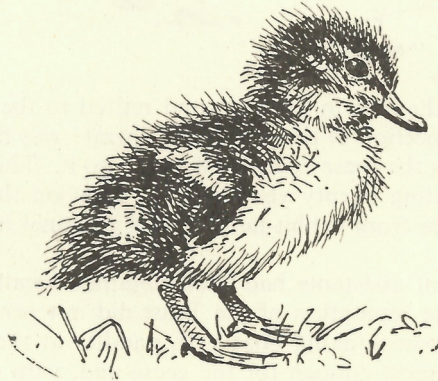Ascot, in April 1952 and another was shot in Autumn 1952 twenty miles south-east at Dogmersfield. Another pair bred at Queensmere, twelve miles away, in 1952 and 1953 when we went specially to catch the five goslings, which were again ringed and colour-ringed.

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EXPERIMENTS ON THE FOLLOWING-REACTION OF DUCKLINGS

By Eric Fabricius and Hugh Boyd

THE useful study of animal behaviour, like any other kind of scientific enquiry, requires a point of view. Because of the complexity which characterises the activities of all living organisms and the comparative novelty of persistent investigation of these activities students of behaviour approach their tasks from many different standpoints. In recent years the most important, because most fruitful, basis of investigations by European workers has been that of *ethology*, the study of the causes of innate behaviour. The principal exponents of this method of approach, Lorenz and Tinbergen, have both published in recent years accounts in English of their aims and methods. In addition to a rather austere paper on ' The comparative method in studying innate behaviour patterns ' (1950), Lorenz has, in *King Solomon's Ring* (1952) provided a wealth of anecdote about what animals do, and why, in a language without technicalities but informed by his exceptional insight. Tinbergen, in *The Study of Instinct* (1951), has provided a more formal ' programme ' and in his very recent *Social Behaviour in Animals* (1953), a survey of some of the results of applying their ' objective ' method. Since these expositions are readily available, it is not necessary here to do more than state the fundamental tenets of the method to which the writers have attempted to adhere in studying some aspects of the behaviour of very young ducklings.

The ethological approach is characterised by especial attention to *innate* behaviour and to the problem of *causation*. ' Innate behaviour is behaviour that has not been changed by learning processes' (Tinbergen, 1951). The ethologist's account of causation is essentially similar to that of the physiologist, but whereas the latter usually concern themselves with the functions of particular organs the ethologist is concerned with the functions of the animal as a whole. This equation of the problem of causation with the study of function may be

philosophically ingenuous, but is justified by the opportunities it creates for the experimental method.

Though the ethologist attaches great importance to innate behaviour this does not imply a lack of interest in learning processes. The interaction of the growth and maturation of innate motor patterns with the effects of learning provides data of crucial importance for the understanding of behaviour. These experiments on the following-reaction of young ducklings were intended to provide additional material in this field.

Attention was first drawn to some peculiar features of the response of young waterfowl to their parents by observations of Heinroth (1911) on the attachment shown by incubator-reared goslings to the first moving object they saw (the observer), resulting in a persistent preference for this object as a ' parent,' rather than for adult geese. Lorenz (1935, and also 1952) followed up this work by rearing goslings with himself as ' parent-companion ' and also carried out a few experiments with Mallard (*Anas platyrhynchos*) ducklings. These provided the only available data on the following-reaction of ducklings (other than incidental anecdotal references in the literature dealing with the rearing of ducklings in captivity) until Fabricius (1951a, 1951b) published the results of a two-year study on young Tufted Ducks (*Aythya fuligula*), Eiders (*Somateria mollissima*), Shovelers (*Anas clypeata*) and Mallards. Subsequently Ramsay (1951) and Nice (1953) have provided further, less extensive, experimental and observational material on various species of ducks. Comparable studies of species other than waterfowl have also been made [see Collias (1952) and Tinbergen (1953)] but will not be discussed here.

Fabricius's (*loc. cit.*) earlier work was based on experiments with ducklings hatched in incubators and confronted on removal with various ' parent-substitutes,' including the experimenter, models of ducks, living ducks and ducklings of other species. The experiments in 1951–53 made use of a similar approach, but with increasing attention to rigour in the conditions of isolation and initial exposure and the greatest possible simplification of the models employed. In 1951 small numbers of Mallards (18 birds), Pintails (*Anas acuta*) (2), and Carolina Ducks (*Aix sponsa*) (12) were used in the experiments and in 1952 8 Mallards and 19 Gadwalls (*Anas strepera*), but in 1953 attention was concentrated on the Mallard, of which 191 were tested in various ways.

For the present account a simple classification of the possible responses to moving objects is sufficient. A full positive response consists of movement towards the object with persistent close following, accompanied by repeated bursts of chirruping calls, called by us ' content notes.' Close following unaccompanied by calls, or with occasional distress calls, ' lost piping,' represents a less intense positive response. Hesitant approach and non-persistent following, for perhaps only a few inches at a time, are still lower positive responses. Failure to follow, the negative response, also varies in intensity, from absence of overt response to violent escape with loud ' lost piping ' and sometimes the ' note of alarm.'

Nearly a third of the ducklings also behaved aggressively towards models. Aggression is usually limited to a threat, with the head lowered and stretched forward, accompanied by more or less vigorous and persistent running towards the model, but sometimes culminates in an attack, when the duckling strikes the model with its bill.

Any one object may elicit all these responses from different ducklings, and indeed most of them, in various sequences, from any one duckling.

The apparatus used for the experiments with moving models in 1953 consisted of a runway 8 feet long, $2\frac{1}{2}$ feet wide and $2\frac{1}{2}$ feet high, of buff-brown fibre board. Two tracks were fitted above the runway, along which trolleys could be pulled, in either direction. The trolleys consisted of model railway trucks adapted so that thin threads could be suspended from them, to which the models were attached by small hooks. The baseboards for the tracks largely obscured the view of the trucks from the floor of the apparatus, so that the trucks themselves were not treated as models by the ducklings. The movement of the trucks was by no means silent, but the noises produced no significant responses from the birds being tested. The models used for most of the experiments were two flat boxes $24 \times 21 \times 4$ cm., one white, the other brown, and a blue balloon of 14 cm. diameter. A series of five smaller models, all brown cubes, was used to discover how small a model could elicit following, and a red box, a brown cylinder, a stuffed stoat and living male and female Mallards were used at other times.

The earlier work with diving ducks (Fabricius *loc. cit.*) had indicated that the potential 'parent' could be a simple model, whose size could vary within very wide limits. In the present experiments a man walking upright was the largest model used (not in the runway !) and produced high-intensity following by some ducklings. The smallest model followed was about the size of a match-box. Still smaller models were avoided, ignored, or pursued as food-objects, like flying insects. From the diving-duck experiments it had appeared that neither features of shape nor the movement of the whole object were of importance for the first release of the following-reaction of the ducklings, but it had seemed that it was necessary for the model to show internal movement, comparable with the relative motion of head and trunk or limbs in living animals. In 1951 we found that a model devoid of such movement (e.g. a simple box, without a 'head' or any movable appendages) could elicit close and persistent following. In the 1953 experiments the flat boxes and the balloon were of about equal effectiveness.

As Fabricius (*loc. cit.*) found in his earlier work, all the models eliciting the following-reaction also elicited escape-reactions, and the responses of most ducklings at the first showing could be described in terms of dominance of one kind of reaction, or alternation between the two, or the gradual replacement of one by the other. The existence of this antagonism creates difficulties in the study of the following-reaction itself. But it appeared from the diving-duck experiments that readiness to respond to models by following diminished rapidly with increase of the interval between hatching and first showing, while the readiness to escape increased (i.e. very young ducklings tended to follow, not to escape, rather older ones tended to escape and not to follow). In the young Tufted Ducks used in 1945 and 1946, birds under 6 hours (from hatching) showed following without escape while those between 6 and 48 hours showed both. Ducklings more than 60 hours old were not employed in the experiments. This indicated the existence of a limited interval to which the capacity to respond by following to the visual stimuli from a 'parent' might be restricted, this *sensitive period* in Tufted Ducks lasting from the time of hatching to at least 36–38 hours, but with the capacity to respond decreasing throughout the period.

Such a result being of considerable interest with respect to interaction between innate behaviour patterns and learning processes, most of the Mallard experiments were with the object of confirming the existence of the sensitive period, finding out its length and seeing how ability to respond by following varied

with age. The picture obtained is less simple than that given by the Tufted Duck experiments.

Restricting attention to the following of ' silent ' models, it was found that about 60% of Mallard ducklings of age 3–25 hours showed following, compared with about 80% of those between 25–50 hours at first showing and 60% of those from 65 to 72 hours. Amongst older birds following was much less liable to occur, but 1 of 6 kept in isolation for 10 days followed a model at first showing. It appears that the sensitive period in the Mallard is not very sharply limited but must extend to at least 72 hours after hatching, ability to respond by following falling off rapidly at greater ages than this. The possible significance of the highest proportion of followers being found amongst ducklings of 25–50 hours, rather than in younger birds (as had been expected) will be considered in detail in a later paper, but the failure of some very young birds is almost certainly due in part to their inability to move readily or rapidly. ' Followers ' varied greatly in the ease with which they began following. Some responded to the very first movement of a model, others might not begin to follow for many minutes. Older birds tended to show initial avoidance more often than following.

A number of experiments were carried out to see if the time spent in following at the first showing affected the persistence of following. Since most of the birds could only be 'exercised' for quite short periods (5, 10, or 15 minutes of following in a day) it is not surprising that no very clear differences were established, especially as most of the ducklings ceased following within the first ten days of life, even if exercised daily. Very few continued following for more than four weeks, though one still followed very well at 18 weeks.

Two experiments with groups of twelve ducklings in each were made in a search for discriminatory responses towards two models. The birds in one group were shown the balloon at first showing, those in the second group the brown box. At subsequent showings after intervals of two days or more, some were given the ' strange ' model, others the ' familiar ' one, and others a choice. While several followed the strange model in addition to the familiar one, in all cases the response to the former was less intense, notably with the absence of content-notes, and in choice experiments the original model was preferred.

In the experiments in 1952 and 1953 the ducklings were tested singly, as it had become apparent in 1951 that if small groups were used misleading results were obtained, due to the ducklings responding to each other as well as to the model. The reactions to siblings were not studied systematically but it became evident that ducklings which failed to follow, or avoided, the models also tended to avoid other ducklings on first meeting them. But even the most ' asocial ' birds (notably those kept isolated for ten days before testing) developed positive responses to siblings within a few hours.

It proved difficult to get live adult Mallard to serve as satisfactory models in the experimental runway, but some cases were found in which the previously-experienced model was unmistakably preferred to the living duck. In other cases, however, ducklings that had failed to follow models followed a duck at once when released nearby (usually, but not always, the duck was calling as well as moving). One duckling taken from a brood that had been swimming with a duck for about 36 hours showed some following of a model, but others of the brood only showed avoidance. Ducklings hatched by a female Mallard, but removed from the nest before they were old enough to have been led away

from it, followed models as often as did birds of the same age hatched in isolation. Some instances were found of model-followers developing a tendency to follow men after some weeks, and these did not seem to be the result of conditioning to man as a food-source.

The limited brooding equipment available made it necessary to rear the ducklings in large groups after they had received their first test. This prevented the study of the effects of continued isolation, and was probably in part responsible for the general falling-off of model-following at an age when wild ducklings would still be very closely devoted to their mother.

Acoustic stimuli may also elicit a following-reaction with or without the presence of a moving object. But strong avoidance of noises was not seen. The experiments were, however, principally concerned with response to visual stimuli, even though, as Lorenz (1935) had found and Fabricius (*loc. cit.*) had confirmed, acoustic stimuli have a stronger 'releasing' effect on the following-reaction of ducklings than do visual ones. This concentration on visual stimuli was decided on because of the relative difficulty of controlling the acoustic stimuli to which the birds might be subjected. The principal results of the experiments with sounds were (1) the confirmation of Fabricius's (*loc. cit.*) finding that the effective acoustic stimuli are very simple (any rhythmical short bubbling sounds or monosyllabic words will serve, no exact imitation of the sounds produced by ducks being necessary), (2) positive response to sounds occurs more readily than response to moving objects, the response often appearing after a very few sounds, and also in long-isolated ducklings that fail to follow models, (3) ducklings failing to follow moving models could be induced to do so by the use of sounds and in some cases followed the 'silent' model closely when the sounds were no longer made.

One of the most interesting and obscure features of the experiments was the great variation in response to models shown by ducklings with similar 'histories.' Of any brood successively shown one model at the same age (measured in hours from hatching) some would follow unhesitatingly, others reluctantly and others not at all. How much of this variation is due to genetic differences remains to be discovered. It is quite possible that some at least may be due to differences in treatment of the egg during incubation, particularly after 'pipping' or chipping and a careful study of the immediate pre-hatching stage might prove informative. During the experiments we became increasingly impressed by the possibility of predicting the performance of a duckling from its appearance on first being transferred from its hatching box to the floor of the runway. Much more intensive observations and experiments will be required before the significance, or indeed the existence, of such a relationship can be established.

Experimental studies such as this deliberately make use of simplified situations. In the wild the young duckling is never presented with so restricted a set of stimuli. Not only does the mother provide shape, movement and sound, but also warmth, conduction to food and away from danger, and perhaps odour, with the likelihood of conditioning being rapidly established. Other members of the brood too provide similar attractions. Thus even ducklings with marked genetic incapacity to follow moving objects, if such ducklings exist, would not necessarily come to grief. One of the most fascinating and rewarding features of severely restricted experimental study is the heightened realisation it affords of the complexity and variety of the interactions between different processes that make up even a simple behaviour pattern.

ACKNOWLEDGMENTS

NOTE

This report consists of no more than a preliminary outline in general terms. A more detailed account of the work is in preparation and will it is hoped be published elsewhere.

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