The Development of Ritualized Displays in Junglefowl

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The development of ritualized displays in Junglefowl

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The courtship of the adult male Junglefowl is characterized by the performance of several intricate and highly stereotyped display activities, specific to the species. When *waltzing*, for example, the male sidles toward the female with the primary feathers of the outer wing fanned downward toward the ground. As the male proceeds to circle the female, the outer foot scrapes through the extended feathers. The sudden approach of the male and the sharp rasp of foot against feathers function as signals which induce the female to crouch, a movement to which the male may respond by mounting and copulation.

A second feature of male display is *tidbitting*. In this the male scratches for and pecks at food, takes it in the bill, and bows up and down while producing a rapidly repeated call. Females often approach a tidbitting male and eat the food which is dropped by him. Thus, this display serves to attract the female and to maintain a bond with her.

Another very striking display is *cornering*, performed by the male under shrubs or at other concealed places. In unplanted pens it is usually oriented to corners. While cornering, the male assumes a half-crouched posture, scratches and stamps with his legs, makes peculiar zigzagging movements with his head and produces a low purring sound. Females often approach the cornering male and make nesting movements at the place chosen by the male. This suggests that cornering can be considered as a signal serving the selection of the nest site.

All these displays are ritualized in the ethological sense: they serve as signals in the communication between individuals and have become adapted during evolution to this function. By comparing the displays of closely related species, it is possible to arrive at a picture about the probable changes that must have taken place during the evolution of such signals (see the contributions of Cullen, Hinde, and Lorenz, to this Symposium).

To find out which factors contributed to the evolution of such signals, and how, is an important biological problem. But equally important is the question of how ritualized displays develop ontogenetically, that is, in the life of the individual. Is it necessary for a bird to see the example of his parents or siblings before he can produce the displays characteristic for his species? Is practice necessary before the full-fledged display occurs? In many cases it appears that this is not so. Ethologists have therefore often used the term 'innate' for species-specific displays, in order to indicate that their ontogeny is not influenced by conditioning, imitation, or similar learning processes. But, in addition, 'innate' sometimes carried the connotation that the development of behaviour takes place entirely without regard to external conditions, provided these conditions were sufficiently favourable for the animal to stay alive. This way of thinking has probably obscured and discouraged a more fertile approach toward ontogenetic problems.

Recently, however, Lorenz (1961) has pointed out that 'innate' should be taken to mean that the ontogeny takes place—not independently of *all* external conditions—but independently of those with respect to which the behaviour in question has been adapted during evolution. Thus, if an animal develops a behaviour pattern when raised in isolation from conspecifics, and if this pattern is clearly adapted to the function of communication between individuals, then, according to Lorenz, such a pattern should be called innate. To take a concrete example, if a male Junglefowl raised in isolation waltzes for the female the first time he encounters one, waltzing should be considered innate.

But if waltzing is innate in this sense, the only thing we learn by applying the term is that social experience is *not* necessary for its development. With this statement, no light at all is thrown on the nature of *positive factors* underlying the development of this pattern. Furthermore, we remain ignorant about the role of the other external factors to which an isolated animal is exposed. The ontogenetic question is not answered by pointing out which factors are not necessary; what we need to know is which factors—internal as well as external—are of importance for the development of the state in which waltzing is produced by the male. That genetic factors are of importance is obvious, but of little help, since these factors are localized in the chromosomes and bear no immediate resemblance to the behaviour.

Although the term 'innate' may have some merit when applied to evolutionary questions (cf. Lorenz 1961; Wickler 1965), its usefulness for ontogenetic questions is extremely limited. Instead of classifying the behaviour patterns into the categories innate and not-innate, it appears to be much more promising to investigate how behaviour develops, and to keep an open mind about the possible influence of external conditions in guiding the development of behaviour.

As a first step in this approach I have studied the development of social behaviour in small groups of incubator-hatched chicks, raised without a mother-hen. In this paper some of the conclusions will be mentioned; for details the reader is referred to a previous paper (Kruijt 1964). I shall limit myself to the male courtship patterns described above.

By observing the chicks from hatching to sexual maturity it became clear that their social behaviour develops in a regular and predictable sequence, starting at a simple level of organization and becoming gradually more complex. At first, social behaviour is limited to mutual attachment, but gradually, aggressive behaviour, fleeing, and copulatory behaviour are added in this order. Each of these groups of patterns can occur more or less in isolation of the others early in development; but later, simultaneous activation of several is the rule. This gives rise to complex interactions between simultaneously activated systems, as a result of which new patterns start to emerge; these can be considered as 'ambivalent' or 'displaced' (see Hinde, in this Symposium).

The courtship displays of the male do not occur in complete form until the stage in which copulatory behaviour is performed, but most of the components of these displays develop much earlier and are then shown during fighting. This suggests that the courtship displays are mainly due to conflicting tendencies of the male to attack the female and to flee from her. The fact that these displays accompany copulatory behaviour so frequently, suggests that conflicts between attack and escape are facilitated by activation of a tendency to copulate with the female.

Of the three displays described earlier, cornering is more dependent on activation of copulatory behaviour than waltzing or tidbitting. The latter two can be shown when the male has no tendency to copulate, but they are more likely to occur as the male's tendency to copulate increases—as judged by his inclination to mount a crouching female. Cornering, on the other hand, is nearly always associated with a strong tendency to copulate; in other words, in the absence of a tendency to copulate, cornering is nearly never shown. Yet, most or perhaps even all components of all displays (included cornering) appear to be expressions of agonistic conflicts, i.e. conflicts between aggression and escape. Therefore, it appears that a strong tendency to copulate can facilitate agonistic conflicts that do not occur normally when the tendency to copulate is absent or weak.

Although this picture throws some light on the causation of the courtship displays of the male, it does not yet show which factors underlie their development. But if the courtship displays are due to complicated interactions between the tendencies to attack, to flee and to copulate, then it will be necessary to study which factors underlie the development of these types of behaviour.

As a next step, therefore, we may ask to what extent the development of these tendencies depends on social experience. To this end a number of males were raised in visual isolation from conspecifics starting on the day of hatching. The behaviour of these males is rather variable, but all develop certain abnormalities which are absent in group-raised males, even if the latter are kept in prolonged isolation at later periods of their life. The following results were obtained.

Many of the isolated males showed excessive fleeing behaviour at some time during the first month of their life. Apparently this behaviour was often aroused by events occurring outside the cage, such as the approach of a human being. Fleeing from outside disturbances of course also occurs in group-raised birds, but in this case fleeing stops soon after the disturbing factor disappears. Isolated males, however, would often continue for long periods after the disappearance of outside disturbances. In other instances no outside inducement was observed at all, but it sometimes seemed that the bird was trying to flee from parts of its own body, especially the tail.

Sooner or later all isolated males start to fight with their own tail. While raising his neck-hackles, the cock turns round and round his own axis, attempts to kick with his legs in the direction of his tail, and pecks viciously at the base of the tail-feathers. Often tail-fighting is initiated when something happens outside the cage, e.g. when humans approach. In alternation with tail-fighting the male may run around the cage while looking backward, as if he were fleeing from his own tail. Once tail-fighting has developed, isolated males usually start to be aggressive toward humans as well.

One of the isolated males even developed copulatory behaviour in the absence of conspecifics. This male often pecked at loose feathers scattered about the cage. Often he would pick one up and perform the copulatory pattern while keeping the feather in the bill.

These observations show that aggressive and fleeing behaviour and, more exceptionally, copulatory behaviour, can develop in the absence of normal social experience; but in the absence of social companions, these types of behaviour show abnormalities especially with regard to the releasing and directing external factors.

The next question which may be raised is whether aggressive, fleeing, and copulatory tendencies are ever aroused simultaneously in isolated males. In other words, do conflicts occur, and how are they expressed?

I mentioned earlier that isolated males may alternate their tail-fighting with behaviour which appears to be an attempt to flee from their own tail. But, moreover, tail-fighting is often interspersed with bouts of tidbitting and the male may waltz around his own axis. In group-raised males these displays are mainly due to a conflict between aggressive and fleeing behaviour. The most parsimonious explanation seems to be that similar conflicts can occur in males raised in isolation, although in this case the conflicting tendencies are aroused by quite different external factors.

Further support for this idea can be derived from the fact that cornering occurs only rarely in isolated males. As discussed earlier, this display is shown by normal males when agonistic and copulatory behaviour are all activated simultaneously and strongly. Most isolated males, however, never showed copulatory behaviour while alone in their cage. The kind of conflicts that produce cornering were usually not arising in these birds and this explains why this display occurred so rarely.

Cornering was also very rare in the isolated cock which copulated with feathers. Again this is understandable since this male attacked humans or his own tail but not loose feathers. Simultaneous activation of agonistic and copulatory behaviour probably never occurred to the same extent in this male as in normal birds where these types of behaviour are elicited by one and the same external object, the social companion.

Thus, this picture leads to the conclusion that Junglefowl males develop ritualized displays both when raised in a group and when raised in isolation, provided the external conditions arouse the conflicts which are necessary to produce displays. Even without social companions the external conditions apparently give many opportunities for such conflicts to arise.

Two further conclusions follow. First, it appears that the development of escape and aggressive behaviour is possibly governed by quite unspecific conditions. I shall return to this conclusion later. Secondly, once aggression and escape are developed, and simultaneously aroused, they interact more or less automatically in such a way that a display, in species-specific form, is performed. This suggests that the processes underlying these interactions are mainly under internal control, and occur independently of the nature of the external factors which gave rise to the conflict.

This should not be taken to mean that the resulting sequences of behaviour are always the same whether the male was raised in isolation or in a group. I sometimes got the impression that the behaviour of isolated males is more erratic and less predictable than that of normal males. This may be due to the fact that the external factors which elicit aggressive and escape behaviour in an isolated male do not allow the type of mutual interactions that are possible between social companions. For example, a male cannot chase away his own tail nor can he flee from it.

Some further observations were made on the behaviour of isolated males toward females. Three males raised in isolation from hatching to the age of 6 to 9 months were subsequently tested with females. All three males copulated successfully after a few encounters, but their behaviour was abnormal. Instead of showing the normal amount of courtship, they often pursued the female frantically. Their attempts to mount were often misoriented and interspersed with aggressive behaviour directed toward their own tail.

Of eleven males isolated until the age of 10 to 16 months only two eventually copulated successfully when subsequently tested with females. The unsuccessful males either ignored or attacked the female. Thus, the ability to copulate is usually lost after prolonged isolation. But this is not true if group-raised males are isolated at later age; other males were raised in male groups and isolated at the age of $2\frac{1}{2}$ months for a period of 13 or 14 months. These males achieved successful copulation after few encounters with females. Their behaviour did not differ from that of group-raised males at the age of 4 months, the age at which they start to perform complete copulatory behaviour.

Recent experiments indicate that prolonged isolation after the age of 6 weeks has the same effect as isolation from hatching, but copulatory ability is not affected if the isolation started at the age of 9 weeks. Apparently, experience gained during social contacts with other males before the age of 9 weeks brings about a change in the organization of the male's behaviour with the result that copulatory ability can develop and be preserved during long periods of isolation after this age. But as mentioned above, males deprived of social experience from hatching can also perform copulatory behaviour, provided contact with the female occurs before the age of 10 months. The final conclusion therefore is that although copulatory ability can develop without early social experience, it cannot be maintained in this case over long periods of isolation. It appears that males which have passed this sensitive period develop abnormal fixations which are difficult or impossible to change.

Waltzing and tidbitting were performed by some of the males in the presence of females, but cornering was always absent or rare. That the female released display at all is not surprising if one considers the fact that these displays were performed in response to very unspecific external factors in general. To an isolated male a female is probably just another object out of a large class of objects which can elicit agonistic behaviour.

More surprising is the fact that isolated males if not older than 10 months were able to copulate. This suggests that copulatory behaviour is released by properties which are more or less unique to the female and can only rarely be released by the external conditions in which a socially deprived male lives.

The variability in the behaviour of isolated males may be due to the fact that many of the disturbances around the cage were not under our control. At present we are starting experiments in which we try to control the environment of an isolated chick much more precisely. One example demonstrating the difficulties in this approach may be mentioned briefly.

Since isolated males attack their own tail, it occurred to us that experience with nearby moving objects gained in early life is possibly an important factor in the development of aggressive behaviour. This was also suggested by the observation that isolated chicks several weeks of age may start to fight with the heating lamp which was attached with flex to the ceiling of their cage. We wondered what would happen if the lamp was attached in such a way that it could no longer move. It was found that isolated chicks raised in this situation had little inclination to fight the lamp, but instead, some of them attacked their transparent drinking bottle, often exactly at the moment that air bubbles floated toward the surface.

This observation suggests an important conclusion: in the absence of social stimulation other external factors are probably influencing the development of aggressive behaviour, and these factors may be very unspecific and difficult to control.

Now, if this is true, then it is also possible that some of these factors are contained in the social experience which group-raised birds gain during their development. If, for example, experience with moving objects influences the development of aggressive behaviour, then it seems quite possible that isolated males can obtain such experience by interacting with their tail, although in normal development the social companions provide the experience. It is, therefore, not possible to conclude that social experience is unimportant if behaviour develops without it. At most we can conclude that such experience is not necessary; but this statement gives very little insight, and should not distract from the real ontogenetic problems.

In summary, it may be said that the ritualized courtship displays of Junglefowl depend for their occurrence on simultaneous activation of agonistic and copulatory behaviour. If the latter are developed, the displays follow more or less automatically and without social experience, although their orientation in socially deprived birds is often abnormal. The interactions between agonistic and copulatory tendencies which produce the displays seem to be mainly under internal control.

The development of agonistic and copulatory behaviour can also take place without social experience. This does not mean that external conditions have no influence at all, but possibly very unspecific conditions are sufficient. For further insight into the development of social behaviour it will therefore be necessary to control the external conditions very precisely, even the unspecific ones.

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