THE DEVELOPMENT OF SOCIAL BEHAVIOR IN BIRDS

BY N. E. COLLIAS

THE purpose of this brief survey is to illustrate by means of selected examples the manner of operation of factors that control development of social bonds in birds. Socialization of the young individual will be considered first, followed by a discussion of sexual and parental bonds. The general problem of gregariousness and bird flocking is considered by J. T. Emlen, Jr., in another paper (Auk, 69: 160–170, 1952) in this symposium on social behavior in birds.

Each of the different aspects of social development can be analyzed into genetic, physiological, and social levels of organization, and into the interactions between these levels. However, our knowledge of the various factors of social development is still very uneven, and no really general treatment is yet possible. In an attempt at a rounded treatment some unpublished notes of my own will be included.

Much of our more analytical knowledge of the biology of reproduction in birds has been derived, for obvious reasons, from studies on the domestic fowl and the domestic pigeon. At the least, these studies may help to provide guideposts in our search for understanding of wild birds existing in a state of nature, although some wide variations between species may be expected to occur. In the writer's opinion, parallel studies on the behavior of unconfined and undomesticated species of birds have generally shown many more similarities than differences compared to studies on confined or domesticated birds.

SOCIALIZATION OF THE YOUNG BIRD

Social development is one aspect of the development of behavior in general, and as such involves behavior patterns that are laid down prior to hatching; and these in turn depend on the development of structures more directly under genetic control. However, most of the major trends in socialization belong to the post-hatching reactive phase in which activity is generally governed or directed by external

Male Boat-tailed Grackle, *Cassidix mexicanus*, in characteristic display. Photographed by Karl Maslowski at Lake Eola, Orlando, Florida, in mid-January. The white feathers in the tail and elsewhere are abnormal.

The "bill-pointing" or "head-up" display of the Boat-tail so admirably caught by Karl Maslowski's camera was noted by Thomas Belt in a closely related Nicaraguan grackle as long ago as 1874. Identical or similar displays occur also in North American grackles of the genus *Quiscalus*, in Brewer's Blackbird, and in certain cowbirds. Usually interpreted as a phase of courtship behavior, it occurs, in the Bronzed Grackle at least, throughout the year and is used by both sexes. Probably it serves as a warning or threat signal.—Charles F. Walker.

stimuli and is subject to social control.   The post-hatching sequence includes certain initial social adjustments, the appearance of new social responses, increasing specificity of social reactions, increasing social independence, and reintegration into new social groups.

Prehatching behavior.   Development of behavior depends on and is associated with development of the neuromuscular system, including the establishment of neural connections, the differentiation of enzyme systems, and the establishment of electrochemical rhythms of activity in the central nervous system.   Among the very early somatic movements of the chick embryo are simple ventral or lateral twitches of the trunk.   Windle and Orr (1934) suggested that these movements were perhaps brought about by the spontaneous discharge of motor neuroblasts, since these authors observed that such movements occurred before the growing sensory nerves had established any central connections in the spinal cord with the motor nerves to the trunk musculature. In the case of certain urodele larvae, Weiss (1941) has found evidence for autonomous activity of fragments of spinal cord placed by this experimenter in the dorsal fin of the larvae.   Presumably, endogenous spinal activity is normally under control of the brain.

The development of myelin about nerve fibers in certain brain tracts and peripheral nerves facilitates the functioning of these nerve fibers.   Differences in social development between different species may parallel differences in rate of myelinization of the nervous system. In the Starling, *Sturnus vulgaris*, in which the eyes do not open until some days after hatching, and in which the first social activity seems to be the act of gaping (Holzapfel, 1939), the optic nerves are not myelinated until the eighth day after hatching; whereas in the chick of the domestic fowl, *Gallus gallus*, which may open its eyes on hatching, the optic nerve is myelinated six days prior to hatching (Schifferli, 1948).   On the other hand, in correspondence with its gaping activities and precociously developed digestive system, myelinization of the hypoglossal and vagus nerves begins earlier in terms of embryonic age in the young Starling than in the chick (*op. cit.*).

Social responsiveness in the newly-hatched chick requires the presence of the basal portions of the cerebral hemispheres, or paleostriata (Collias, 1950a), and this finding emphasizes the importance of studies of the development of the cerebrum in relation to social development. At the time of hatching in the chick, myelinization has proceeded in all parts of the brain, with the exception of the rostral part of the corpus striatum (Schifferli, 1948).   In contrast, the young Starling hatches with its brain in a much more embryonic state, with myelinated sheaths present only in the brain stem (*op. cit.*).   This species difference in

myelinization of the brain is associated with a marked difference in degree of behavioral and social development at the time of hatching, and may turn out to be a typical difference between nidicolous and nidifugous birds.

There are expansive and restrictive phases to behavioral development. In the chick embryo, movements of the head, trunk, fore limbs, hind limbs, and tail develop on the average in that order (Kuo, 1932). As development proceeds the percentage of independent movements of wing, leg, tail, beak, and eye increases rapidly up to the time when the generalized, active movements of hatching begin (Kuo, 1939). Inspection of Kuo's table (1932:400–405) of the chronology of chick behavior suggests that the development of the prehatching behavior of the chick passes through inactive, active (endogenous), and reactive (responsive to external stimuli) phases.

The extensive studies of Kuo (1932) on the prehatching behavior of the chick, involving about 3,000 eggs, indicate that the basis of social behavior must be laid down in the development of the chick embryo before hatching. Movement responses to touch and pressure generally appear before, but distance receptors for sound and light normally do not function until after, tearing of the egg membranes by the chick in the last few days of incubation. Vocalizations, which are the chief means whereby the newly-hatched chick can emit social signals effective at a distance, appear after the onset of respiratory movements, and usually shortly after the tearing of the egg membranes.

In many respects social development resembles embryonic development. There are many parallels between trends in the physiology of development and trends in social development. As will be brought out in subsequent pages, such principles of embryology as early plasticity, increasing complexity, induction, functional segregation, and functional reintegration of parts resemble the principles of social development.

Initial social adjustments and responses after hatching. Apparently spontaneous movements of the legs, wings, head, and neck during hatching alternate with periods of rest and enable the young chick to hatch. The newly-hatched chick is likely to remain attached to the egg shell by the extra-embryonic membranes for some minutes after hatching; normally it soon pulls loose. Motivation for this activity is indicated by the giving of "contentment" or "pleasure" notes whenever one places traction on these membranes before the chick has broken loose. The normal pulling away tendency of the chick is therefore not entirely an accidental thing. One hen was observed to aid a hatching chick by pecking at the membranes.

Aside from the initial disturbance occasioned by hatching, many young birds at first seem to spend much of their time sleeping.

Spontaneous gaping in young Starlings appeared during the first few hours after being hatched in isolation in a quiet and darkened room (Holzapfel, 1939). Spontaneous gaping tended to disappear in these isolated birds after four or five days, indicating that an inhibitory control had become established, and gaping thereafter appeared in closer relationship to environmental stimuli.

The young of many nidifugous species of birds give characteristic distress calls when isolated from the parent or from the rest of the brood—for example, in young of the: domestic hen, Ring-necked Pheasant, *Phasianus colchicus* (personal obs.); Bob-white Quail, *Colinus virginianus* (Stoddard, 1931); Blue-winged Teal, *Anas discors* (Hochbaum, 1944); Woodcock, *Philohela minor* (Pettingill, 1936); Sandhill Crane, *Grus canadensis* (Walkinshaw, 1949); and European Coot, *Fulica atra* (Alley and Boyd, 1950). In these species the parents have characteristic notes that serve to attract the young. The same reciprocal relationship probably occurs in many other kinds of birds. The young of some nidicolous species may give distress calls; a downy young Marsh Hawk, *Circus cyaneus*, which I placed a few feet from its nest kept up a continual twittering, similar to food-begging notes, while it slowly crawled back to the nest containing the rest of its brood and, having once regained the nest and the company of its nestmates, promptly ceased its vocalizations.

A special study was made of the social behavior of chicks of the domestic fowl. This study was aided by a grant from the Research Committee of the Graduate School of the University of Wisconsin, from funds supplied by the Wisconsin Alumni Research Foundation. The social responses of about 1000 chicks were studied in the course of this work. Only preliminary abstracts have appeared (Collias, 1950a, b), and it seems useful to present some further details here, although more complete data will be published later. I am greatly indebted to my wife, Mrs. Elsie Collias, for her assistance with some of the experiments, and for preparation of the original figures.

These studies clearly show that the distress calls of baby chicks stimulate clucking by a mother hen. The clucking of a broody hen inhibits the distress calls of her chicks and also causes them to emit notes of very different character which, for reasons to be mentioned, are termed "pleasure" notes. Distress calls are loud, insistent peeps which are given repeatedly and carry a considerable distance. Pleasure notes are much lighter peeps of a different quality, are given in much more rapid sequence, and carry only a short distance. The
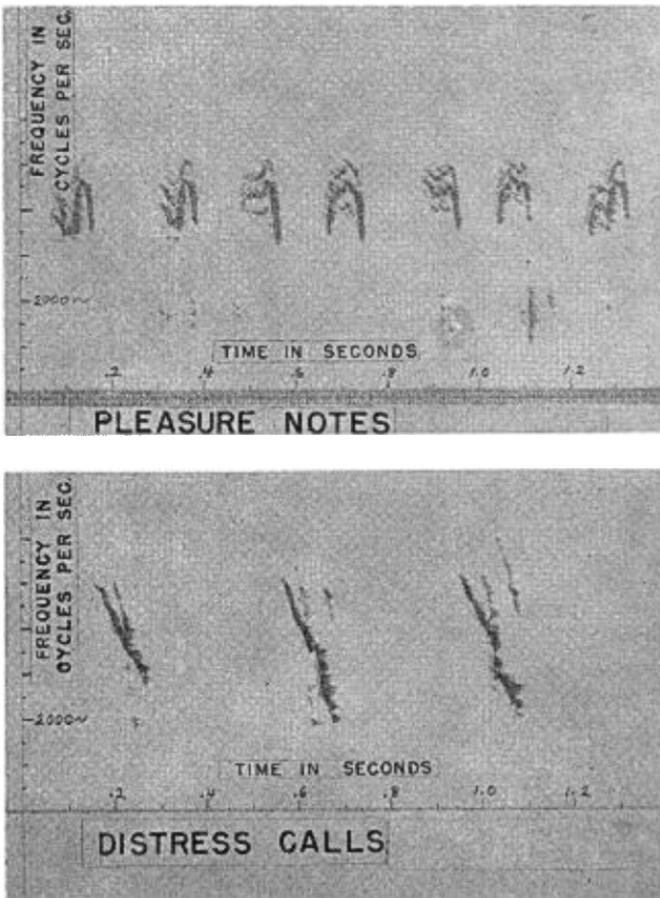
FIGURE 1.   Sound spectrograms of pleasure notes (upper) and distress calls (lower) of a chick of the domestic fowl.

sound spectrograms of these two sounds give a precise idea of the energy at each frequency for a given instant of time (Fig. 1).   It may be noted from these records that a distress call characteristically differs from a pleasure note in that it is composed of descending frequencies only, and in descending to a lower frequency than that present in any part of a pleasure note.   I wish to thank Professor Martin Joos for making these and other spectrograms of the sound signals of the domestic fowl and for aid in the interpretation of these spectrograms.

Upon hatching on a table under direct observation, chicks were found to give their characteristic distress calls apparently because of loss of contact with the eggshell and because of cooling of the moist down.   Figure 2 illustrates the initial social responses of chicks within the first five to fifteen minutes after hatching.   The two temperature

tests were each taken in the first five minutes after hatching.   In the
other tests the chicks were tested for successive five-minute periods as
represented by the vertical bars, reading from left to right, with the
first five minutes post-hatching being represented by the first bar to
the left, within each box.   At least ten chicks were used for each type
of test.

When a chick was hatched under a warm lamp (100° F.) the number
of distress calls was very greatly reduced, as compared with a chick
allowed to hatch at the subnormal temperature of 78–82° F.   If a
chick were kept warm and the hand placed over the chick immediately
after hatching, few if any distress calls were given.

These social responses can be traced back into the pipped egg.   If
such an egg be held in the hand and its position changed, presumably
shifting the pressure points in the contact of the chick with its shell,
the chick inside frequently will give a flurry of pleasure notes.   Again,
if a pipped egg is alternately cooled and warmed the chick within may
sometimes give distress calls or pleasure notes in close correspondence
to the temperate changes.

Recently hatched (incubator) chicks paid no apparent attention to
mounted specimens of hens.   Indeed, a chick placed beneath a
mounted hen may desert this foster mother for a warm heating pad
placed a few inches away.

Figure 2 shows that positive responses to clucking may be given
within 5 to 10 minutes after hatching.   Occasionally there is found a
pipped egg containing a chick which will respond consistently to
clucks by cessation of distress calls.   Here again the social response
can be traced back into the egg.

If a pipped egg be hold next to the ear, one frequently hears tapping
sounds given repeatedly and often at a rate about like that of the
normal rate of clucking of a broody hen; these sounds also resemble
clucking in their low frequency.   These tapping sounds appear to be
made by the clapping of the bill, a behavior pattern which Kuo (1932)
observed to arise as early as the ninth day of incubation, long before
the chick shows any evidence of reaction to external sounds.   As
mentioned below, repeated tapping sounds usually will quiet the dis-
tress calls of recently-hatched chicks.   It follows that repetitive sounds
of low frequency represent a stimulus situation to which a chick is
normally exposed long before hatching.

The response to moving objects developed more slowly than did
social responses to other sensory modalities, since it was not evidenced
in these tests (Fig. 2) by consistent cessation of distress calls at 5 to
10 minutes after hatching.   However, by one hour after hatching,

sight of any object moving near by usually causes a chick to stop its distress calls. Chicks usually open their eyes at the time of hatching, but in the first few hours after hatching they are likely to spend much time resting quietly with eyes closed.
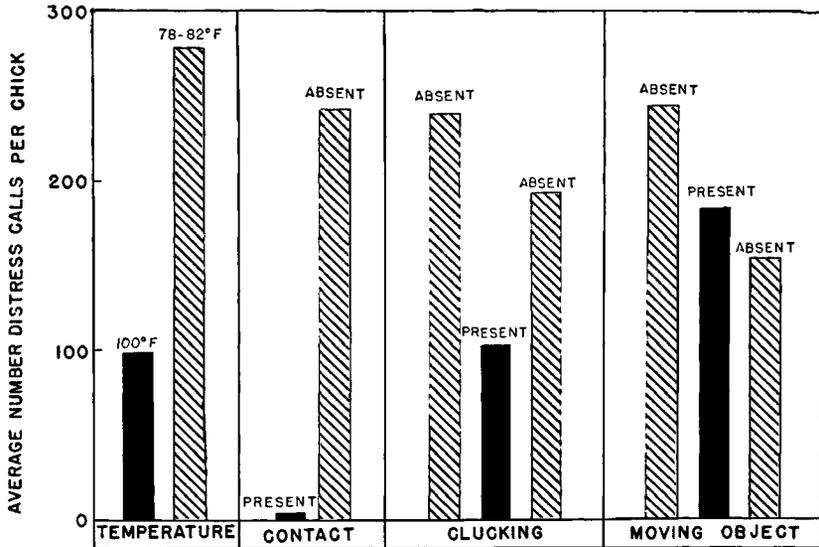

FIGURE 2. Social responses of chicks of the domestic fowl upon hatching in isolation under specified conditions (see text).

The significance of clucking by a hen in the life of baby chicks justified a fuller analysis and account of the properties of this vocalization as a social signal. The initial reactions of each chick were tested separately. An individual chick was removed from the incubator, placed on a lighted table 18 to 24 inches from a loudspeaker connected with a record player, and a record was played to the chick for a definite time interval, during which its responses on initial exposure to a given type of sound were observed through a cheese cloth screen. The degree of approach to the loud-speaker was recorded and notes were taken on vocalizations. As a rule, ten or more chicks in the first three days after hatching were used for each type of test. These tests with phonograph records have shown clucking to have an optimal quality, rate, and loudness. Chicks in the first few days of life respond to wide variations in these sound properties. Interestingly enough, chicks responded well to far greater rates and amplitudes of clucking than are ever given normally by a hen.

Tests with various artificial sounds gave some idea of the response of chicks to different qualitative properties of the sound. Any loud,

harsh sound, such as the warning screen to "aerial predators" of an adult chicken, the scraping of a chair over the floor, a sneeze, or the blaring of an automobile horn, often resulted in escape reactions, *i.e.*, the chick would make an abrupt short run and frequently would hide under or against some object. To repeated hissing sounds the chicks were rather indifferent. To records of a hen clucking, to human imitations of clucking, and even to records of repeated pencil tapping the chicks responded readily with cessation of distress calls, by giving pleasure notes, and by approaching close to the source of the sound. The food call of a broody hen and the low purring sound she uses to attract her chicks when settled in one spot for the night also promptly inhibit distress calls.

In one test series, ten chicks were exposed individually to a specific sound stimulus for one minute, after a minute of isolation to stimulate distress calls. Under these conditions, the frequency of distress calls was decreased 98% by clucking, 85% by clinking two glass bowls together, 65% by an intermittent artificial tone of 256 cycles, and only 25% by the same tone given continuously. All of these sounds were played from disc records.

Very slow or very fast clucking was produced by taking a tape record of the normal rate (1 to 3 per second) and inserting or removing sections of blank tape between the sounds. Chicks responded much better to fast than to slow clucking, but the response slowed down at extremely rapid artificial rates (approximately 10 per sec.).

Loudness of recorded clucking was readily varied by use of the volume amplifier on the record player. Often a chick which was giving repeated distress calls in one spot some little distance from the weak clucking which emanated from the loud speaker abruptly ceased its distress calls and moved toward the loud speaker, as soon as the volume of the clucking was amplified. But extremely loud clucking was less effective, and in chicks a few days old sometimes resulted in escape reactions.

Chicks responded with pleasure notes or cessation of distress calls to very low frequencies of artificial, short, repetitive tones played from disc records, but were generally silent or gave distress calls to high frequency tones (above 400 cycles per second), otherwise similar in pattern. This preference for low tones is correlated with the occurrence of very low frequencies (down to 0 cycles per second) in the clucking of a broody hen, as was revealed by a sound spectrogram of normal clucking (Fig. 3). In contrast, the sound spectrogram of the warning call to hawks as given by a rooster was found to contain only frequencies at or above 400 cycles per second. The prolonged nature
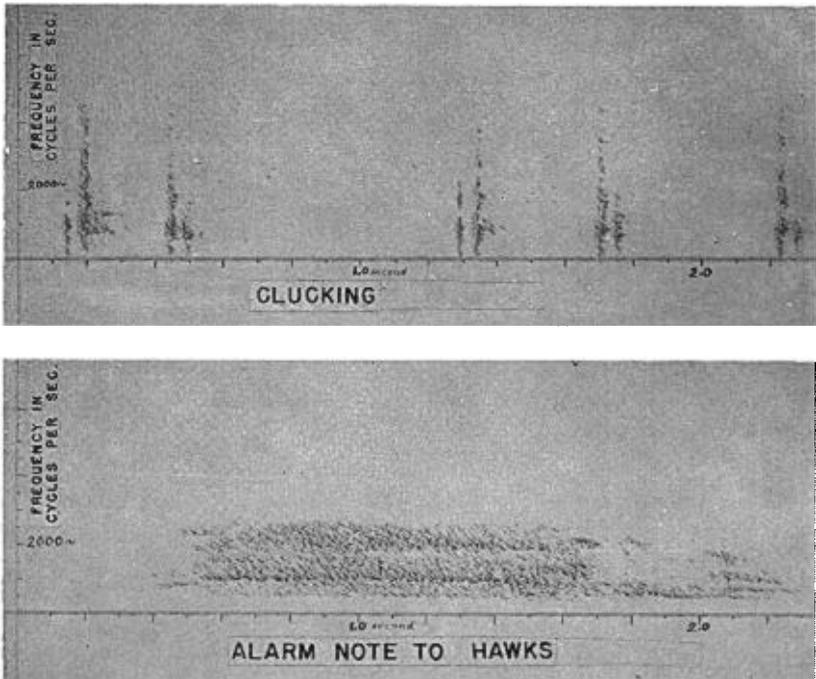
FIGURE 3.   Sound spectrograms of the clucking of a domestic hen (upper) and of the alarm cry to an aerial predator as given by a domestic cock (lower).

of the hawk call also seems to be a factor inhibiting pleasure notes. In taking the initial recordings, the "hawk" was merely a piece of cloth thrown up past the cage of the rooster.   This simple procedure was found to be very effective for inducing this particular warning cry. The domestic hen gives a warning scream similar to that of the male.

Many of the properties of social responses in baby chicks may conveniently be classified under the same categories used in the analysis of the general properties of the central nervous system.   *Latency* is illustrated by the pause of several seconds to several minutes that usually precedes the beginning of distress calls when a chick is isolated. *Rhythmicity* is illustrated by the fact that these distress calls are given repeatedly at fairly regular intervals, showing some tendency to recur in groups.   *Fluctuating threshold* is illustrated by the alternation of periods of distress calls with periods of pleasure notes when a chick was kept isolated from its companions for an hour or more (Fig. 4).   After preliminary handling this chick was isolated for two hours in a clean cardboard box in a quiet room.   In Figure 4 the horizontal line represents the time scale reading from left to right.   Vertical lines are each

one minute apart.   Vertical lines extending *above* the horizontal line each represent the number of distress calls emitted by the chick for that particular minute.   Vertical lines extending *below* the horizontal line each represent the number of five-second intervals in that particular minute during which pleasure notes were emitted; this method of

DISTRESS CALLS
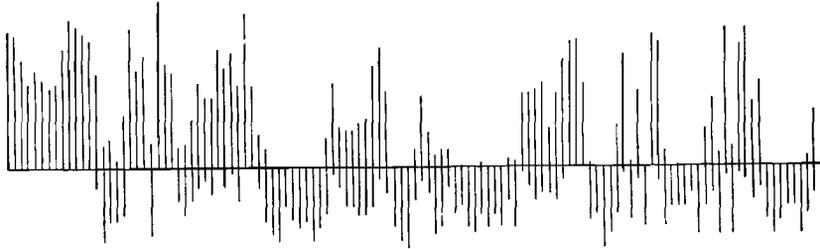
PLEASURE NOTES

FIGURE 4.   Response reversal in a domestic chick isolated for two hours on the day of hatching.   Fluctuation between states of "insecurity" and "security" is clearly evident, despite lack of any apparent change in the external stimulus situation (see text).

measurement was adopted because pleasure notes are frequently given at a rate too rapid to be accurately counted without instrumental aid. The actual *reversal of response* secured in this instance suggests oscillation between two balanced neural systems, and is reminiscent of the phenomenon of negative after-image in human visual physiology.

Summation is illustrated by the greater tendency of a chick, which was placed on a table between vertically moving forefingers, to move toward the finger which was allowed to tap the substrate, in contradistinction to the opposite forefinger which was simultaneously moved up and down without permitting it to touch the table.   When I alternated the finger that tapped the table the chick would often be induced to run back and forth following sound plus movement versus movement alone.   But a baby chick would often go to movement alone, when this was not placed in competition with another stronger stimulus situation.   *Afterdischarge* is illustrated by the tendency of chicks which had been petted for a while to continue giving pleasure notes for a few seconds when this contact stimulus was discontinued and the chick was abruptly isolated.   *Inhibition* is illustrated by the fact that distress calls and pleasure notes seem to be incompatible— situations that stimulate the one type of vocalization as a rule promptly inhibit the other.   Another illustration is the usually prompt inhibi-

tion of all vocalizations by baby chicks when the mother hen gives a warning note. *Specific fatigue* or *refractoriness* may be illustrated by some chicks which stopped giving pleasure notes and sometimes resumed distress calls on long continued exposure to clucking. These chicks were kept under a warm lamp to prevent chilling. The alternation of periods of distress calls with periods of pleasure notes, shown in Figure 4 for an isolated baby chick, could be interpreted as reflecting a corresponding alternation in the state of fatigue, or of an accommodation process, in two balanced and opposing neural systems. Lorenz (1950) has emphasized the importance and extent of occurrence of specific exhaustability of social responses. He observed that repeated elicitation of the "following response" in a hand-raised young Jackdaw, *Corvus monedula*, required progressively greater stimulation. The feeding responses of chicks of the Herring Gull, *Larus argentatus*, can be elicited with cardboard models of the head of the adult, but with repeated stimulation there occurs a steady drop in responsiveness (Tinbergen and Perdeck, 1950).

The characteristic distress calls of baby chicks may be given repeatedly under many conditions of distress that at the same time inhibit pleasure notes: isolation from companions, cold, hunger, thirst, pain, restraint, or approach of a large object. Conversely, the opposite situations as a rule lead to pleasure notes and inhibit distress calls. To some extent, but not completely, at least some of these various stimulus situations can substitute for each other, *e. g.*, a cold chick may cease its distress calls for a short time on being exposed to clucking. The giving of distress calls seems to indicate lowering of the threshold of social responsiveness. Thus, if a baby chick immediately after isolation does not stop its distress calls promptly at sight of an object gently moving near by, it often responds better after it has been isolated and has given its distress calls for a few minutes.

The facts of the preceding paragraphs, taken as a group, suggest the existence of two antithetical neural systems balanced against each other, and corresponding to what in man would be called security-insecurity feelings and responses. This balance provides a delicate mechanism for rapid and adaptive responses to environmental changes.

In general, a chick moves toward stimulus situations that cause it to emit pleasure notes, and away from such situations as bring about distress calls. What a chick does in a complex social situation will evidently depend on the balance of the total external and internal conditions, as expressed objectively in the balance of approach and avoidance tendencies.

We have been dealing in some detail with intitial social responses to an auditory social signal. An excellent example of initial social responses to a *visual* social signal may be drawn from the work of Tinbergen and Perdeck (1950) on the feeding responses of recently-hatched chicks of the Herring Gull. These chicks are not fed until several hours after hatching, and by selecting for testing those chicks that had just dried or were nearly dry these observers believed that a fair proportion of inexperienced chicks was secured. The parent Herring Gull has a red spot on each side of the lower mandible near the tip, and that spot helps stimulate and guide the feeding responses of the chick. By enumerating the relative frequency of pecking responses by the chicks to different types of flat cardboard models of heads of adult Herring Gulls presented in succession under standard controlled conditions, some idea was secured of the stimulus properties of the red spot as a social signal. Absence of this red spot decreased the percentage of positive responses by three-fourths. Color, background contrast, and position of the spot proved important, but differences in color of the bill or head had little or no influence, except that a red bill was somewhat more effective than bills of other colors. A red bill-spot was more effective than any other, including black which has greater contrast value. The importance of contrast was brought out by using a series of models with gray bills and bill-spots of eight different shades of gray ranging between white and black. The percentage of responses increased with the degree of contrast in both directions, *i.e.*, from a gray to a white bill-spot and from a gray to a black bill-spot. The number of responses was decreased three-fourths by shifting the red spot from its normal position near the tip of the bill to a place on the forehead. If the model were held still, responses decreased some 70%, indicating the importance of movement.

Initial social adjustments may involve the development of tolerance for the young by the parents. One broody domestic hen which was incubating eggs at first pecked at chicks placed in front of her, but soon adopted them and ceased to peck at them. I have observed that hens developing broodiness, induced by confining them with baby chicks, at first frequently attack the chicks, then develop tolerance for the chicks, and finally begin to cluck and actively care for the chicks.

The reciprocal nature of parent-young adjustments should be stressed. In a pair of Mourning Doves, *Zenaidura macroura*, which I watched at their nest in a garden in Ohio, the parents took the initiative in feeding the young on the day the young hatched. The parents stimulated the initial feeding responses of the young by pecking gently at the angle of the mouth and particularly by gently pinching the cere

of the young between the parental mandibles. The parents at first inserted the upper mandible, at least, in the beak of the young. On the following and in subsequent days the young helped initiate more of the feedings, and also took a more active rôle by inserting the beak into the mouth of the parent in typical columbiform fashion.

Strengthening of initial responses with social experience. Social attachment quickly increases with social experience in recently-hatched chicks. In the course of routine tests it was noted that at first, responses of chicks to clucking or to sight of a moving object were slow, but after some minutes of repeated exposure a chick responded much more rapidly and over greater distances. At the same time the need for the operative social stimulus was increased, as indicated by much more frequent distress calls between stimulus periods.

Six chicks which I raised by hand until they were ten days of age, when subsequently placed with a broody hen, responded much more slowly or not at all to food-calls of the hen for the first week in her company, as compared to six controls of the same hatch which were placed with the hen on their first day of life and kept with her for the same length of time. The same thing was found in a similar experiment to be true of pheasant chicks placed with a domestic hen. Normally, a broody hen represents to the chick an adaptable complex of attractive stimuli, including warmth, contact, clucking, and movement; and repeated exposure to these stimuli, as well as the food guidance and protection that a hen gives her chicks, helps to strengthen the family bond. At the New York Zoological Park I observed in a pair of Black-footed Penguins, *Spheniscus demersus*, that the parents spent much time preening the head and neck of their young; this probably strengthens the attachment of the young to the parent.

The responses of chicks to each other are part of the family bond and of their socialization. Young chicks of the domestic fowl were very slow to approach one another or failed to come together, even when only five or six inches apart, until after they had experienced some minutes of bodily contact, following which the members of each pair rapidly came together when separated by short distances. This problem was tested with ten pairs of chicks, aged two to three hours, and ten pairs of chicks aged three to four days.

Early social plasticity. Chicks 1, 2, 4, 6, 8, and 10 days of age were tested individually for response on first exposure to clucking. These tests were made in a runway, one foot wide and ten feet long, flanked by cheesecloth walls and with a loud-speaker at either end of the runway, both loud-speakers being connected with a record player. A toggle switch enabled the recorded clucking to be switched back and

100

80

PERCENTAGE

OF TRIALS

60

IN WHICH CHICK

CAME TO STIMULUS

40

20

0

- - - - - - TO CLUCKS

————— TO LARGE RETREATING OBJECT

2   4   6   8   10

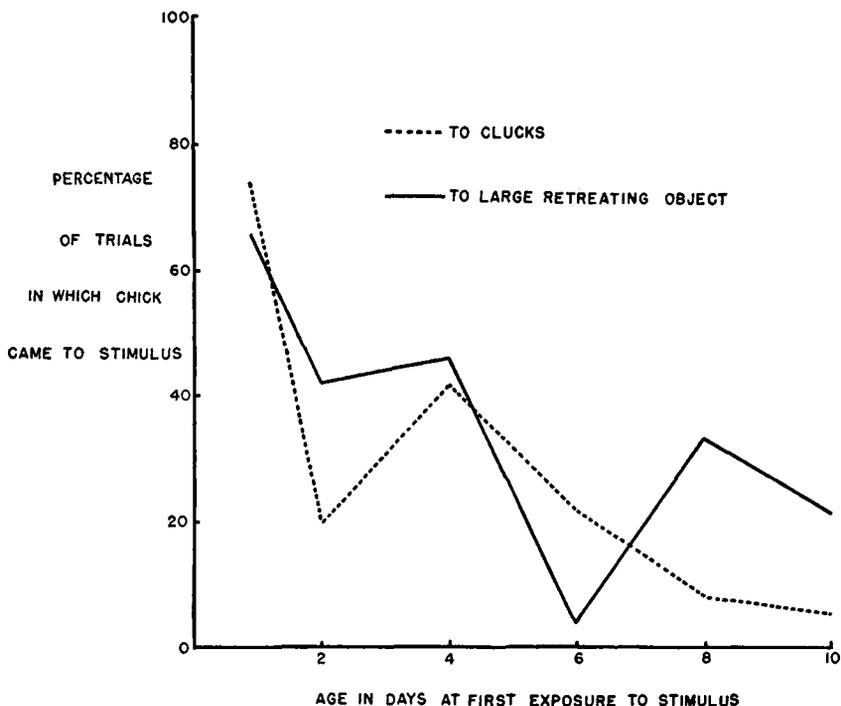AGE IN DAYS AT FIRST EXPOSURE TO STIMULUS

FIGURE 5. Social responsiveness of domestic chicks on initial exposure to a parental object is greatest in the first few days after hatching. See text for explanation of figure.

forth at will from one loud-speaker to the other. Each chick was placed in the center of the runway and was given 10 trials during each of which it was exposed to clucking for one minute. Each trial in which the chick approached to within one foot of the loud-speaker was considered a positive response.

For testing the first responses of these same chicks to a large, retreating object, the observer placed a chick on the floor and then placed himself directly in front of and facing away from the chick. The observer then proceeded slowly away from the chick, often stopping momentarily, or even backing up a few steps, this being continued until about 10 feet had been covered. The usual response of a normal chick in the first few days of life is to follow the observer.

About 100 chicks were given 10 tests, each being tested for response both to clucking and to movements; the results are summarized in Figure 5. The marked decrease in social responsiveness with increasing age is readily evident.

The changing balance of social attraction with fear responses is probably involved in the phenomenon of early social plasticity. In chicks of the domestic fowl, fear responses, such as the tendency to avoid any large approaching object, are very weak on the day of hatching and become stronger by the time the chick is a few days older. The importance of the development of fear responses in relation to early social plasticity has also been indicated in field studies on young Coots by Alley and Boyd (1950).

The younger birds and mammals are, when first taken from their natural parents, the easier they are to tame, *i.e.*, to develop social attachments to human beings. Lorenz (1935) has given a graphic illustration of this phenomenon in Jackdaws. According to Alley and Boyd (1950) young European Coots are wild and difficult to tame after eight hours from the time of hatching. Some species of hand-reared birds may develop social attachments to other species of birds kept in the same room in addition to attachment to the human caretaker (Nice, 1950).

The relative rôles of learning and of more direct genetic control in species attraction vary greatly between different species. Thus, a domestic pigeon reared by Ring Doves, *Streptopelia risoria*, once it matures may continue to associate and try to mate with Ring Doves, rather than with its own species (Craig, 1908; Whitman, 1919). But a Cowbird, *Molothrus ater*, and other parasitic species of birds, normally reared by foster parents, return to their own species for purposes of mating. Birds tend to find and maintain contact with their own species by means of distinctive vocalizations, and the degree to which the song can be modified by abnormal circumstances of rearing seems to vary greatly between different species (Nice, 1943).

Appearance of new social responses. Very young Starlings gape in response to contact, to gentle shaking, to scratching sounds, and to parental vocal signals, but after the eyes open they also gape in response to moving objects. At the same time they become less sensitive to contact stimuli. Orientation responses appear; a young Starling with eyes open at 10 days of age will not follow the pincers with which it is fed, but at 14 days of age it will do so (Holzapfel, 1939).

As a young Robin, *Turdus migratorius*, grows larger it needs more food, and develops louder hunger notes which then seem to indicate a greater degree of hunger for the following reasons. After being fed, the young Robin is silent for a time, then gives light peeps, followed after some minutes by much louder one-syllabled notes, and finally by a series of still louder two-syllabled notes (Fig. 6). A young Robin raised by me in the summer of 1950 and assumed to be two or three
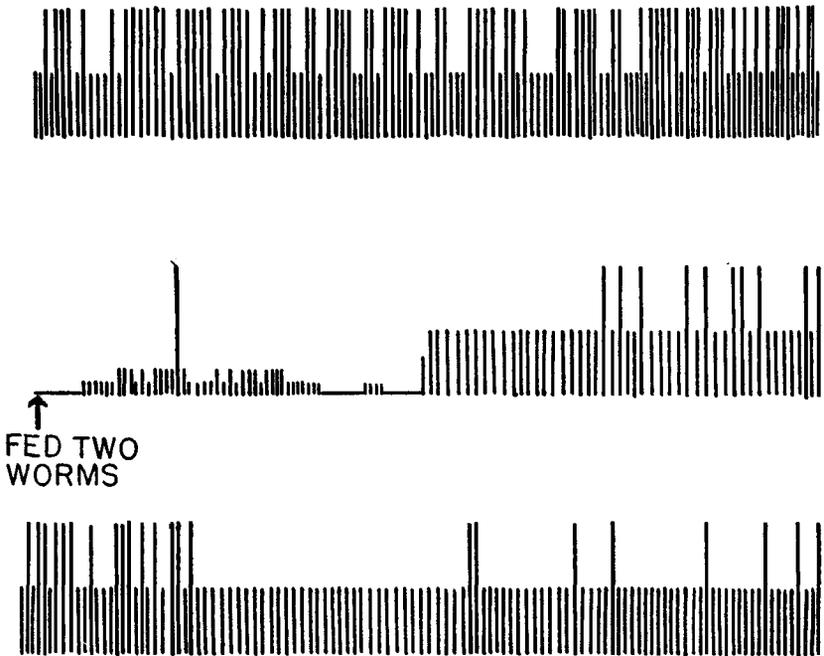
FED TWO
WORMS

FIGURE 6. Effect of hunger and of feeding on vocalizations by a fledgling Robin. The strength or loudness of each note is indicated by a vertical line, the record proceeding from left to right and from top to bottom; the longest such lines represent loud notes of two syllables and are apparently indicative of greatest hunger. Horizontal lines represent periods of prolonged silence, the period of silence being roughly proportional to the length of the line.

days old when first secured, at first gaped silently and gave the light "hunger" notes after it had been fed; two days later it gave what seemed to be the same notes before being fed, and after some days developed the louder notes, at first the one-syllabled and then the two-syllabled loud call. The latter call appeared at about 11 days of age, assuming the original estimate of age to be correct. Thus the ontogenetic sequence of hunger notes paralleled the same sequence which in the older nestling seemed to reflect the degree of hunger; perhaps this parallelism indicates a gradually increasing development of the internal hunger mechanism. At the same time it is not unlikely that the loud two-syllabled call, which appeared as the latest of the hunger notes, functions to facilitate the parent-young bond in response to the added stress involved when the young bird has left the nest. Figure 7 shows that the loud hunger calls are in all probability hunger-location calls; it could often be observed, as in this instance, that the

young Robin would cease its insistent calling shortly after the caretaker hid himself, only to resume its vocalizations once he reappeared.

Aggressive behavior appears in young birds long after initial responses to the parent. In young passerines pecking at objects replaces gaping. Normally, aggressive behavior makes its first ap-

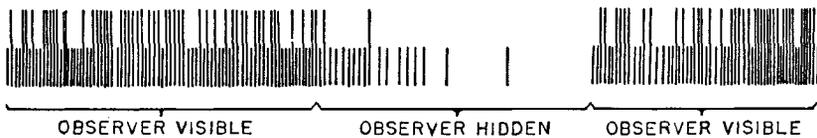OBSERVER VISIBLE   OBSERVER HIDDEN   OBSERVER VISIBLE

FIGURE 7. Demonstration that hunger notes of a fledgling Robin could function to inform the parent as to the location of the fledgling. See Figure 6 for explanation of vertical lines. The length of periods of silence is roughly proportional to the space between the vertical lines.

pearance in chicks of the domestic fowl as "play-fighting." Unlike the fights of adult chickens, play-fights do not seem to lead to a definite decision concerning dominance relations. We have observed that as the chicks mature their skirmishes gradually become more "serious," and following a prolonged period of instability a definite dominance hierarchy emerges in the flock. The development of a dominance hierarchy depends on the development of aggressive tendencies in the individual birds of the flock and on their ability to learn each other as individuals.

Sexual and parental behavioral responses may appear in very young birds of some species (Meyer-Holzapfel, 1949). Meyer-Holzapfel suggested that such precocity may be due to the delayed maturation of internal inhibitory mechanisms relative to mechanisms for the sex and parental drives, respectively.

Reproductive behavior is stimulated by the development of pituitary and gonads and of mechanisms responsive to the secretions of these endocrine glands. Birds may differ widely in the time relations concerned. For example, in the Ring Dove and Pigeon the testes do not grow appreciably until two or more months of age. In male chicks of the domestic fowl, growth and secretion in the testes begin within a week of hatching, and by 90 days of age the testis weight has increased some 80 times (Breneman, 1945). At the same time, the difference between these species in testicular growth reflects differences in the pituitary development and differentiation which helps control gonadal growth (Breneman, 1945). This difference in pituitary-gonadal development may prove to be one characteristic difference between nidicolous and nidifugous species of birds.

Increasing specificity of social responses. Following the first ap-
pearance of a new social response comes a period of increasing speci-
ficity of this response.

This can be illustrated by the development of song from indefinite
to definite form in the Song Sparrow, *Melospiza melodia* (Nice, 1943).
The first song in this species, as in many other passerines, is an in-
definite, nonspecific warble. This is followed by the gradual intro-
duction of short songs, then come longer more adult-type songs sepa-
rated by greater intervals of quietude but with an undetermined and
variable repertoire, and finally adult songs with a relatively fixed
repertoire. The degree to which the species song is self-differentiated,
or is acquired by hearing other members of the species sing, varies
greatly with different passerines. The selective learning by some
young passerines of many of the features of the song of their own
species deserves critical and extensive investigation.

An increasing social discrimination by young birds is evident when
they learn to distinguish different individuals of their species. Craig
(1908) noted in families of Ring Doves that the mother becomes
unwilling to feed the young long before the father does so, and that
the young soon learn to distinguish between their parents, as indicated
by their food-begging behavior. The importance of feeding motiva-
tion and reinforcement for learning is indicated by the experiments of
Holzapfel (1939) on young hand-raised Starlings in which gaping at
first occurred in response to a variety of unspecific stimuli; but it
finally became restricted to the pincers with which they were fed, or to
objects resembling the pincers. Craig also observed that young Ring
Doves may at first beg from strange doves, but since the latter refuse
to feed them and may even drive them off, the young are familiarized
with a further distinction of individuals. Under natural conditions
it has been observed that young European Coots will at first follow
and beg from any adult Coot, but soon learn to avoid adults in an
attitude of attack, and after a while cease to follow or beg except from
the parents and avoid strangers without waiting to be attacked
(Alley and Boyd, 1950).

The existence of dominance hierarchies within bird flocks indicates
that the powers of recognition and discrimination may be extended to
many individuals. At a bait station in a marsh during late winter
and early spring, we observed a consistent dominance hierarchy
among 14 individually marked pheasant hens which regularly visited
the corn used as bait (Collias and Taber, 1951).

Cues involved in individual recognition include voice, color, and
facial characteristics. Domestic chicks of different broods when

mixed in the dark show some tendency to sort themselves out and go to their own mother, at least when hens of different breeds are used. But some of the chicks may simply go to the nearest hen. In another experiment, I took three well-established broods of chicks from broody hens of three different colors and placed them in the same enclosure with three strange broody hens of the same three colors. The chicks taken from a black mother followed the strange black hen, those taken from a red mother followed the strange red hen, and those taken from a white mother followed the strange white hen. These responses were predominant but not completely exclusive. Schjelderup-Ebbe (1922) observed that alterations in coloration of the face were effective in stimulating attacks on flock mates in a flock of domestic hens. We have observed that changes in coloration of the body plumage or changes in plumage during the molt are quite ineffective in this respect.

Additional evidence of increasing social discrimination is the weakening or lack of social responses by domestic chicks to abnormal stimuli when early social experience has been normal. Craig (1913) stated that young Ring Doves that have never mated are more likely to enter into abnormal matings, as with their own sex, with alien species, or with the hand, or to lay without a nest, as compared with birds which have had mating experience. Young Red-winged Blackbirds, *Agelaius phoeniceus*, just after hatching gape readily to artificial sounds—a hiss, a clap of the hands, or a whistle—as well as to the cluck of the parents, but the response to the artificial sounds disappears in a few days, unlike the response to the parental cluck, which presumably was given more often than the artificial sounds and was reinforced by feeding (Kuhlmann, 1909).

Rôle of leadership in socialization. The strength of the social bond between young and parents is undoubtedly increased by the benefits of the relationship to the young; thus, learning of a diet suitable for a species may be facilitated by parental example, and it functions to reinforce the social bond. Baby chicks will run toward their mother and peck at the spot at which their mother pecks and at her beak. A chick that has never seen lettuce may be very slow in responding to a piece of lettuce placed in its cage, but if one merely taps on this lettuce with one forefinger the chick will run to and peck the lettuce and thereafter eats it with avidity. Movement and the tapping sound are the orienting stimuli here, and eating of the lettuce is the reinforcing stimulus. The parent in many nidifugous species of birds leads the young to a safe roosting spot each evening. Parentless ducklings of the Canvas-back, *Aythya valisineria*, are much less wary than are ducklings still attended by a mother (Hochbaum, 1944:107).

In fact, parent birds furnish guidance to their young in so many phases of life, that they may be said to act in the socialization of young birds somewhat as do special organizers or inductors in embryological development.

The importance of normal parental relations in the life of young birds is suggested in certain game birds by the lesser survival of incubator-hatched, pen-raised birds, as compared to wild-trapped stock, after transplantation, although there are other factors and the matter needs analysis. In one study on banded Ring-necked Pheasants wild-trapped birds showed up to three times the survival rate of game farm birds of comparable age released on the same area at about the same time, mid-summer. Survival was checked during the hunting season in the latter part of November from the percentage of band returns (Harper, Hart, and Shaffer, 1951). According to Studholme (1948) it is practically worthless to release for restocking purposes pheasants under eight weeks of age. However, it seems that young stock is more capable of establishing itself and reverting to the wild than is adult stock, and one study (*op. cit.*) indicated that birds approximately 12 to 14 weeks of age were most suitable for restocking.

In many species of passerine birds the young males normally learn much of the characteristic song of the species from older males of the same species (Nice, 1943). Not all social learning is effected on a parental basis; it may continue during the near-adult period after parental bonds are broken in many passerine species of birds, as in the traditional build up of numbers at a winter feeding station (J. Hickey, pers. comm.). The use of a certain winter roost by Crows, *Corvus brachyrhynchos*, for 50 years or more (Emlen, 1938) is a good example of the effectiveness of older leaders in simplifying what for many birds is a living problem of much importance.

The contagiousness of behavior in domestic chicks facilitates aggregation and socialization. For example, when one chick pecks at the ground its neighbors tend to run over and do likewise. The chicks follow each other as they move along. Some lag more than do others. In 10 groups of chicks, each consisting of 10 to 12 marked individuals which I tested for their response to warmth, each group had one or more individuals which consistently and conspicuously lagged behind the others. These tests were conducted in a narrow runway 10 feet long and 1 foot wide with cheesecloth walls; at each end of the runway there was placed an electric lamp. These lamps provided heat for the chicks which would crowd beneath the lamp that was on. The two lamps were turned on alternately, and when one lamp was turned off the chicks would move to the other lamp which was then on.

Some individuals tended to respond a little sooner than others, and interestingly enough, a few of these leaders would sometimes repeatedly leave the group under the warm lamp and go to the laggard in the cold, which then tended to follow the leader back to the group. From these results it appears that a leader is *less stimulus-bound* than are followers. Such behavior of the leader would be expected to favor survival of the group as a whole.

Increasing social independence. In many species of birds, as the young become older the aggregation tendency is reduced. Thus, a raft of downy young ducklings of the Mallard, *Anas platyrhynchos*, in which the individual young are frequently in physical contact, tends to break up as the ducklings grow, and the individuals are then generally more widely spaced.

Infantile responses may disappear or become latent. Distress calls which are given by domestic chicks on isolation become reduced in frequency as the chicks grow older (Fig. 8). Gaping in young passerines disappears and is replaced by independent feeding responses. In young Starlings raised in the laboratory, pecking began at 20 days, but gaping normally lasted 4 weeks; it was suggested that the overlap in gaping and self-feeding reactions provides a factor of safety during the change to the adult mode of nourishment (Meyer-Holzapfel, 1949). Leaving the nest may in the case of some nidicolous species be facilitated by parental "luring" either with or without food (Nice, 1943:245).

The disappearance of infantile responses may in part be due to cessation of parental care. The disappearance of gaping in young hand-raised Starlings can be greatly accelerated or greatly delayed, by restricting or increasing the amount of hand-feeding, respectively (Holzapfel, 1939).

Regression may appear under stress. It has been observed for a number of species of passerines that young birds in process of learning to feed themselves, when very hungry do not pick up and eat food, but instead start to beg (Nice, 1943:40). The rally call of scattered Bobwhite Quail, according to Stoddard (1931), is merely a modified form of the distress call of the chicks. The biological significance of regression may be that of increasing survival value by rejecting the temporary weakness of the developing individual in favor of the greater survival value of recourse to parental care.

Gradually increasing independence of the young, combined with an increasing indifference of the parents, may lead to breakup of the family. The parent may desert the young as does the female Canvasback (Hochbaum, 1944); young Manx Shearwaters, *Puffinus puffinus*,
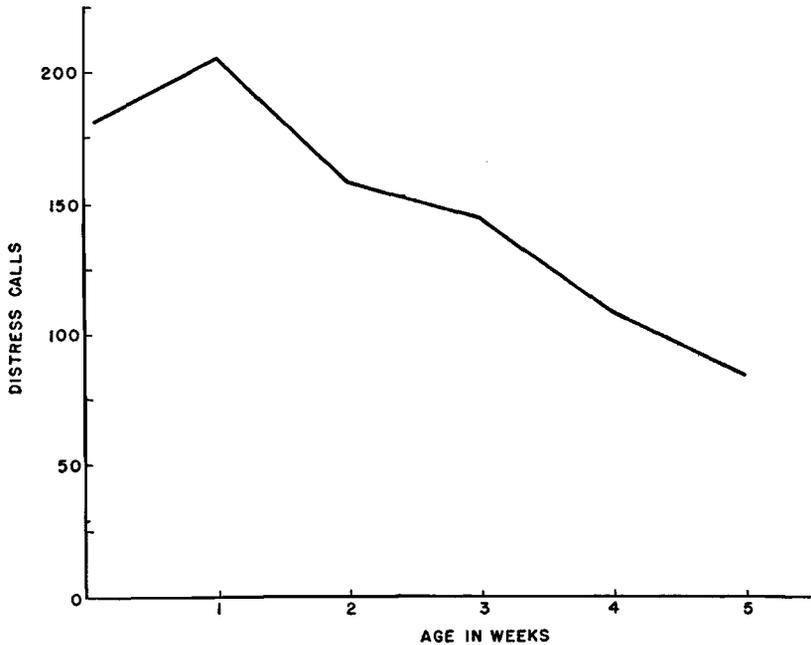
FIGURE 8. Frequency of distress calls by domestic chicks on being isolated changes with age, after the first week. Ten to 17 chicks were tested each week, except that only 6 chicks were tested in the fifth week.

are literally starved out of their nest holes as a result of parental desertion (Lockley, 1942:51).

In some species the parents may even drive off the young at a certain stage, as in the Moor-hen, *Gallinula chloropus* (Howard, 1940). The balance between aggression and parental care may fluctuate during the transitional phase. Howard (*op. cit.*) observed a male Moor-hen chase and peck each young one immediately after feeding it. Song Sparrows drive off their own full-grown young as readily as they drive away strangers (Nice, 1943:253). Loss of parental tolerance for young birds was associated with start of a new nesting season in one pair of Blue Geese, *Chen caerulescens* (Jenkins, 1944). To some extent, rise of aggressiveness, sexual motivation, and exploratory tendencies in the young may contribute to break-up of the family.

Reintegration of the young bird into new social groups.   The formation of post-breeding flocks or of breeding pairs or groups requires a certain amount of readjustment, particularly with reference to the balance between cooperative and competitive tendencies of the flock.   Species attraction has already been determined by this time, and largely as a

result of socialization within the family (with the exception of parasitic species) the young bird is well acquainted with the habitat, voice, and appearance of its own species.

Increased tolerance for strangers, associated with decreased attachment to the maturing young, may permit the post-breeding combining of families seen in covies of Bob-white Quail by Stoddard (1931) or in flocks of Canada Geese, *Branta canadensis* by Elder and Elder (1949). Previous acquaintance helps determine persistence of subgroups in the flock. When I combined two small flocks of young White Leghorn pullets from two pens into one pen, the two flocks, although often intermixed in the daytime, for months roosted separately at night.

Entrance into a new social group not only requires tolerance of the new individual by the group, but also may be accompanied by the attainment by the newcomer of a definite social status within the group, as has been shown in nature for California Quail, *Lophortyx californica* by Howard and Emlen (1942). For newcomers the initial social status is usually low in the dominance hierarchy.

Social facilitation may aid entrance into new social groups. When two previously acquainted domestic hens are introduced together into a strange flock, the more dominant individual may facilitate rise of its partner in the social scale (Douglis, 1948).

An experienced partner may facilitate formation of a new social bond. According to Levi (1941) young female domestic pigeons placed in a pen with older males will pair more quickly, than if placed with young males.

DEVELOPMENT OF SEXUAL AND PARENTAL BONDS

Just as in human society, the development of appropriate sexual and parental bonds among birds is an integral part of social development in the life history of the individual. The external factors concerned have often been reviewed; emphasis here will be placed on internal factors. The development of sexual and parental bonds is to a considerable extent dependent on changes in the endocrine system, although many non-endocrine factors facilitate or are necessary for the formation of these bonds. Recent literature relating mechanisms of reproductive behavior in birds to hormones has been reviewed elsewhere in some detail (Collias, 1950c) and it will generally not be cited here again, although some of the major concepts will be mentioned.

Sexual bonds. Pair formation involves location of a member of the opposite sex, fighting or threatening away possible rivals, and development of specific tolerance for and attachment to the mate. Location of a mate is facilitated by distinctive vocalizations, generally by the

male, and these special vocalizations are known in many species to
decline greatly in frequency once a mate is secured.   In a number of
species it has been shown that these vocalizations are stimulated by
male hormone—for example, the crowing of the domestic rooster, the
Ring-necked Pheasant, and the California Quail, the booming of the
Prairie Chicken (*Tympanuchus cupido*), the snap-hiss ceremony of the
Black-crowned Night Heron (*Nycticorax nycticorax*), the whistle of the
Redhead drake (*Aythya americana*), the breeding calls of the male
Herring Gull and Laughing Gull (*Larus atricilla*), the bowing coo of
the Ring Dove and the Domestic Pigeon, and the song of the Canary
(*Serinus canarius*) and the Chaffinch (*Fringilla coelebs*).

Male hormone has also been shown to stimulate aggressive behavior
in a variety of birds, including both males and females, although it is
possible that a high level of male hormone induces a specific tolerance
for females (Collias, 1944).   Male Ring-necked Pheasants cease to
peck females as the males come into breeding condition (Collias and
Taber, 1951).   The domestic hen has been proved to secrete female
hormone from the cortex of the ovary and male hormone from the
medulla of the ovary; female birds in a few other species of diverse
types have likewise been demonstrated to be endocrine bisexuals.
Therefore, it seems likely that to some extent territorial defense by the
females in some species of birds is stimulated by male hormone.

Special displays which may function in sex recognition have been
shown to be stimulated by male hormone in the domestic cock,
Prairie Chicken, Black-crowned Night Heron, Laughing Gull, Red-
head drake, Ring Dove, and Domestic Pigeon.   Copulation in the
male position has been stimulated by male hormone in the rooster,
Ring Dove, and Black-crowned Night Heron.   Receptive crouching
in the domestic hen is stimulated by female hormone.   Pair formation
requires hormonal motivation in pigeons at least, since pigeons do not
pair if previously castrated or hypophysectomized.

It seems therefore that sex hormones may stimulate the whole com-
plex of sexual behavior, as has been shown most critically for the
domestic fowl.

Sexual behavior in birds often involves display of conspicuous
features of plumage or of special ornaments, which in many instances
have been shown to depend on hormonal control.

Parental bonds.   Parental bonds involve attachments to the eggs
and young.   When eggs are allowed to pile up in breeding pens of
Bob-white Quail, some of the birds may start incubating (Stoddard,
1931:459).   On the other hand, daily removal of the eggs tends to
stimulate laying of an abnormally large number of eggs in this species

as well as in a wide variety of other species of birds. Many species of birds will continue to incubate sterile eggs long past the length of incubation period normal for the species. Broodiness can be induced and maintained for months (as much as six months in one of my hens) in domestic hens by keeping them with baby chicks, but according to Patel's experiments (1936), parental behavior cannot be prolonged in pigeons by giving them a succession of young squabs. Very young chicks are most effective with domestic hens, and as the chicks of a hen grow up and lose their downy plumage the mother shows an increased tendency to peck and drive them from her.

Prolactin secretion induces broodiness in domestic hens, even in the absence of accumulations of eggs or of chicks. In Domestic Pigeons and Ring Doves prolactin induces formation of the crop secretions that are used to nourish the young squabs. In fact, crop growth is a standard, specific, and delicate measure of prolactin secretion.

A certain amount of progress has been made in the analysis of the genetic basis of parental behavior in domestic fowl. In certain breeds of domestic fowl broodiness has been found to depend to some extent on sex-linked factors (Roberts and Card, 1934). According to Hays (1940), broodiness in his strain of Rhode Island Reds depended largely on two pairs of dominant, complementary autosomal genes, with no clear evidence for sex-linkage. Possibly a number of quantitative modifiers are involved. It would seem most probable that in the ancestral type of fowl all these types of genes would be involved.

There is some evidence available on the physiological genetics of broodiness in domestic fowl. The pituitary of non-broody strains of fowl contains less prolactin than does the pituitary of broody strains of fowl (Burrows and Byerly, 1936). Normally, the pituitary of a rooster contains less prolactin and more gonadotrophin than does the pituitary of a broody hen (Burrows and Byerly, 1936). Large doses of prolactin will make a rooster brood and care for chicks (Nalbandov and Card, 1945). Capons may likewise brood and care for chicks; in domestic hens it is known that a high level of sex hormones inhibits broodiness. It is possible therefore that a rooster does not normally brood chicks in part because of differences in the relative amounts of pituitary hormones secreted, as compared to a hen. The Domestic Pigeon belongs to a species in which the male helps to incubate the eggs and feed the young; and in contrast to the situation in domestic fowl large doses of male hormone do not seem to inhibit broodiness.

A difference in response to prolactin is also associated with differences in genetic constitution. Riddle and his co-workers (Riddle and Bates, 1939) found that it was easier to induce broodiness with pro-
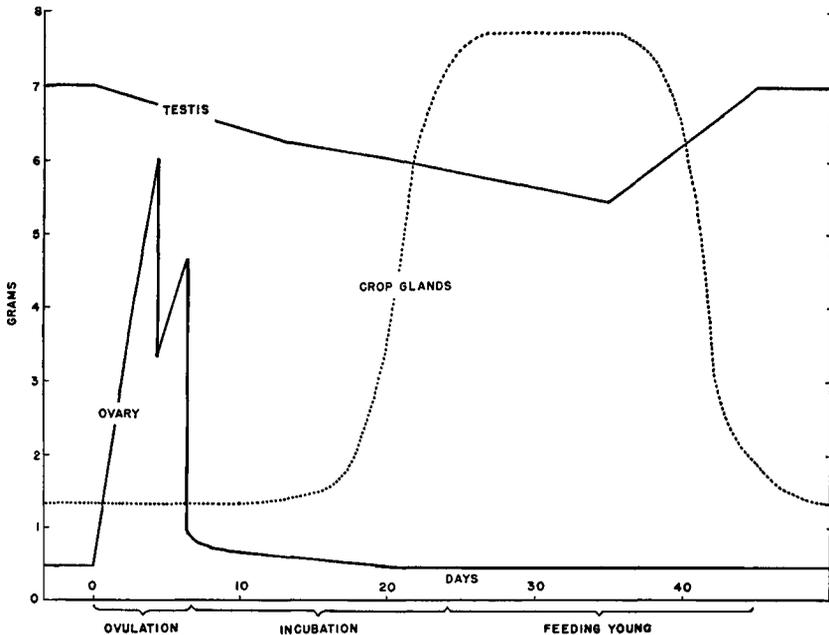
FIGURE 9. The inverse relationship between sexual and parental phases of the breeding cycle in the domestic pigeon. The sexual phase may be measured roughly by changes in gonadal weight. The parental phase may be measured quite specifically by growth of the crop glands (After J. P. Schooley, 1937).

lactin in hens of broody strains than in non-broody strains. Nalbandov and Card (1945) observed that a much larger dose of prolactin was required to induce broodiness in roosters than in hens, and that the amount of prolactin required to induce broodiness in roosters was inversely proportional to the number of genes for broodiness which these roosters were assumed to carry.

Interaction of factors controlling breeding behavior. There is an inverse relationship between the sexual and parental phases of breeding behavior controlled by a parallel inverse relationship in the underlying hormonal changes, as has been demonstrated for the Domestic Pigeon (Fig. 9) and the domestic hen (Collias, 1950c, 1951).

Balanced interaction between hormones of the anterior pituitary and gonadal hormones acts as a basic control mechanism of breeding rhythm in pigeons and Ring Doves. Prolactin secretion in these species is stimulated by secretions from the testis and ovary, but as the level of prolactin rises it inhibits the gonadotrophic output of the pituitary, thereby exerting a strong anti-gonadal effect and reducing its own source of stimulation. Probably a similar mechanism operates

in domestic hens and many other birds.   Figure 10 illustrates the case
of a domestic hen kept with the same brood of chicks for approxi-
mately 120 days.   It will be noticed that in this case broodiness and
egg-laying, which probably indicate prolactin and gonadotrophic
activity of the anterior pituitary, respectively, were inversely related
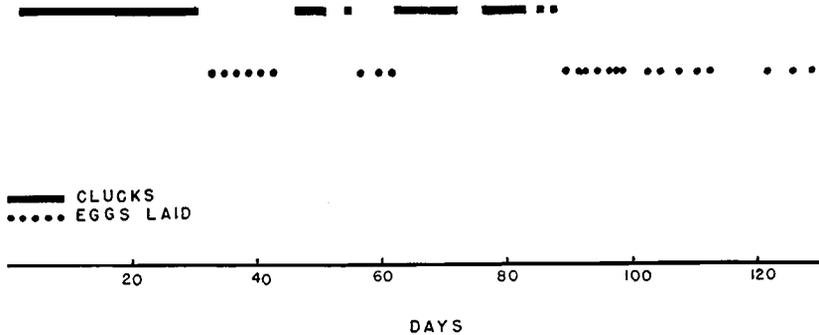

FIGURE 10.   The fluctuation or oscillation between the broody phase (indicated
by clucking) and the sexual phase (indicated by egg-laying) in one domestic hen, as
her chicks grew older and her broodiness gradually disappeared.

and that the hen oscillated between the two phases of reproductive
behavior for a time before her broodiness, indicated by clucking, was
finally terminated.   Such oscillation is characteristic of self-regulatory
systems, and reflects the lag in the controlling factors.

Social control of endocrine secretion probably operates through the
pituitary gland which is closely related to the central nervous system.
The sexual behavior of male Ring Doves increases the rate of ovulation
by females, presumably by stimulating the output of pituitary gonado-
trophin.   Prolactin secretion as indicated by crop growth and secre-
tion can be stimulated in Domestic Pigeons by incubation of the eggs
and by sight of the mate incubating the eggs ("psychological brood-
ing"), as has been experimentally demonstrated by Patel (1936).
The gonads, by stimulating pair formation, facilitate subsequent de-
velopment of broody behavior in pigeons.   It is possible also that the
broody response to prolactin is facilitated by the priming action of
sex hormones, as in the domestic fowl.

The occurrence of multiple broods is probably related to a variety
of factors.   The greater number of broods in the Ring Dove as com-
pared to the Mourning Dove under identical laboratory conditions is
associated with seasonal breeding periodicity in the latter species
which is more subject to control by changes in day length (Cole, 1933).
The Domestic Pigeon is probably relatively unresponsive to artificial

changes in day-length (Levi, 1941) as compared with the domestic fowl; this fact, and the relative inability of young squabs to prolong parental behavior, in contrast to that ability of young chicks, help to explain the greater number of broods in the pigeon.

Figure 11 is a simplified diagram summarizing interactions of some important factors that control breeding cycles in pigeons and doves.

INCREASED——►GONADOTROPHIN ◄————————►SEXUAL BEHAVIOR
DAY LENGTH   ▲   ＼   ／
                          (–) │   ＼GONADS／
                              │   ／   ＼
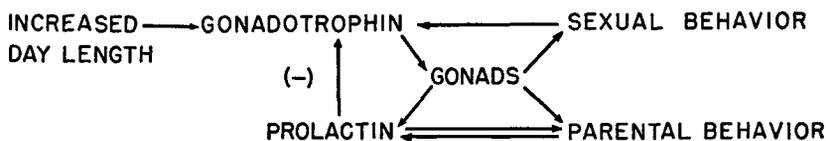   PROLACTIN◄═══════════════►PARENTAL BEHAVIOR

FIGURE 11. Diagram of the interaction of some factors controlling breeding behavior in pigeons and doves.

Each arrow represents a stimulating effect unless an inhibiting effect is indicated by a minus sign. Different species of doves and pigeons may differ in details or quantitatively, particularly in the response to day length. The breeding behavior of the domestic fowl is regulated by a system of factors showing considerable similarity to those operative in pigeons but differing in certain important aspects, as brought out in the preceding pages.

Seasonal adjustment of social bonds. The nature of the factors regulating the seasonal development of breeding and flocking behavior should be mentioned. In this respect the importance of changes in day-length in temperate zones and of wet and dry seasons in the tropics has often been discussed. Social factors generally may play only a secondary rôle; thus, when the Mourning Dove, a seasonal breeder, was mated with the Ring Dove, which at least in captivity is a non-seasonal breeder, seasonal periodicity in egg-laying and fertility of the Mourning Dove under laboratory conditions was maintained (Cole, 1933).

Studies on the annual breeding periodicity of cock Ring-necked Pheasants near Madison, Wisconsin, have shown a general parallelism between changes in day-length, changes in testis-size and pituitary activity, and changes in breeding behavior (Taber, 1949; Collias, 1951). This is a causal sequence with respect to the onset of breeding activity, since it is known for this species that increase in day-length will stimulate testicular activity presumably via the pituitary, and the testicular hormone in turn stimulates breeding behavior in the males.

Little is known as yet concerning the mechanism of the effect of light. Some experiments on immature domestic ducks have indicated that testicular growth may result from very localized light stimulation

restricted to the pituitary gland or to the hypothalamus (Benoit and Kehl, 1939). The hypophysis, unlike the brain and spinal cord, has a special affinity for porphyrins introduced into the body (Klüver, 1944). Porphyrins include some powerful photo-chemicals, and would appear to merit consideration in connection with the problem of the absorption of light energy and its transformation into breeding activity.

Such studies as those of Chapin (1946) on the 9.6-month breeding cycle of the Sooty Terns, *Sterna fuscata*, on Ascension Island (8° S. Lat.) indicate the existence of an internal rhythm of breeding periodicity, and suggest that the ordinary function of changes in day-length is to synchronize and adjust this internal rhythm with seasonal rhythms in the external environment.

Unless habitat conditions are suitable some species of birds may not breed, despite onset of the normal breeding season. In very dry years Gambel's Quail, *Lophortyx gambelii*, of the southwestern United States fail to breed, apparently because of a lack of green food, the growth of which is normally stimulated by rainfall (MacGregor and Inlay, 1951).

It seems to be a general rule that natural selection has so regulated the season of breeding that young birds are generally hatched in the most favorable season for their growth and survival. For example, the peak in numbers of nestlings in Blue Titmice, *Parus caeruleus*, coincides with the peak in numbers of *Cheimatobia* caterpillars that furnish the principal food of the nestlings (Gibb, 1950).

Following the breeding season, the decline in gonadal activity removes an important stimulus to territorial and certain other forms of aggressiveness, thereby facilitating the tolerance that permits flock formation (Emlen and Lorenz, 1942; Collias, 1944).

In summary, the orderly development of social bonds involved in the reproductive behavior of birds depends on the balance and interplay between physical, endocrine, and social factors forming an interacting system that aids ecological adjustment in the sense that it leads to the production of young birds during the season best fitted for their survival.

CONCLUSIONS

1. Social development is part of the development of behavior in general, and as such may be traced back through physiological and chemical levels of organization to genetic factors. What genes determine in this indirect fashion is the tendency to respond to more or less specific social situations; and the interaction between different levels leads to social development.

2. Shifts in physiological balance points, such as those determined by the rate of secretion of specific hormones, play a large rôle in determining the social situation. Thus, sexual and parental phases of the breeding cycle are largely controlled by sex hormones and by prolactin, respectively. In turn, specific social situations react back on and help control the rate of secretion of these hormones. By influencing endocrine secretion, changes in the physical environment may synchronize with internally determined endocrine rhythms in such a way that most breeding activity occurs at the time of year best suited to survival of the young. Flocking of many birds outside the breeding season is associated with the increased tolerance of other individuals that accompanies decline of gonadal activity.

3. The patterning of social behavior parallels the principles of operation of the central nervous system as studied by physiologists, and the development of behavior, including socialization of the young bird, likewise parallels the physiology of development as studied by embryologists.

4. The basis for social reactions is largely developed by the embryo before hatching takes place. The trends in socialization of the young bird after hatching may be summarized as follows: (1) a period of relative inactivity, and sometimes of "spontaneous" or apparently endogenous activity, is followed by (2) the appearance and development of initial, rather generalized, social responses which, passing through an early plastic period, become strengthened, fixated, directed, and specified by social experience. This period of increased social discrimination is followed by (3) a period of gradually increasing social independence that may result in break-up of the family, and finally (4) reintegration into new social groups, a process which in most species of birds seems to be largely governed by the preceding socialization within the family and by the balance between cooperative and competitive tendencies. Social development is greatly facilitated by example and leadership.

5. The results of social development are individuals and groups that respond adaptively to the habitat, habits, and recognition marks of the species, and are therefore ecologically adjusted.

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