 1949). In any real information channel it can be shown that there will inevitably be errors made by the receiver in reading signals and it is possible to give a precise method of measuring this ambiguity or 'equivocation' as Shannon calls it. However, in our present state of knowledge about animal communication it is not possible to apply this approach except in a very few cases. Moles (1963) has pointed out some of the pre-requisites for doing so, such as determining the minimum discriminable unit in the sensory dimension involved, and the corresponding 'time quantum' necessary for the animal to perceive such units. There seem to have been only two attempts to measure the information content of animal signals, one by Haldane & Spurway (1954) for the bee-dance, the other by Wilson (1962) for a chemical signal, an odour trail indicating distance and direction of food, in the Fire-ant (*Solenopsis saevissima*). Perhaps one of the main values of such exercises is to show the kind of facts which are necessary and to make explicit the assumptions on which such calculations are based. Such data are at present regrettably rare in studies of animal signalling, and no attempt will therefore be made to estimate ambiguity quantitatively for the signals to be considered in the remainder of this paper.

SELECTION PRESSURES FOR THE ELIMINATION OF AMBIGUITY

The ambiguity inherent in any communication channel is aggravated in animal communication because of the nature of the historical development of the signals themselves. Comparative studies on a number of species, mainly arthropods and vertebrates, have shown that it is possible in many cases to trace the evolutionary history of signals, and this has frequently indicated that two signals in the same species or a signal in two different species have a common evolutionary origin (e.g. Lorenz 1941; Tinbergen 1960; Alexander 1962). As has often been pointed out, this process is exactly comparable to the cultural evolution of language with diversification of words from a common origin. Signals which have a common origin in time are intrinsically likely to be similar and give rise to ambiguity if they need to be distinguished from the 'parental' or from the 'sister' form. The reduction of this ambiguity has been due to a number of different selection pressures: for distinguishing members of different species, members of the two sexes or other subgroups within a species, between individuals in different physiological states and even between individuals themselves.

Species separation

The best known of these selection pressures are those responsible for reproductive isolation between species, preventing hydridization. Differences in ritualized courtship signals, visual and auditory are widespread in sympatric species (Lanyon & Tavolga 1960; Blair 1961; Mayr 1963; Busnel 1963 *a*). In species which overlap in parts of their breeding range the differences are sometimes enhanced in the area of overlap (Blair 1964). Courtship usually consists of a loosely knit chain of reactions involving distinct signals by both partners. Reproductive isolation is achieved by differences in signals and the response to them at one or more stages in the chain. It has been found in several groups that the signals which come early in the courtship sequences show more variation from one species to another than do the actions immediately preceding copulation (Hinde 1959; Alexander 1962). Selection has acted to prevent mistakes as early as possible. However, double-assurance mechanisms are also well known, reducing still further the chance of a hybrid mating.

Until recently the evidence for the function of ritualized signals in reproductive isolation was mainly circumstantial, but it has now been possible to demonstrate this experimentally. The male *Scleropus* lizard nods his head on encountering another individual on his territory. The temporal patterning of nods varies from species to species, and with a cam suitably shaped Hunsaker (1962) was able to make a model simulate the nodding patterns of the different species, and show that the females responded to the pattern of their own species. On the whole sound signals are easier to manipulate than visual ones, and many workers have studied species recognition of songs and calls. Sometimes it has been possible to investigate female choice (e.g. Perdeck 1958; Blair & Littlejohn 1960) but often the test of 'species recognition' has been whether or not males show aggressive behaviour or counter-sing, which they normally do only in reply to songs of their own species. For instance, Dilger (1956) tested the response of five species of thrushes when a song was played from near a stuffed specimen of one of the five species placed in a male's territory. The songs of the species are more different than their appearances, and it depended on the species of song alone whether or not the mounted thrush would be attacked.

The experimental investigation of signals makes it possible to analyse what features of a signal are carrying the essential message, by progressively eliminating one or other of the potentially relevant parameters and testing the animal's response to the altered signal. A promising start has been made for some of the calls of Orthoptera and birds and shown clearly that some aspects of song are of little importance while others greatly affect the response. For example, Falls (1963) studied the monotonous song of the Ovenbird (*Seiurus aurocapillus*), which consists of a series of trisyllabic phrases, and found that elimination of the first syllable did not affect the response of other males to the song. The presence of the other two syllables was important and so was their order—reversed songs evoked a reduced response.

The full exploitation of this type of analysis depends not only on testing the responses to natural calls which have been altered, but to synthetic sound signals of any desired frequency and amplitude pattern. This poses considerable technical problems, but some first steps have been taken in work with Orthoptera (Busnel 1963 *b*). Capranica (1965) has made an elegant analysis of the part of the mating call of the male Bullfrog (*Rana catesbiana*) necessary for evoking the song of other conspecific males in reply. By using POVO, an electric analog sound generator developed by the Massachussetts Institute of Technology in connexion with speech research, he was able to show that the message resided in the frequency structure within the individual croaks, and depended upon a complicated balance between the relative sound energies in three neighbouring frequency regions.

Species recognition has sometimes played a part in the evolution of signals in another way. (The following argument has been modified slightly from that of Hamilton (1962).) When closely related species occur in the same habitat but differ in ecology, e.g. in food, they need to develop isolating mechanisms to avoid wasting time by provoking each other's aggression, and possibly being injured in fights. Thus they will tend to diverge in threat signals and response to threat signals. In Britain four species of Paridae with different food habits, breed within a habitat with overlapping territories with little inter-specific aggression between them. On the other hand, in North America the Paridae are ecologically more similar and rarely coexist within the same habitat without territorial exclusion. The crucial point seems to be whether by fighting with the other species they are driving away a competitor for some limited commodity. In colonial nesting gulls the function of territory is to secure a space around the nest in which the young can space themselves out as they hide from predators (Tinbergen 1956). In this area a member of a closely related species is as dangerous as a member of ones own, and correspondingly where *Larus argentatus* and *L. fuscus* form mixed colonies their territories form non-overlapping mosaics.

Among coral reef fishes in which the sexes are alike there are often striking differences in the gaudy patterns of related species, e.g. Chaetodontidae. These differences are thought to be due to the need for avoiding aggression towards species which are not ecological competitors (Lorenz 1964 *b*; Zumpe 1965).

Separation within a species

Within a species there is often considerable differentiation in the social role of members differing in age, sex, etc., and there are many differences in the structure, appearance and behaviour of such groups which enable them to be recognized. Two examples will be described, in which the role of the signals has been experimentally verified.

In the Zebra Finch (*Taeniopygia castanotis*) flocks consist of pairs, which spend much of their time sitting together, and juveniles, which clump side by side in larger groups. Young and adults differ in plumage and beak colour. When the young moult out of their first plumage and their beak changes at the same time from the juvenile black to the adult red, they lose their readiness to clump and begin to search for a mate. These changes in appearance, which are typical of many vertebrates, have been shown by Immelmann (1959) to act as signals affecting the behaviour of young and adult to each other. Beak colour was particularly important: a male would start to court one of his own fledged young if its beak were artificially coloured red, though only intermittently. Conversely, young would cease to beg from one of their parents whose beak was coloured black. There are also differences in plumage between the sexes and a slight but distinct difference in the shade of red of the beaks. By altering the appearance of normal birds of either sex and of three types of mutants and by presenting models, Immelmann showed the role of these differences in sex recognition. Immelman's results by no means exclude the role of behaviour in recognition. Coloration was often found to determine the initial response of one bird to another, but its effect would wane, particularly in females selecting males, if the behaviour of the partner was inappropriate.

The break-down of sex recognition can be more serious in spiders where the female may treat a courting male as food. Crane (1949) described the courtship of fifteen species of jumping spiders (Salticidae) showing how the strikingly marked first legs, palps or chelicerae of the male are displayed. *Epiblemum scenicum* holds its black-and-white banded legs out sideways and waves them up and down as it approaches the female. A female will hunt and attack a wide range of moving objects (Drees 1952). If a small disk with a wire projecting on either side, a 'male model', is presented she will stalk and jump on this too. But by making the wires move like the courting male's first legs (by switching on and off an electromagnet beneath the experimental table), Drees showed that the female's attack could be stopped and she would permit the male model to come right up to her.

Intraspecific signals play a role in many situations, and need to be distinct from each other. This is the Principle of Antithesis recognized by Darwin (1873). Many animals 'walk tall' when confidently threatening, but 'fold up' when beaten. When aggressive the offensive weapons are directed towards the opponent, when submissive they are turned away (Tinbergen 1959). The same principle can apply to sounds. Alexander (1962) concluded that the structure of the evolutionarily more primitive 'calling song', which is the most important signal possessed by field crickets, seems largely to have determined the methods by which the species could evolve distinctive sounds operating unambiguously in other situations.

Selection pressures so far considered have favoured unambiguous recognition, the evolution of a signal which is as distinct as possible from, say, other signals within the species with which it might be confused. Such signals may be called 'disjunctive'. But there is an important type of signal, which will be considered next, where 'conjunctiveness' has advantages where variability is beneficial when it expresses the fluctuating state of the displaying animal and therefore predicts what it is likely to do in the near future. Such signals are widespread in the courtship and threat of vertebrates, where it can be shown that the animals are simultaneously aroused to behave in different ways—to attack and flee in the case of threat, to attack, flee and mate in the case of courtship (Tinbergen 1952; Morris 1956; Hinde 1959; Wiepkema 1961). As the relative strengths of the arousal of these different tendencies is continually changing, this is reflected in the form of the display. Thus Stokes (1962), quantifying the components of the threat display of the Blue Tit (*Parus caeruleus*), found that if the body is horizontal and orientated towards the opponent with the wings raised and tail fanned, the display is likely to be followed by an attack; but if these features are lacking and instead the feathers are fluffed and the crest raised, the displaying bird is more likely to flee. Should the bird have its nape feathers raised and open its beak, this means that it is unlikely to attack or flee, but will defend the spot where it is (usually at food).

The importance of this variability of form is that it can be read by the observer, and doubtless by a fellow member of the species, as indicating future behaviour, and appropriate action can be taken in advance. During the highly ritualized fighting of many Cichlid fish such as *Aequidens latifrons* there is a gradual escalation of threat which allows either contestant to withdraw if it is not prepared, as it were, to raise its stakes (Oehlert 1958; Ohm 1958–59).

The development of ritualized fighting in highly social animals, with its diminished risk of injury for the individual, both winner and loser, has been reiterated by Lorenz (e.g. 1964*a*). Within a taxonomic family one can see this trend for species with smaller territories to have more ritualized threat displays and/or conspicuous signal structures demonstrated in threat. Dr Bryan Nelson has drawn my attention to it in the Sulidae, and it can be seen in other birds: Sterninae (Cullen 1956), Ploceinae (Crook 1964). From Oehlert's (1958) descriptions it appears to hold in some genera of Cichlids. Presumably in dense territories with steep attack-flee gradients, misunderstanding a signal is quickly penalized by an attack, so that displays have become more ritualized to reduce this danger.

Sometimes the transitions in motivation from fleeing to attacking or mating can be read in a smooth transition in the form of the display, but Morris (1957) has pointed out the important principle that many displays develop 'typical intensity' or 'typical compromise'.* Instead of reflecting the minor changes in motivation, the form of the display has become stabilised. For instance the S-posture threat display of the Poecilid fish *Xiphophorus helleri* and *montezumae* has become fixed with the rivals side by side, parallel or anti-parallel, each with its swordtail bent slightly towards the other and its head away, and they maintain this 'typical form' until one attacks or the other flees (Franck 1964; contrast Morris 1957). In other species, *X. pygmaeus*, *maculatus* and *xiphidium*, the S-posture has not developed a 'typical form', or not to the same extent. Their threat displays, though basically similar to the S-posture of the first two species, are more variable and express in the head orientation and general positioning of the body the momentary attack-flee balance.

This evolution of 'typical form' is a trend away from the conjunctive signal code to a disjunctive one. As Morris points out this implies that the reduction in information provided about the state of the signaller is more than compensated by the elimination of signal ambiguity. Moreover, he adds, the state of the signaller can still be represented in other

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* 'Typical form' (Tinbergen 1964) seems a better general name, which would include both the others.

parameters of the display such as its frequency. It is not clear why some species have evolved 'typical form' signals while others have not. A stimulating discussion of what is essentially the same problem is to be found in Alexander (1962) where he discusses the evolution and diversification of the four main types of cricket calls, occurring in the situations of advertisement, courtship, aggression and after copulation.

Individual differences

The existence of individual differences in a signalling code can seriously impair its accuracy, as has been shown in the experiments of Schweiger (1958) already discussed. But Marler (1961) has pointed out that a call can encode both the individuality of the caller and the main message provided that different parts of the signal are utilized. From sound-spectrograph analyses this seems to be the case for the songs of *Pipilo fuscus*, a species with considerable individual variation (Marler & Isaac 1960 *a*, *b*). In other species an individual may have a variety of songs, many of them peculiar to himself, all sharing broad species-specific or population-specific characteristics (Marler & Tamura 1962; Mulligan 1963).

In birds the identity of the caller is often an important piece of information. Precise evidence that individuals can recognize one another by voice is not abundant (Marler 1956; Thorpe 1961; Tschanz 1964), but there is much circumstantial evidence that at least in those species with a lasting pair bond, the mates recognize one another in this way. Male-male recognition may also be important in stabilizing the territorial structure of a neighbourhood, and Weeden & Falls (1959) showed that Ovenbirds distinguished between played-back songs of their neighbours and more distant males, being more likely to ignore a neighbour's song.

Limits to diversity: direction of signal evolution

The diversification of ritualized signals has been encouraged by the selection pressures outlined above, but it has been restricted to some extent by the signal-generating structures and sense organs available to a species. The vocal apparatus of fish and Amphibia limits most of their utterances to croaks and grunts (Moulton 1963; Bogert 1960), while the more specialized syrinx and larynx of birds and mammals allow elaborate frequency-modulated whistles and howls (Thorpe 1961; Kelemen 1963; Tembrock 1963). Correspondingly, while the ears of birds and mammals are very sensitive to frequency changes, the sound-detectors of insects are not, and respond chiefly to amplitude modulation (Autrum 1963). The tympanal organs of Orthoptera, the insect group most specialized for sound signalling, are particularly sensitive to rapid changes in amplitude and can distinguish between differences in such transients, so that the messages can be coded in the rhythm of the song, the steepness of the transients and the duration of individual sound pulses (Autrum 1963). Differences in temporal resolution, the ability to separate successive stimuli so that they are perceived as distinct rather than continuous, may account for differences in signals between birds and mammals. Pumphrey (1961) estimated that a bird song would need to be slowed up at least ten times before the human ear could fully resolve the detail a young Chaffinch (*Fringilla coelebs*) hears and reproduces.

Since many visual displays have apparently originated from 'intention movements' of locomotion (Daanje 1950), this might be expected to have restricted diversification. Very similar displays seem indeed to have evolved independently. For instance, in birds the upward stretched posture with beak pointing vertically is found widely in passerines, herons, terns and gannets (Andrew 1961; Meyerriecks 1960; Moynihan 1955; Dorward 1962) and seems to have originated in each group from a flying-up movement. However, in cases where diversification of signals is at a premium, as in reproductive isolation between related species, a great variety of modifications can be achieved on the same basic patterns (e.g. in surface-feeding ducks—Lorenz (1941)).

Much of this variety appears arbitrary, with no indication of why one species should ritualize its behaviour in this way, and another in that, but some general trends can be recognized. (For further examples see Wickler (1961).) Habitat and general habits play an important part. Within a family of birds the smaller species are usually more agile on the wing, and these are the ones which have the most elaborate aerial displays (Moynihan 1955; Meyerriecks 1960). Passerine species living in open country with few bushes and trees for song-posts have song-flights instead (Howard 1920). Fish living in rapidly flowing streams have, in different families, developed a parallel-swimming threat display, sometimes with their bodies in contact along their length and with tail beats precisely synchronized (Wickler 1959). This parallel orientation is doubtless connected with the way these fish have to head into the current to maintain position. The calling songs of male crickets, by which females are attracted, are much louder in the relatively solitary desert species than in those which aggregate in leaf litter (Alexander 1962). In the mating calls of frogs, the dominant frequency and pulse rate vary widely from species to species, but show a negative correlation with body size (Blair 1964).

By their very nature signals will make an animal not only more conspicuous to its own species but also to predators, so that signals which have evolved must be considered a compromise between conspicuousness and concealment. An interesting example concerns the hawk-alarm-call of a number of bird species, which warns other members of the flock but must also to some extent endanger the individual which calls. This call is surprisingly similar in different taxonomic families, and Marler (1956) has shown that its amplitude and frequency structure are precisely those which make it difficult for a vertebrate predator to pinpoint, using the three known methods of sound localization which would be available to it.

Species which are less vulnerable from predators may in consequence be able to afford more conspicuous signals. Hoogland, Morris & Tinbergen (1956–57) proved that the stout spines of the Stickleback (*Gasterosteus aculeatus*) help to protect it against fish predators, and that the weaker spines of the related *Pygosteus pungitius* are less effective. *Gasterosteus* also differs from *Pygosteus* in being less timid, in nesting in the open instead of in weed and in being more conspicuous in breeding coloration. Hoogland *et al.* suggested that this was because the strong spines permitted a more exposed way of life. Work in progress (K. Wilz, personal communication) indicates that some of the differences in the courtship of the two species can also be ascribed to the change which lead to the greater aggressiveness of *Gasterosteus*. Shifts in the balance of attacking, fleeing and mating tendencies account for many differences in the courtship displays of related species, e.g. Fringillid finches (Hinde 1955–56, 1959) and Cichlid fish (Baerends & Blockzijl 1963).

The behaviour of the cliff-nesting Kittiwake Gull (*Rissa tridactyla*) in contrast to its more typical ground nesting relatives illustrates how a hierarchy of adaptive modifications may be brought about by a single major change (E. Cullen 1957). The shift to the new nesting habitat safe from predators led to over thirty changes, including alteration of fighting technique, threat and appeasement displays, male advertisement, food begging posture and calls, and the development of an appeasement posture by the young with a special black band on the nape to reinforce its effect. In the related group of terns a somewhat similar aberrant cliff- and tree-nesting species was found to have undergone some of the same modifications as the Kittiwake (Cullen & Ashmole 1963).

The interaction of different behaviour systems is shown on a grander scale in a long series of papers by Crook, culminating in 1964, on fifty species of weaver birds, showing the correlation between food, habitat and social structure. Differences in the advertisement displays of the males were linked with nests of different structures and these in turn were associated with a particular type of breeding social organization.

Sometimes correlated differences may be difficult to interpret. Crane (1957) reported that in two taxonomic groups of fiddler crabs (*Uca*) the displays were particularly elaborate in species living on the shores of bays protected from waves, but only when salinity was high. This puzzling pattern was repeated in two geographical areas. Alexander (1962), with data from about 100 species of crickets, found particular structural types of calls has arisen independently in different groups, and tentatively attributes this to the way the crickets auditory system functions in making certain kinds of sounds more easily decoded than others. Whether or not this view is correct, this kind of correlation analysis, combined with a detailed knowledge of the animal's ecology and sensory physiology, offers the best hope for understanding the diversification of such complicated signals.

In the past, with a few exceptions, comparative studies of ritualized behaviour were made either on many species in captive or semi-wild conditions where their ecology was more or less distorted, or else under natural conditions but with far fewer species. It is now clear that the evolutionary processes which have shaped and are shaping the behaviour we see today can only be properly assessed when an animal's behaviour in its normal surroundings are thoroughly known, together with the capabilities of its sensory systems and signal-generating organs. Moreover, since the only way we can trace the evolution of behaviour is by comparing existing species, we need to have this information for related species living in different habitats, and unrelated species living in the same habitat. In view of our virtual ignorance of many of these facts, it is small wonder that there are still many unsolved puzzles about ritualized behaviour.

Abstract

Ritualization consists of the evolution of increased conspicuousness of signals and decreased ambiguity. Errors of signalling occur, even in that most remarkable of known animal signalling systems, the bee dance. Selection pressures moulding the reduction of ambiguity;

(1) Between species: reproductive isolation to prevent hybridization, and isolation to reduce aggressive encounters between closely related, ecologically non-competing species.

(2) Within species: Darwin's principle of antithesis leads to displays with the opposite meaning looking as different as possible. The ritualization of fighting is widespread, especially in densely territorial species. 'Disjunctive' and 'conjunctive' signals are distinguished, the former being

relatively distinct from each other, the latter intergrading. Displays signalling an individual's precise motivational state at a certain moment make use of conjunctive systems, though these may break into disjunctive 'typical forms'.

(3) Individual differences, if not introducing ambiguity in signalling, can be important, as the identity of the signaller is often a relevant piece of information in higher vertebrates with developed personal relationships.

The nature of the sense organs and potential signal-generator organs of the species limit the types of signal produced and the way the message is coded in them. In spite of the apparent arbitrariness of many of the signals used by different species, detailed examination of some has shown that it is sometimes possible to identify the selection pressures which shaped them.

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