

THE SIGNIFICANCE OF COLOUR PATTERNS IN FISH FOR THE STUDY OF SOME FUNDAMENTAL ISSUES IN BEHAVIOUR

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In this lecture I shall try to serve two purposes: (1) I hope to give you an impression of the way ethologists study the behaviour of fish, (2) I want to show you why fish can be extremely valuable subjects for the study of a number of behaviour problems of crucial fundamental importance. As this special suitability is based on the capacity of changing rapidly and reversibly the body colouration and its (usually black) marking patterns, I shall restrict myself to examples of the relation between colours and behaviour in fish.

The first species of fish which was intensively put into use for ethologically oriented behaviour studies is the three-spined stickleback (*Gasterosteus aculeatus*), Niko TINBERGEN and his first pupils chose it because it was abundantly available, easy to catch, to keep and to rear and because it possesses a fascinating reproductive behaviour pattern, combined with the pronounced sexual colour dimorphy during the reproductive period. In the course of years other characteristics, including a relative rigidity of the behaviour pattern, have further contributed to a position of the three-spined stickleback in some ethological laboratories (Leiden: TER PELKWIJK and TINBERGEN, 1937; VAN IERSEL, 1953; SEVENSTER, 1961, 1968; SEVENSTER-BOL, 1962; VAN DEN ASSEM, 1967; Groningen: BAGGERMAN, 1957, 1965; and Oxford: WILZ, 1970), which is comparable to that of the white rat in the laboratories of the other branch of objective behaviour studies: experimental psychology or 'behaviorism'.

The colour differences between male and female, assumed at the approach of the reproductive season suggested the first experimental research, the investigation of the fundamental question of how animals identify the various objects of biological significance to them in their natural environment. In other words: which stimuli in the environment are effective in eliciting a response and on what does this sensitivity of the animal depend. The obvious approach to an answer is to present to the animal models or dummies, imitating the object more or less closely, and in which features can be changed at will. The results of these experiments are well known now, they appear in every textbook. Male three-spined sticklebacks were found to attack, and ripe females to court, dummies with red on them, almost irrespective of their shape. The males courted silvery dummies, especially when the dummy showed a ventral swelling, as occurs in the real female with the ripe gonads.

These findings seemed to fit the Lorenzian concept (LORENZ, 1937) of 'an innate releasing mechanism'; a postulated mechanism for information processing, evaluating or filtering the stimuli received from the environment by the receptors. Different behaviour patterns were thought to be evoked through different channels with, at least partly, different filters. The value of a

feature was found to depend not only on its presence but also on characteristics such as size, intensity or place on the model, the latter implying sensitivity for "Gestalt" aspects of the stimulus situation. The effective stimuli are called key-stimuli, they are always characteristic for the object and LORENZ has argued that in the course of evolution they have often developed in these objects for the purpose of triggering a particular response in another animal (the "receiver"), usually a conspecific, provided this response was beneficial to the "sender", e.g. in social communication (social releasers, "Auslöser").

The effect of a dummy was found to depend not so much on this completeness, and thus similarity with the natural object, than on the sum value of the features present (rule of heterogeneous summation). Features which could not be perceived by the sensory organs of the animals of course had no releasing value, but of those perceptible, the value might differ dramatically between different behaviour patterns. This was a surprising discovery at the time it was made, particularly because this way of identifying objects had never been recognized in human beings. Although the phenomenon has chiefly been studied for visual characteristics, largely because of the dominant role of visual perception in the human experimenter, there is sufficient evidence that it also holds good for other sensory modalities.

The technique of the early experiments with sticklebacks referred to above, was not very sophisticated. The models were moved by hand in an only roughly standardized way, the results were not yet quantified in accordance with the rigorous standards later adopted in ethology, following the example of the comparative psychologists. I, therefore, prefer to choose for a discussion of the work on object identification the results of the, in general more sophisticatedly executed, experiments by a number of authors on the release of the responses of young fry to Cichlid to follow and stay close to the parent. In these experiments the latency period and intensity of the response to dummies were carefully measured and choice tests between models were also carried out.

The first experiments of this kind were done by NOBLE and CURTIS (1939) on the red Acara or jewel fish, *Hemichromis bimaculatus* GILL, and in a rather dark, greenish brown Cichlid species they called *Cichlasoma bimaculatum* (L.) but which was probably the species now called *Aequidens portalegrensis* (HENSEL). BAERENDS and BAERENDS-VAN ROON (1950) worked with these species and with the greyish-blue *Aequidens latifrons*, the dark greenish-violet *Cichlasoma biocellatum* REGAN and the grey + red *Cichlasoma meeki* (BRIND.). The most sophisticated techniques were used by KÜHME (1962) on *Cichlasoma biocellatum* and *Hemichromis bimaculatus* and by KUENZER on the yellow *Apistogramma reitzigi* AHL, the yellow + black *Apistogramma borelli* (REGAN) (KUENZER, 1962), the black + white checkerboard patterned *Nannacara anomala* REGAN (KUENZER, 1968) and the yellowish-brown oral incubator *Hemihaplochromis multicolor* (HILGENDORF) (KUENZER, 1975). I want to restrict myself here to the results obtained on the effect of the overall colors of dummies eliciting the following response in the fry. Form was evidently not an important cue but some characteristics of parental movement as well as odours, were. In general, when samples of young were taken from the parental school and confronted in a test tank with a model, they showed a responsiveness to colours which was roughly related to the dominant colour of their species in the reproductive phase. *Hemichromis* fry showed a preference for red, *A. reitzigi* for yellow, *Aequidens latifrons*, *A. portalegrensis* and *C. biocellatum* followed blue, green, dark-grey and black models about equally well but clearly preferred them over colours of longer wavelength. *Apistogramma borelli* young preferred dummies in which both yellow and black occurred, young of *Cichlasoma meeki* responded most intensively to dummies combining grey and red. KUENZER found that *Nannacara* young, although able to distinguish the checkerboard pattern of the parent, for the following response evaluated it only in terms of its overall brightness with respect to the background. Evaluation of brightness instead of wavelength was demonstrated by KUENZER for *Nannacara* (although this species is able to distinguish the *wavelengths* blue and green) and *Hemihaplochromis*. Sensitivity for a certain brightness range could also explain the results with those species in which a preference for blue and green dummies over red, orange and yellow ones was reported above; for these species responded equally to some of the grey models of a graded series of different brightness.

Knowing the preferences of the young, the interesting problem emerges how they got

them. This is a fundamental problem which became undesirably emotional when as a result of the false dichotomy of instinct versus learning, it was called the "nature or nurture" problem. Is the effectiveness of a particular wavelength and/or brightness range the result of experience with the coloration of the parents, or of other kinds of experiences with colours, or does it develop independently of any experience of wavelength differences? The latter question is probably insoluble, because of endless possibilities, part of which one might think of without finding a way to attack them experimentally, and part of which one will overlook. However, the influence of experience with the adequate object for the following response is experimentally testable; the obvious technique is the isolation experiment. An elegant way to carry it out is to induce pairs of substrate spawning species to oviposit on two closely adjoined stones and immediately after spawning separate one stone with part of the clutch in an isolation tank with a strong aerator while leaving the other stone with the parents for control. Isolation of individual young is not advisable because it was found to lead to an almost 100 % mortality.

The results of such experiments differed between species. The preferences for the longer wavelengths in *Hemichromis* and *Apistogramma* (and also for yellow + black in *A. borelli*) and for the shorter wavelengths and/or a particular brightness range in *Nannacara*, were all shown by young raised from the egg in isolation of the parents. This, however, does not necessarily imply that the strength of the colour preference remains unchanged while the young are growing

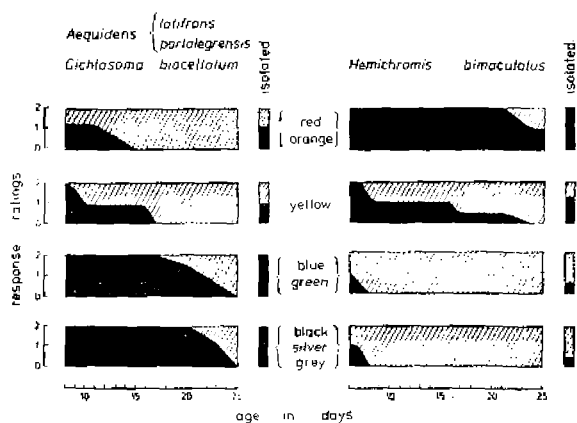


FIG. 1. — Response to differently coloured models (black area) of young of three Cichlid species reared with the parents, at different ages; the constant response of isolated young of the same species is summarized for day 9 and 13.

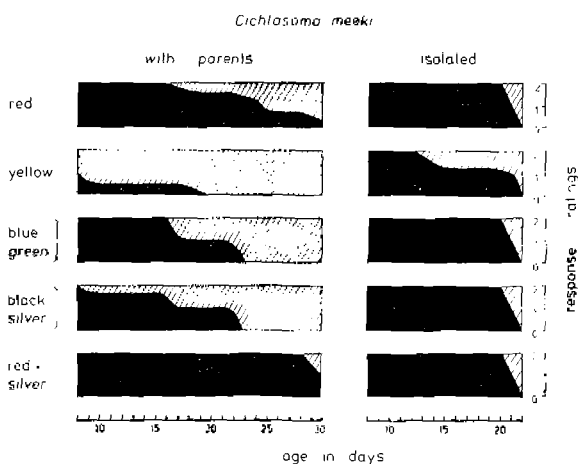


FIG. 2. — Response to differently coloured models of young *Cichlasoma meeki*, reared with the parents and in isolation, at different ages.

up. Experiments by BAERENDS and BAERENDS-VAN ROON (1950) in which new samples of young were taken from the same school and tested at intervals of a few days show (fig. 1) that the preferences of *C. biocellatum* and the two *Aequidens* species for blue, green, silver, grey and black, and of *Hemichromis* for red become more pronounced and exclusive with advancing age. As this happened in absence of the parents and of other coloured objects (experience with black and grey, however, seems impossible to avoid) the increase of the preference for wavelength must be due to an inborn mechanism and the changes in selectiveness with age to its maturation.

In contrast, the results of the experiments with *Cichlasoma meeki* gave different results (fig. 2). In this species the isolates remained almost maximally responsive to all colours used during the four week period they were tested. Young raised with their parents, however, gradually lost their interest for blue, green, black and entirely silver dummies; the interest for yellow, which had always remained low, was the first to disappear. The initially strong attraction of red also decreased at the end of the period and only the high releasing

and directing effect of models in which silver and red were combined remained. Obviously, young of this species learn that the colour pattern of their parents is a combination of red and grey. No difference could be found between models on which the red patch was applied in different places, provided the red colour was not distributed among several isolated spots. KÜHME (1962) was able to train *Cichlasoma biocellatum* fry to change their preference for models in colours of shorter wavelength for a red model by replacing the parents on the first day of free swimming by such a (moving) model. *Hemichromis* young proved to be much more resistant to similar attempts through training to change their primary red preference.

These results point to the potential existence in young Cichlids of two possibilities to identify the parent fish: (1) by means of an evaluation mechanism which does not depend on experience with the parent, and (2) through acquiring knowledge about parental features by means of a learning process. Some species appear to depend largely on the first, others on the second possibility and a species like *C. meeki* uses both. The differences between species in the use of the learning potentialities during the period of parental care must be due to differences in the genes. With this interpretation in mind it is interesting to study parent identification in Cichlid species in which colour polymorphism occurs.

Such a species is the grey, vertically barred "Convict Cichlid" *Cichlasoma nigrofasciatum*, in which, at least in captivity, an almost white form occurs which, probably due to one mutant gene, lacks all melanophores. In my laboratory RIDDERBOS and VAN HUIS (unpubl.) have carried out dummy experiments on the following response of samples of fry produced by naturally coloured pairs and by white pairs, raised by their parents, as well as in isolation. Young from all groups highly evaluated dark models and all preferred vertically barred models over models with a longitudinal black bar (another marking pattern common in Cichlids), but this latter pattern was preferred over plain coloured models. The same was true for young produced by mixed pairs. The independence of these preferences from experience with the parents reveals that a powerful genetical component must be underlying it. Only young produced by white pairs, and raised by their parents, did not clearly prefer darker models (with or without markings) over brighter ones. They had obviously acquired some knowledge of their parents being white and details of the results of the test suggest that this learned knowledge conflicted with the innate knowledge. This would make it extremely interesting to rear young with foster parents of the other morph. The exchange of clutches, however, is difficult and so far our attempts have failed.

Such experiments were in particular stimulated by the well-known work of KONRAD LORENZ (1935) on imprinting in goslings following their own or foster mother and the implications he made about the effect of such imprinted engrams for species- and partner recognition in later life, such as the disastrous irreversibility of imprinting on inadequate objects.

Cross-fostering, however, in Cichlids has with some success been accomplished by other authors to test whether the knowledge the parents have of their own kind of fry (and which makes cross-fostering so difficult) might be obtained through an imprinting process during the first experiences with their own clutch. NOBLE and CURTIS (1939), GREENBERG (1963) and MYRBERG (1966) have cross-fostered *Hemichromis bimaculatus* and *Aequidens portalegrensis*. Unfortunately the results obtained by these authors are contradictory. The data of NOBLE and CURTIS and some of MYRBERG' data seem to support the imprinting hypothesis, but GREENBERG' results argue against it. The contradictions might be due to differences between the experiments in the interference of chemical factors which are also involved (KÜHME, 1963).

Very much in line with the findings in birds are the results obtained in imprinting experiment carried out by SJÖLANDER and FERNO (1973) with four young of the oral incubator *Haplochromis burtoni* (GÜNTHER) taken from the mouth of the female and each individually raised with 10-15 equally large young of the substrate spawner *Cichlosoma nigrofasciatum* (GÜNTHER). In contrast to controls these *Haplochromis* young, when sexually mature, all showed a preference for the company of *C. nigrofasciatum* and also performed sexual behaviour towards this species. It was not further analysed, however, on what features of the alien species this imprinting had taken place.

The red colour in reproductive males and females of *Hemichromis bimaculatus* is also important in recognition of the mate. NOBLE and CURTIS (1939) have shown that females select the redder of two males. ROWLAND (1975) was able to evoke attack, sexual and escape behaviour in males of this species by presenting red as well as greyish-green dummies. However, the response frequency towards each of these models was different for different activities. For example, the courting activity «quivering» reached much higher levels in response to red dummies than to green ones. The incidence of attack towards red and green models showed a more complicated picture; it varied a great deal between presentations and, in particular, between individual males. Mostly the males tended to attack green dummies. Sometimes they seemed to be inhibited in attacking red dummies, sometimes, however, males showed a higher attack rate towards red than towards green. This could be induced in males which had previously courted red dummies by allowing them to spawn with a female. Such data reveal that in addition to external stimuli internal factors also determine the type and the parameters of the response.

The study of this so-called «motivation» of behaviour, in a qualitative (type of motivational system or systems activated) as well as a quantitative, sense (level of activation) is another fundamental issue in theories on behaviour. To solve the important questions asked one is in great need to identify and «titer» motivation, particularly before an activity occurs. For when this happens one measures only the effect of internal and external stimulation in combination. Now in fish, colour patterns, and especially the black markings, seem to reflect motivation; the same pattern may last for a period in which various activities are performed. As an example of the way colour patterns can be used in the study of motivation I will briefly discuss some results we obtained in the analysis of the courtship behaviour of the male of the guppy, *Lebistes reticulatus* (PETERS), (BAERENDS, BROUWER and WATERBOLK, 1955).

Since WINGE's work (WINGE, 1927) on the genetics of this species the variety of colour patterns between different morphs is well known. In spite of this, a considerable amount of consistency can be found in the black markings displayed during interactions between the fish, at least in the morphs we have seen. In the material used, we distinguished 6 different black markings which could be displayed in various intensities and even disappear entirely. In addition changes were possible in the darkness of the iris of the eye and a system of melanophores distributed all over the body was able to cover all other markings as if it were a veil. Although all markings have been observed to be present alone, the majority of them tended to occur in combination with others. The incidence of the various thinkable combinations varied with its type, some markings appeared to be incompatible with one another, especially when fully developed.

Male courtship consists of two phases (fig. 3). In the first phase the male tries to separate a female by leading her away from a concentration of guppies. He starts with following a female from behind and below, touching her a few times near the genital papilla. Then, via swimming above and beside the female the male tries to get in front of her and, if she moves slowly enough, posture face to face, while alternately approaching and retreating over short distances («luring»). Suddenly the male turns about 180° and, while its body axis is aligned with that of the female he bends his body in a S-curve («sigmoid»). If he has been able to perform this chain of activities successfully the male completes the first phase by abruptly jumping away over a distance of at least 10 cm. For proceeding to the second courtship phase the female needs to respond by following. The male then again assumes the «sigmoid», but no longer oriented in line but at a right angle with the body axis of the female, thus checking its forward movement. From this position the male suddenly charges around and finally comes from behind towards the female, bringing its gonopodium in contact with her genital pore by swinging it forward. If the copulation is successful the male finishes by making a few short jerking jumps. This order of the various activities is not absolutely rigid, it is an order of high probability. The chain can be broken off at nearly all links, but breaks are more likely in some than in other places. For continuation the response of the female is important, but also the motivational state of the male.

In the course of both phases a consistent pattern of changes also occurs in the black markings. During following, luring, sigmoid and the jump, in the first phase of courtship,

a rounded patch on the tail just at the base of the caudal fin is visible. After entering the second phase this patch disappears and instead a roughly rectangular lateral patch dominates. In both phases when the intensity of the activities rises, a longitudinal stripe appears in addition to the other markings present. Finally a black edge along the dorsal side of the caudal fin may be displayed, but in contrast to phase I, this band is never fully developed during the more intense parts of phase II.

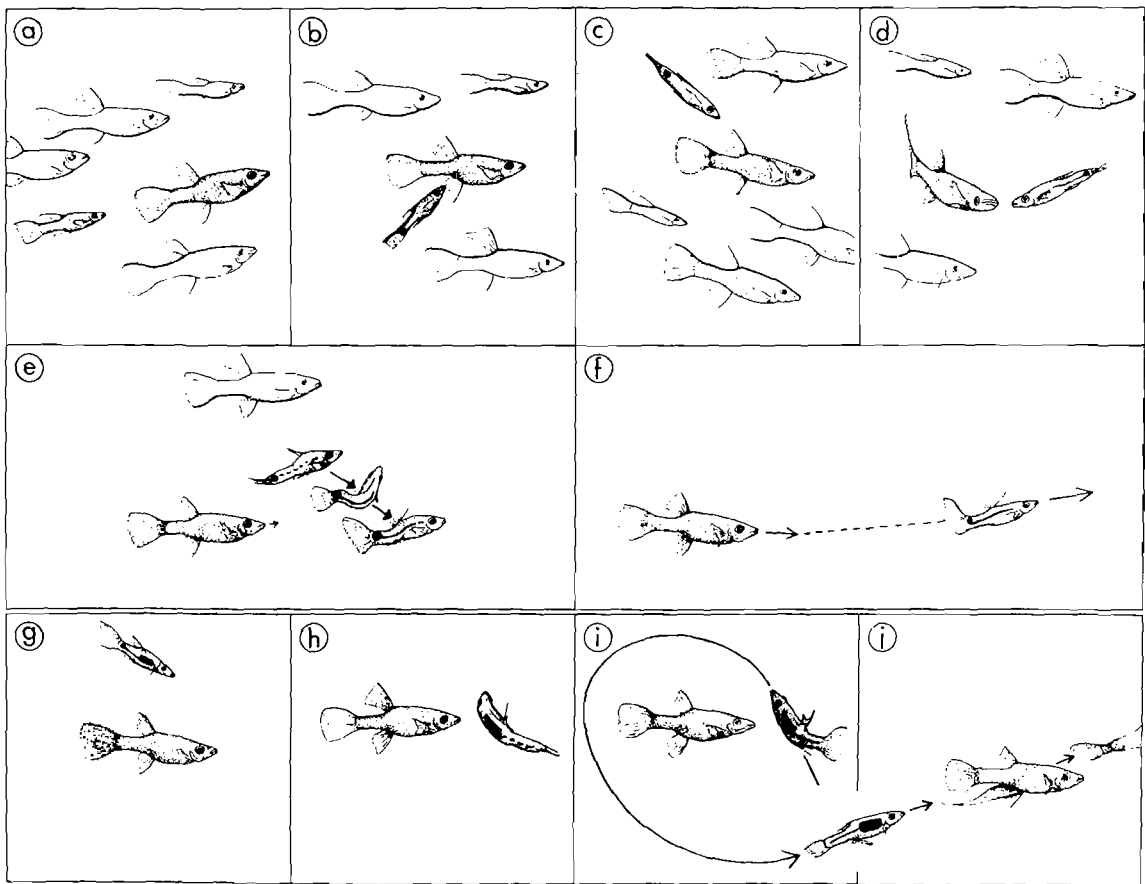


FIG. 3. — *The courtship of the male Lebistes reticulatus. First phase: (a, b, c) following the female, (d) posturing, (e) sigmoid, (f) display jump. Second phase: (g) approach, (h) checking, (i) copulation attempt.*

The gradual shift of the marking pattern in the course of the courtship performances suggests that these patterns reflect motivational stages. This hypothesis was tested by counting the number of times each of the more frequently occurring marking patterns were present when each of three acts: the intention sigmoid, the sigmoid and the copulation attempt, occurred. As shown in figure 4 this allows ordering of these marking patterns along a scale which can be taken to represent, and thus be used for measuring, the tendency to fertilize in the male. This combined with another finding, viz. that the stimulus value for mating increases with the size of the female, gives us the possibility to study the interaction between internal and external factors quantitatively.

To this end males, which while courting not optimally responsive females, have developed a particular marking pattern, were suddenly, under standard conditions, confronted with one of a series of females of different sizes enclosed in a glass tube.

In the upper part of the figure 4 the relation of the response evoked by this treatment with the size of the female and the marking pattern present in the male is given for three activities. It is clear that the same activity can be reached with different proportions of internal and external stimulation. Passing from a less to a more advanced link in the chain of courtship activities can be achieved by increase of each kind of stimulation separately and by a combination of both.

The «isoclines» represent the motivational state of the fish at the moment a particular activity occur. Although the hyperbolic shape of the «isocline» suggests a multiplicative relation between internal and external factors one should not jump to this conclusion without realizing that this form depends on the characteristics of the scale and thus on the way the variables were measured and plotted (see also Houston and McFarland, 1976).

TINBERGEN and some of his pupils (TINBERGEN, 1952, see also BAERENDS, 1975) have suggested that the motivation underlying an activity may have a complex character, being a compromise resulting from the interaction of the simultaneous activity of more or less incompatible motivational systems in the animal (such as those for attack and for fleeing). Here we touch on another fundamental issue in ethology: the question whether behaviour is organized in motivation systems.

The courtship of the *Lebistes* male contains elements which can be understood on the basis of interaction of conflicting motivations. In the first phase biting often occurs; the black dorsal edge of the tail fin mentioned above is also a marking typical of fighting males. Jumping looks like a ritualized flight (to which the tail patch seems to have been added as a conspicuous social releaser) and the patterns and orientation of luring and of the sigmoids have an ambivalent appearance. One can argue that during courtship the tendencies to attack and to flee, aroused by the reduced distance to the other fish while interacting, become reduced and thus enable the tendency to fertilize to produce overt copulation behaviour.

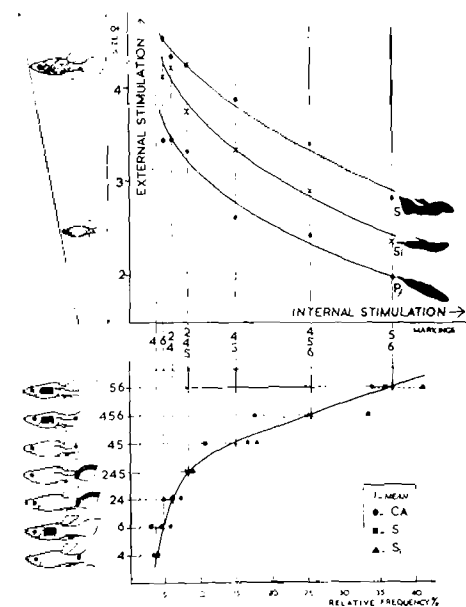


FIG. 4. — The relation between different marking patterns and the occurrence of sigmoid displays or copulation attempts (lower part), and the relation between this «internal tendency for sexual behaviour» with the strength of the external stimulus (size of the female) in producing three displays: posturing, intention sigmoid and full sigmoid.

Lebistes is a rather small and too rapidly moving fish to be a very promising subject for penetrating further in the issue of motivations. The much larger Cichlids, which also display different colour and marking patterns in support of complex social and sexual behaviour, are likely to be more suitable for this purpose. To make this clear I shall attempt to give a rough general survey of some essentials of Cichlid behaviour.

On the basis of the type of reproductive behaviour, two groups of Cichlids can be distinguished. The phylogenetically more primitive type are substrate spawners. The fishes defend territories of some size. Pairs are usually formed in these territories several days before spawning takes place. The other type, which has developed in more than one taxonomically identified group, are the oral incubators. Both groups have a similar repertoire of agonistic behaviour. With regard to sexual behaviour a distinction can be made between communication activities occurring before the formation of the pair and which are subserving the selection of a member of the same species, of opposite sex and of the right condition, and communication activities chiefly performed after pair formation, which are supposed to promote endocrine and motivational synchronization of the pair (GREENBERG, ZIJLSTRA and BAERENDS, 1965) and give the partners the possibility to become individually acquainted with one another. The former activities are sexually dimorphic and activities of the male and of the female follow each other as links in a stimulus response chain.

The activities occurring after pair formation are monomorph and are performed by both sexes, often simultaneously.

Substrate spawners have territories of some size in which pair formation takes place several days before spawning and in which the parents co-operate in taking care of the young, often for a month or more. In this group the behaviour initiating the formation of the pair tends to be poor in components and, to the human observer, relatively inconspicuous. In contrast the behaviour of the established pair (e.g. quivering, digging, cleaning the substrate and pseudo-spawning) is repeatedly shown; it often flares up after agonistic encounters with neighbours. The colour patterns of most substrate spawners are sexually monomorph.

Oral incubators also have territories but these are usually smaller and in a great many species only defended by the resident (male) fish. Several of such territories closely adjoin each other, such that the term «lek» or arena, as borrowed from ornithology, can be applied. The resident males compete strongly to attract passing females to their territories, for the greater part occupied by a dug out pit or cleaned area. Sexually dimorph communicative activities dominate in encounters with females and are supported by a conspicuous sexual dimorphism in colour and marking pattern. When a female has decided on a mate she usually does not stay longer than a few hours in his territory. During this period sexually monomorphic activities can be seen. Like in the substrate spawners they are probably important in facilitating spawning, but they take a much less time. Immediately after a batch of eggs have appeared the female turns around and takes them into the mouth, together with the sperm ejaculated by the male while circling with her over the bottom of the «nest». After the female has spent all the ripe eggs she leaves the area to take shelter elsewhere with her brood.

Detailed analysis of the form and orientation of several of these activities gives support to TINBERGEN's hypothesis that they could have been derived from interactions between opposing behaviour systems, in particular the tendencies to attack and to flee, through (simultaneous or successive) ambivalent combinations of incomplete modal action patterns of systems, or ambivalent orientations (which may lead to re-direction), through displacement caused by disinhibition or through any combinations of these phenomena (BAERENDS and BAERENDS-VAN ROON, 1950, see also BAERENDS, 1971). Activities resulting from these kinds of interactions without having evolved in adaptation to signal functions are well known. It is usually thought that when, in evolution, they have turned into ritualized signals they have become emancipated from the motivational factors originally involved. However, the evidence for this emancipation phenomenon is only weak and, moreover, there are theoretical reasons for questioning the concept (BAERENDS, 1975). If marking patterns can be taken to represent motivational systems, studies of the correlation between the occurrence of such patterns and activities with communicative functions seem a feasible way for testing the emancipation hypothesis and, if it should not be rejected, for developing it further.

With this purpose in mind a couple of years ago, studies of a number of Cichlid species were started in my laboratory. Figure 5 gives, as an example some data obtained by ENGELSMA (unpubl.) on *Cichlasoma meeki* males and females in reproductive condition. Two elements of the marking pattern are always present: the «eye» patch on the gill covers and the black patch caudally on the tail. The big, black, so called «cichlid patch» laterally on the body is usually present, but can disappear. The same is true for the horizontal row of smaller black patches, in which the «cichlid patch» is situated, although it may vary its intensity independently. The occurrence of this row of patches on a plain grey background is one of the important marking patterns of this species. Black bars through these patches form a second important pattern. Sometimes it appears in a form in which the bars do not extend ventrally beyond the lateral row of patches. A third important marking pattern is a darkening of the entire body, which may vary in intensity. The vertical bars and the overall darkness always occur in combination with the lateral patch-row, which may, however, vary in intensity. Figure 5 gives a summarizing picture of the percentage occurrence of the various marking patterns shown in the left column when agonistic behaviour (attacking and threatening), overt escape (fleeing and hiding), courtship or parental care was performed.

The lateral patch-row is the only pattern occurring unmixed with others. This is the case in the resident male in its territory, behaving neutrally or sexually. In the female this pattern

is, under the same circumstances, always mixed to some extent with overall darkness. The figure shows that this darkening also is correlated with escape in both sexes, but particularly in the female. When agonistic behaviour occurs vertical bars are likely to appear, but when this behaviour turns into flight these bars do not extend ventrally, and the «cichlid patch» is likely to fade. In both sexes during escape behaviour vertical bars and overall darkness occur in combination; however, this happened in only 16% of the times males showed escape behaviour, compared with 65% for the females. In both sexes escape also occurs when only the overall darkness is superimposed on the lateral patch row. This more often happens in the female, even when she is behaving sexually and particularly when she is caring for the brood. We

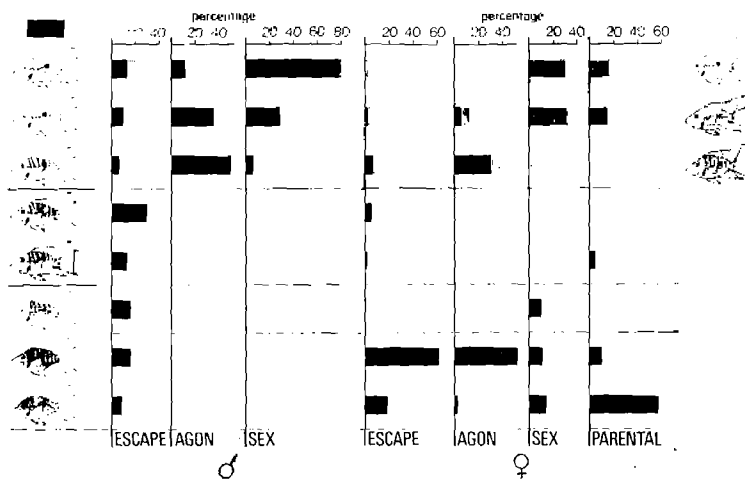


FIG. 5. The relation between different marking patterns and three types of social behaviour in *Cichlasoma meeki* (after Engelsma, unpublished).

think that the overall darkness expresses a strong tendency to stay put in the territory, perhaps combined with a tendency *not* to attack, whereas the vertical bars would express leaving and fleeing. A study by BALDACCINI (1973) on the correlations between behaviour patterns and markings in *Tilapia mariae* (BOULENGER) gave a similar picture. In both cases, as well as in several other Cichlids we are working on, the frequent occurrence of mixtures of tendencies is clearly visible in the marking patterns. Much more work will have to be done to unravel how far common mechanisms are underlying the occurrence of the markings and the activities. It is obvious that if such mechanisms exist, and this is one of our fundamental questions of the organization of behaviour, they allow for a considerable amount of overlap and plasticity, which makes their analysis very difficult.

Another complication which undoubtedly occurs if one tries to use the markings as indicators for causal mechanisms, is that markings in general do not only serve to communicate true messages about the presence and the motivation of a fish, but also the false message suggesting that the fish is absent, through giving it a cryptic appearance. It is not unlikely that in the course of evolution this was the primary function of markings. If so, it is possible that in spite of secondarily added 'positive' communication functions, this original function is still present in the mechanisms through which the markings are now caused. Consequently it will always be wise, when considering function and causation of colour and marking patterns, to realize that they may be the result of a compromise between advertisement and camouflage. This notion was earlier suggested for the occurrence of cryptic and aposematic characteristics in the larvae of closely related species of Tenthredinids by PROP (1959).

Some Cichlid species have extended this compromise in a very interesting way. On top of the possibility for individuals to change their colour and patterning within a short time span,

they may change their basic coloration in the course of their life time, and/or they may have distributed different colorations over different individuals by becoming polymorphic. We have already seen the case of the white mutant of *Cichlasoma nigrofasciatum* which originated in aquaria. However, *Cichlasoma citrinellum*, the Midas Cichlid was found wild in Central America with dark and "golden" morphs (BARLOW, BAUER and MCKAYE, 1976) and VAN LIER RIBBINK (1975) found *Pseudocrenilabrus philander* to be polytypic in areas of southern Africa. The work on this fascinating phenomenon of polymorphism has only recently started. It, of course, lays an emphasis on the evolution and function of colour patterns, but for the latter, insight into causation is equally important. Function can only be properly understood through field work; it is promising that this necessary complement to laboratory work is now developing in tropical regions of the old and the new world.

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