

A LABORATORY APPROACH TO THE STUDY OF IMPRINTING¹

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ACCORDING to Lorenz (1937), imprinting differs from other forms of acquired behavior in that: (1) it occurs very rapidly; (2) it occurs only in a very limited part of the animal's life; and (3) it is irreversible, or, at least, it is difficult to extinguish. Although imprinting was for some time thought to be found exclusively in birds, it now seems that it may be a more universal type of behavior. Suggestions from the literature point to the possibility that it may exist in such diverse forms as insects, fishes, and mammals (Thorpe, 1950). The characteristics of imprinting listed above make it an extremely important subject in the study of behavior. This is emphasized by Thorpe (1950) who wrote, "It needs and would repay full and precise experimental investigation more almost than any other aspect of animal behaviour." For this reason we decided to begin a careful analysis of the problem. The experiments to be described represent attempts to develop laboratory techniques to study the following problems:

- (1) What is the critical age for imprinting to occur?
- (2) What characteristics are necessary in the imprinting object if it is to release the reaction of following?
- (3) How long must young birds be exposed to the imprinting object, if imprinting is to be complete and irreversible?

PROCEDURE

The Mallard ducklings (*Anas platyrhynchos*) used in these experiments were hatched from eggs incubated in a forced-air incubator. Two days before hatching, the eggs were transferred to a still-air incubator fitted with glass doors and shutters. This latter incubator was kept very humid, as the ducklings had to be removed and isolated as they hatched. Each duckling was given a number, and this number, as well as the day and hour of hatching, was noted on the cardboard box in which the duckling was placed. This information was also recorded in the permanent records. The box containing the duckling was then placed in a third incubator, used as a brooder until imprinting and testing was completed, and only then was the duckling placed in daylight and given food and water.

During school hours and during the night, it was not feasible to watch the hatching incubator constantly. At these times the incubator was examined every 1-2 hours and the age of the duckling was estimated by the degree of dryness of the duckling.

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For the experiments, papier-mâché Mallard duck decoys were secured. These models were then fitted with off-center wheels that caused them to waddle when moved. The models also contained loud-speakers that could be attached to tape-recorders. The latter were fitted with circular tapes which allowed the same pattern of sound to be presented repeatedly. Some of the models had articulated heads that moved on springs with the motion of the decoy. In addition, a male model was fitted with a heating element and a felt apron so that the duckling could go under the decoy for warmth.

The imprinting runs, as well as the test runs, were made in a $1.5 \times 1.5 \times 12$ ft. runway. This was covered on the bottom and sides with monk's cloth and provided with a hinged cover of screen wire. It rested on legs 3 feet above the floor. Fifteen watt bulbs were present overhead at either end and in the center. The remainder of the room was kept dark whenever the eggs were hatching, or when the imprinting or testing of ducklings was in progress.

In the standard imprinting trials, the optimum male model, fitted with a heating element and a felt apron, was provided with an arbitrarily chosen series of calls, best represented as *GOCK, gock, gock, gock, gock*. Two main methods of imprinting were used. In the first series, the duckling was kept with the model 10 minutes, and although the movement of the model was accommodated to that of the individual duckling, it was kept in motion as much as possible for the entire period. The duckling usually traveled 150 to 250 feet in the time allotted. In the second series, the duckling was kept with the imprinting object for 30 minutes and the model was moved a short distance every 5 minutes for a total of 12 feet.

Five to 70 hours after imprinting, each duckling was given the following 4 tests, which we estimated to be in order of increasing difficulty. These tests are graphically presented in Figure 1. The time of response and the character of the call note (*i.e.*, whether pleasure tone or distress note) of the duckling were recorded.

In the test situation a female model was used as well as the imprinting object or male model. The male model was connected to a tape recorder upon which was recorded the standard *gock*, and the female model was connected to a tape recorder which played the sound of a female Mallard calling her young. (In order to secure the latter record, a female Mallard with young was penned up, her young removed, and her call notes were recorded from a short distance.) In each test, as much as 2 minutes was allowed for a response.

Test 1.—In this test both models were motionless at first and both were calling. The duckling in a cardboard box was placed one foot from each model in the center of the runway. The box was then removed to release the

duckling. After it had made a choice, the model chosen was moved slowly to the end of the runway to test the reaction of following in the duckling. Throughout the experiments the ducklings were never touched by hand but were picked up and released by means of the cardboard box mentioned.

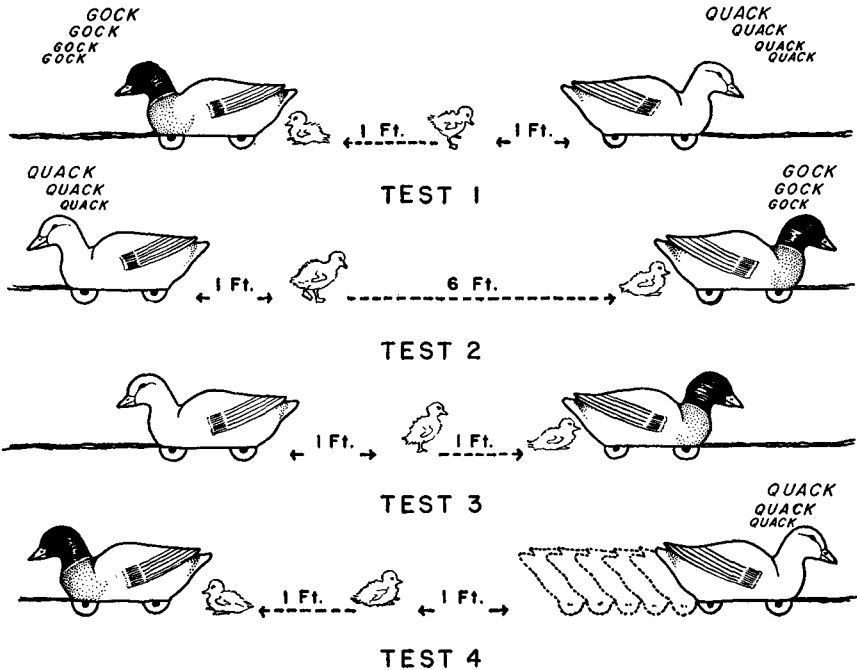


FIG. 1. Diagram of procedures used to test amount of imprinting.

Test 2.—This test was similar to Test 1 except the male model was now placed at the far end of the runway, 6 feet from the ducklings. This test was designed to determine if the duckling would respond to the imprinting object even though the female model was now closer and louder.

Test 3.—In the third test both models were kept silent and the ability of the duckling to make a response on the basis of visual cues alone was tested. The models and the ducklings were in the same starting position as in Test 1. After the duckling made a choice, the silent model was then moved to test the response of following.

Test 4.—In the last test the duckling was released from the center, as before, and the models were in the same starting position. However, in this test only the female was calling and when the duckling was released the female model was moved down the runway. Thus, to score a positive response, the duck-

ling had to go to the male although confronted with a variety of conflicting stimuli.

If the duckling gave a positive response to the imprinting object (the male Mallard) in all tests, imprinting was regarded as complete. Such ducklings, when released, remained apart from parent female Mallards; the imprinting may, therefore, be regarded as irreversible. Only a few ducklings were difficult to score on a quantitative basis. For these few, a response was considered partial and scored as 0.5 if the duckling went in the direction of the imprinting object before the model was moved and remained there. Other qualitative differences in response were also noted. For instance, of the 92 ducklings tested in the standard series, a total of 35 chose the male model in Test 3 and only 8 of these gave a distress note, even though no sound was used in this test. In contrast, only 16 ducklings went to the female model in this test, and 10 of these gave a distress note.

CRITICAL PERIOD

Ninety-two ducklings were imprinted in the standard series, 54 by 10 minutes of following (Table 1), and 38 by the 30 minute method (Table 2). In both of these series 13–16 hours proved to be the best age for imprinting. Approximately 50 per cent of the 21 ducklings imprinted in this age-group were completely imprinted. Only 3 other ducks made perfect scores, and none imprinted before 12 hours of age or after 18 hours of age made perfect scores. Beyond 28 hours no imprinting occurred. In addition, 3 ducklings were exposed to the standard *gock* call continuously for over 24 hours before and up to the time of hatching. No imprinting occurred in these ducklings. In fact, 2 of the 3 responded to the recorded call of the female Mallard in preference to the call to which they had been exposed. The other duckling did not respond to either call.

Under the conditions of the experiment, therefore, the period 13–16 hours is definitely the period for maximum imprinting in Mallards. This is made obvious by the graphs which include all of the 92 animals imprinted in the standard series. Figure 2 shows the percentage of animals in each age group that made perfect imprinting scores. Figure 3 shows the percentage of positive responses made by these same ducklings in each age group. These results will be reported elsewhere (Hess and Ramsay).

Our results contradict the findings of Fabricius (1951a) who reported that ages before 12 hours are most favorable for imprinting in several species of ducks including Mallards. It may be that the tests we used were more sensitive than those used by Fabricius. We also wonder about the condition of his young birds; he reported that normal walking and running was not established until the ducklings were 16 to 28 hours old. All of our ducklings

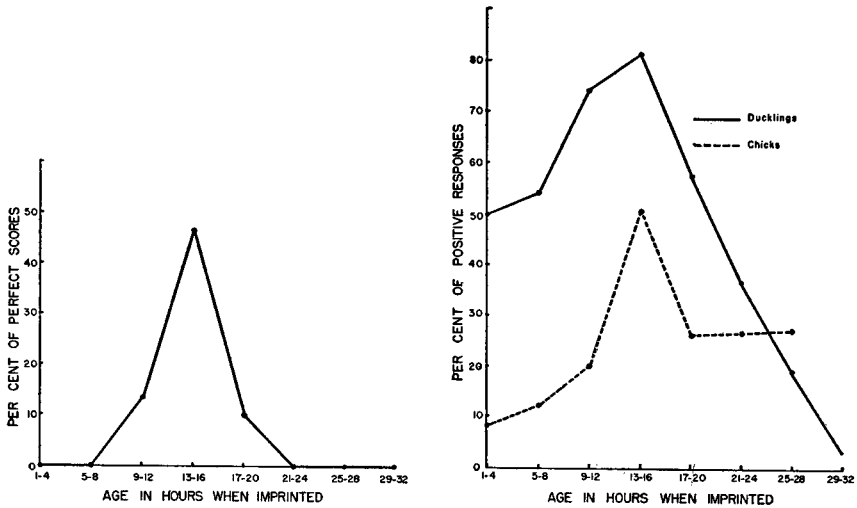


FIG. 2. Percentage of "perfect" scores for Mallards imprinted in various age groups.

FIG. 3. Percentage of positive responses made by ducklings and chicks in test series.

could walk and run many hours before that, although we recorded that 4 of the 8 ducklings imprinted before they were 2 hours old could not even crawl in a straight line at first but circled in a clockwise direction. Six ducklings, 3 to 4 hours old, imprinted by the 10 minute method, traveled an average distance of 75 feet in the time allowed. Maximum distance traveled was 250 feet, minimum 16 feet. Fabricius also reported (1951a) that fear responses first appeared in his Tufted Ducks (*Aythya fuligula*) and Eiders (*Somateria mollissima*) at 12 hours. Fear responses to the imprinting model did not appear in our Mallards until 24 hours. Eleven of the 14 ducklings imprinted in this age-group showed strong fear responses. Of over 100 other Mallard ducklings (imprinted earlier) only 3 (ages, 16, 20, and 16 hours) showed alarm. It seems significant that the only ducklings that showed any appreciable imprinting in the 21 to 24 hour group were the same individuals that showed no alarm.

SOCIAL FACILITATION IN IMPRINTING

Two groups of 2 animals each, well past the optimum imprinting age, were partially imprinted by being placed with 2 well imprinted ducklings and the imprinting object during the imprinting period. These all made much better scores than could be expected otherwise. Each of the 2 imprinted at 28 hours made a score of 3 positive responses. Each of the 2 ducklings imprinted at 38 hours made a score of 2 positive responses in the test period.

TABLE 1

No. of ducklings	Age in hours	TESTS OF DUCKLINGS IMPRINTED FOR 10 MINUTES				Average
		Number of positive responses				
		Test 1	Test 2	Test 3	Test 4	
5	1- 4	5	4	3	0	2.4
8	5- 8	8	8	3	0	2.4
8	9-12	8	8	5	2	2.9
10	13-16	10	10	8.5	4	3.3
10	17-20	9	9	3	2	2.3
6	21-24	4	3	2	0	1.5
3	25-28	1	1	0	1	1.
4	29-32	0	0.5	0	0	0.13

TABLE 2

No. of ducklings	Age in hours	TESTS OF DUCKLINGS IMPRINTED FOR 30 MINUTES				Average
		Number of positive responses				
		Test 1	Test 2	Test 3	Test 4	
8	1- 4	7	7	0	1	1.9
12	5- 8	10.5	10.5	3	0	2.
7 ¹	9-12	7	7	3	4.5	3.1
5	13-16	5	5	3	3	3.2
0	17-20	---	---	---	---	---
5	21-24	3	2	1	1	1.4
1	25-28	0	0	0	0	0

¹Six of these 7 birds were 12 hours old when imprinted and very close to the age for maximum imprinting.

TABLE 3

No. of chicks	Age in hours	TESTS OF CHICK IMPRINTED FOR 10 MINUTES					Average
		Number of positive responses					
		Test 1	Test 2	Test 3	Test 4	Test 5	
5	1- 4	1	0	0	0	1	0.4
5	5- 8	1	0	0	0	2	0.6
3	9-12	0.5	0	0	0	2.5	1.0
4	13-16	3	2	1	0	4	2.5
3	17-20	0.5	0	1.5	0	2	1.3
3	21-24	2.5	0.5	0	0	1	1.3
3	25-28	1	1	0	0	2	1.3

Nice (1953) observed imprinting in a 6-day old Shoveller (*Spatula clypeata*), apparently through social facilitation. We plan further study to determine the effects of maturation of fear responses, and decline in tendency to respond to the imprinting object on imprinting as the duckling grows older.

RELEASE OF THE REACTION OF FOLLOWING

Experiments on this subject were exploratory in nature and no final conclusions can be drawn as comparatively few ducklings were used in each experiment.

Sound.—Seven ducklings of various ages were imprinted only on the recorded natural quack of a female Mallard calling her young. Of these, only 4 responded to the imprinting object at all in the test period. These 4 made fair scores in the tests (average score 2). The other 3 did not respond to either model. In contrast, of 38 Mallard ducklings similarly imprinted on the male model calling *gock*, only one failed to respond at all, and the group score averaged 2.3.

Twenty-four ducklings of various ages were carefully tested for inherent preferences. These ducklings were first tested with the models silent and then with the male model calling *gock* and the female model calling *quack*. The calls were then reversed in the models 2 or more times. At no time were the models moved and each duckling was allowed as much as 5 minutes to make a response. No talking occurred in the laboratory where the ducklings were kept until after they were tested. We could not eliminate talking outside the room.

None of the 24 ducklings made any move toward either the male or female models as long as the latter were silent. Fifteen showed no preference between the call notes. Of the 15, 10 made no move toward either sound, and 5 responded to each call once. Of the remainder of the 24, 8 chose the *gock* consistently and only one chose the *quack* repeatedly. Of 15 ducklings similarly tested for preferences between the recorded duck quack and a spoken simulated quack, 2 definitely chose the simulated quack and one the recorded quack. Thus, the ducklings showed no real preference.

Motion.—Four ducklings were kept with a motionless male model without heating element and with fixed head for 30 minutes. This model was giving the standard *gock* call. When the ducklings were tested, all gave positive scores on Tests 1, 2 and 3. However, only one was imprinted at the critical age, and again, this is the only duckling that gave a perfect score. If articulated motion, or motion within the organism, is one of the key stimuli in releasing the following reaction, as claimed by Fabricius (1951a), by the principle of heterogeneous summation, these ducklings should not have done nearly as well as they did. In our records it is recorded that 2 of these 4 ducklings followed poorly in their first following response when they were about 2 days old at the test period. It remains to be determined accurately whether any difference in this response is due to lack of exercise or practice by the duckling, or due to a lack of willingness to respond.

Three additional ducklings were imprinted by this same method on the

non-moving, non-articulated male model, calling the standard *gock* for 30 minutes, and 3 others were imprinted by the same method on a small box fitted with a speaker. This box was approximately the same size as the male model, and the ducklings were all near the most favorable age for imprinting. When they were approximately 2 days old they were given the following tests: (1) male model and box both call the standard *gock*, (2) male model silent, box calls, and (3) male model calls, box silent.

In the test situation, those imprinted on the male model scored a total of 5.5 positive responses (and one negative). The ducklings imprinted on the box scored a total of 2.5 positive responses (and 2 negative). In other words, the ducklings imprinted on the male model were almost twice as strongly imprinted as those imprinted on the box. It also seems significant that 2 of the ducklings imprinted on the male model responded to the silent male even when the box was calling (Test 2), but none of those imprinted on the box responded to the silent box when the male model was calling (Test 3). These limited data seems to contradict Fabricius' (1951a) conclusion that ducklings have no inherent preference as to the form of the object.

FIELD STUDIES

Two groups of ducklings, kept with the male model during the entire imprinting period, remained with the male model and followed it in preference to parent female Mallards that tried to lead them away. These parent females had young of the same age as the experimental ducklings. During this experiment, as well as during the imprinting, the male model was calling *gock* intermittently. One day-old unimprinted duckling, used as a control, went by the male model calling *gock* and on to join the parent Mallard duck. One of these experimental groups that had been given less than 10 minutes practice during the imprinting runs in following a silent male model in the runway, went to a silent floating male model and followed it in spite of the female's attempt to lure them away. The second group with no practice in following a silent model went to the floating model, followed it briefly, and then left it to return to the more familiar model with wheels on nearby land.

These results are not surprising when we recall that young of various species will follow non-articulated, smoothly moving objects, such as balls and boxes drawn along a cable (Ramsay, 1951), and that Grey Lag-Geese (*Anser anser*) if caught at the critical age will follow boats (Lorenz, 1937).

A parent female Mallard duck, while resting quietly on land will sometimes spread her tail and move her folded wings slowly back and forth an inch or more from her body. In a previous experiment, 2 Mallards hatched by a Wood Duck (*Aix sponsa*) seemed to be attracted to a parent female Mallard which was displaying in this fashion but which, as far as we could observe, was not calling. This is an example of a *releaser* in the classical sense (Lorenz,

1937). It seems very likely, therefore, that Fabricius was dealing with 2 separate innate releasing mechanisms, and not with 2 key stimuli in the same releasing mechanism, when he stated that articulated motion, or motion within the organism, is one of the 2 key stimuli in the release of the reaction of following. As Tinbergen has emphasized (1951), unless the innate responses of the organism are carefully analyzed into separate components, it will appear that the animal is reacting to a complex of stimuli.

COMPARATIVE STUDIES

In contrast to these results with Mallard ducklings, 26 Cochin Bantam chicks, similarly treated as a group, showed comparatively little imprinting (see Table 3). None of the chicks chose the imprinting object in preference to the moving clucking female in Test 4, and only one chick responded to the male model in Tests 1, 2 and 3. In order to compare the chicks more adequately, an additional test followed Test 4. In Test 5 the female model was quiet and immobile and the male alone was calling. Even with the few animals tested, it is apparent that the critical age for imprinting in chicks corresponds closely to that for ducklings (Fig. 3).

Of 13 chicks tested for inherent preferences, all but 2 chose the recorded cluck of a mother hen in preference to the standard *gock*. It seems logical to assume, therefore, that this very strong innate preference in chicks for the cluck resulted in these low scores and that by substituting another call that was not preferred, one might find that considerable imprinting had occurred. Since chicks are readily available in large groups as experimental animals, it would be worthwhile to devise suitable testing procedures for the study of imprinting in these animals.

SUMMARY

Ninety two Mallard ducklings were imprinted on a male Mallard decoy speaking a rhythmical *GOCK, gock, gock, gock, gock*, through a loud-speaker installed in the decoy. In order to secure maximum imprinting, this model was provided with an articulated head, an internal heating element, and off-center wheels that produced a waddling motion. For testing, a female model with loudspeaker also was used.

From 5 to 70 hours after imprinting, each duckling was given the following 4 tests, which we estimate to be in order of increasing difficulty:

- (1) Both models motionless, both call; duckling 1 foot away from each.
- (2) Female model louder and closer.
- (3) Both models silent.
- (4) Female model only calling and moving.

In the test situation the imprinting object, or male model, was used against the female model. The female was provided with the recorded call notes of a female Mallard calling her young and the male was provided with the standard *gock*.

Thirteen to 16 hours proved to be the critical age for imprinting in Mallards. Approximately half of the ducklings imprinted in this age-group were completely imprinted and went to the imprinting object in all tests. Only 3 of the remaining ducklings gave perfect scores.

Three ducklings exposed to the standard *gock* call for 24 hours before and up to the instant of hatching showed no imprinting on that sound.

Mallard ducklings were running normally in 3 to 4 hours. Fear responses did not appear until 24 hours.

Beyond 28 hours no imprinting occurred ordinarily and only one duckling showed any imprinting beyond 24 hours. Four older ducklings (28 and 38 hours) were partially imprinted by association with well-imprinted ducklings during the imprinting runs.

Twenty-four ducklings were tested for inherent preferences. None responded to either the male or female model when it was still and silent. In addition, 15 showed no preference to either call note when they were simultaneously presented. Ten of the 15 gave no response and 5 responded once to each call. Eight ducklings showed a consistent preference for the *gock* and one responded repeatedly to the *quack*.

Four ducklings were imprinted on a motionless, non-articulated male model sounding the standard call. These four all made positive scores in Test 1, 2 and 3 and one, imprinted during the critical age, made a perfect score. Three additional ducklings imprinted by this method made scores over twice as good as another group of 3 ducklings imprinted on a box of the size of the model, giving the same call through an internal loudspeaker.

Five ducklings in two different groups were imprinted for 24 hours on a male model. These ducklings stayed with this male model in preference to live parent females with ducklings of their own age. One group of these, with some experience in following a silent model, followed a silent floating model although one of the parent female ducks tried to lure them away. The other group followed the floating model briefly and then returned to the similar model with wheels on shore but did not go to the live parent duck.

All but 2 of 13 bantam chicks tested for inherent preferences chose the recorded cluck of a mother hen in preference to the *gock*. None chose the *gock* in every test. Twenty-six bantam chicks were imprinted on the male model giving the standard call. These showed considerably less imprinting than Mallard ducklings. The critical age for imprinting chicks corresponds to that for ducklings.

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