SOME MECHANISMS OF FAMILY INTEGRATION IN DUCKS

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THE family life of ducks has been analyzed, to some extent, by various investigators. Some very useful studies have been made in Finland by Fabricius (1951), who has also summarized much of the earlier literature on the subject. Many of his observations were of birds trained to follow him while he acted as substitute-parent and observer. In the application of this profitable method he followed the earlier lead of Heinroth (1911) and of Lorenz (1935), who have given much impetus to the analytic study of avian social behavior, particularly in Europe. In North America, Mrs. Nice (1953) has successfully applied this same method to 12 ducklings of five different species.

In our own study, we have also made use of ducklings trained to follow a human observer. In addition, we have relied on the observation of duck families in nature and in pens. Many of our working hypotheses were derived from an earlier study of the development of social behavior in chicks of the domestic fowl (Collias, 1950, 1952). The justification for this application was shown by the remarkable degree of similarity in the results for these rather widely different types of bird.

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The observations to be described were made at the Delta Waterfowl Research Station in Manitoba. This station operates a series of incubators in which are hatched duck eggs collected from nests in the surrounding marshlands, thus providing a good opportunity to study the behavior of young ducklings under controlled conditions from the time of hatching. Furthermore, the abundant population of nesting ducks of various species in the immediate vicinity of the research station greatly facilitates field studies on the behavior of wild ducks under natural conditions. During three successive summers, we were able to use the facilities of the station through the kindness of the director, H. Albert Hochbaum, and with the support of the Wildlife Management Institute and the North American Wildlife Foundation. The director and Peter Ward, hatchery superintendent at Delta, were very helpful in giving us many useful suggestions during the course of our work. We wish to thank Milton Weller, James Teer, Arthur Hawkins, and Charles Evans for facilitating our field studies of ducks in nature, Arthur Hallerberg and James Crow for advice on the statistical treatment of our data, Milton Weller and Frank Mc-

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FIELD OBSERVATIONS

We focussed our attention on the response of following the parent, since ducklings which do not follow the mother and become lost are thereby automatically divested of all the vital benefits of family life. The most crucial period for the response of following would seem to be the time of leaving the nest. For this reason, field observations were made from a blind on the leaving of the nest under natural conditions by two broods of ducks, one representing a diving duck and the other a surface-feeding duck. The species concerned were the Canvasback (*Aythya valisineria*) and the Blue-winged Teal (*Anas discors*). We were particularly interested in the nature of the call notes used by the mother to attract the young.

The Canvasback brood was watched from a blind some 16 or 17 feet from the nest. The nest was placed over water in a dense growth of cattails. The brood left the nest on June 18, 1953. Two days earlier at 8 P.M., 9 of the 15 eggs had been pipped, and next morning 5 of the eggs were hatched. These 5 ducklings were dry when counted at 1 P.M. It follows that at least some of the 10 ducklings that left the nest at 9 A.M. the next morning had spent close to 24 hours in the nest before their final departure. This Canvasback nest, as is not uncommon in this area, had been parasitized by the Redhead (*Aythya americana*), and 6 Redhead ducklings hatched in addition to 4 Canvasback ducklings.

The female Canvasback was not heard to vocalize until the actual departure of the brood from the nest. The observer was in the blind for three hours on June 17, the day before the brood left (female was on nest 2 hours, 20 minutes). On leaving, the observer slipped quietly from the blind and stood to one side in full view of the female on her nest, which now contained 5 hatched young ones. She sat still and alert, with neck erect, and as the observer slowly took two steps toward her she flew directly up from the nest into the air, and then circled the nest several times at a distance of 40 to 60 yards, occasionally giving her alarm note, a rather harsh *kurr*. The young remained in the nest.

On June 18, the observer entered the blind at 5:45 A.M. The female had apparently left unseen at his approach and did not return for 2 hours. In the meantime, the ducklings were left in the nest unattended. After the observer had been in the blind for 20 minutes one duckling left the nest and the company of its nestmates. It soon began giving distress calls which promptly ceased when it climbed back into the nest and rejoined the others, a few minutes after having left. Some 45 minutes later, six of the young left the nest together and commenced feeding; this local excursion extended to a distance of at least six feet from the nest. Whenever one of the ducklings became separated from the others it gave distress calls until it had regained the company of its fellows. The young returned to the nest about 20 minutes after leaving. The mother was nowhere to be seen or heard during all this time, and before she returned, some of the young made another local excursion, this time lasting about 15 minutes. As they climbed back into the nest on their return and crowded together, the ducklings gave contentment notes.

Just after the last duckling was in the nest, the mother finally returned, silently. The young gave contentment notes as she got up on the nest. She stood and preened herself for six minutes before settling down to brood the young. From time to time the ducklings were heard to give contentment notes. For one hour, the mother, apparently silent, brooded the young. At first she was quite alert and then gradually dozed off, head and beak turned backwards and resting on her back or shoulder.

She then roused and became very alert with neck upstretched, looking this way and that for 10 minutes, particularly toward the blind. At 9:01 A.M. she left the nest, and within one minute all of the ducklings had followed her into the water. To quote from the (N.C.) field notes:

> As the female enters the water she commences to call, at the same time swimming slowly and quite steadily, directly away from the nest. . . . She calls a low-pitched *kuk-kuk-kuk-kuk-kuk-kuk*, etc., about six times per second, i.e., as fast or faster than a man can say it. Her call is so faint, that although I can hear it very definitely and distinctly in the blind, 15 to 20 feet away, I doubt if I would be able to hear it, had I been as much as 30 feet away. In general, her accent is quite steady with no special emphasis on any one note. The rhythm of the *kuk-kuk* . . . is occasionally broken as if she had sometimes to take a breath, and once or twice her voice broke into a louder but still faint, somewhat quacking note. In the *kuk-kuk* . . . call, I occasionally hear higher overtones, but these are weaker than the fundamental. This call is *not at all harsh*, thus differing strongly from her usual alarm note. The ducklings follow the female *at once* with no evident hesitation, but they do trail out in single file rather than in a compact mass, and I hear a few distress calls, probably from ducklings that are temporarily a few inches or a foot behind in the fast moving procession. The entire act of leaving the nest takes only about one minute. The female moves off to the left in the cattails, calling continually, and disappears from view almost at once, and within two minutes the family can no longer be seen or heard.
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> At 9:45 the female returns silently to the nest, apparently alone; she climbs up on

the nest and gives several very faint, low-pitched notes that are not at all harsh and sound like purring. Within 10 to 20 seconds, the ducklings all show up, coming from the same direction as that from which the female had appeared. Some ducklings at once climb up after her, others swim about the nest 2 or 3 feet away, before returning to the nest. The excursion led by the female was about 45 minutes long.

After returning to the nest the female preens herself vigorously for 10 minutes just before and while she broods the ducklings. Then she dozes, occasionally rousing herself to preen or to look about with neck erect in alert fashion. After one-half hour she appears to be asleep, with bill tucked back, but she does open her eyes at a noise.

At 10:47, after a period of alertness lasting about 10 minutes, the female stands up and then leaves the nest. Several times before actually leaving the nest she takes a step as if to leave the nest, and some of the ducklings precede her into the water as if stimulated by her intention movements and eager to leave. This time she does not start her whispered *kuk-kuk-* etc., until actually in the water, and her calling is so faint that I can barely hear it 20 feet away. As she swims off with the ducklings she makes a slight splashing noise which perhaps also serves to attract the ducklings. She leaves the nest more to the rear this time, i.e., in a direction away from the blind.

12:00 noon. One hour and 13 minutes later she has not returned to the nest with her brood, and I leave the blind.

The Blue-winged Teal brood was watched from a blind only four feet from the nest, which was located in a field of grass. By placing the blind between the nest and a road about 20 feet from the nest, the observer made it possible to enter and leave the blind at will without flushing the hen from the nest.

All of the 11 eggs were pipped on July 13, 1954, at 9:15 A.M., but none were hatched when checked at 10 A.M. on the next day. However, some of the ducklings hatched in the afternoon, and in contrast to her relatively sleek appearance before the hatching, the female was now puffed out, and the feathers of her body, especially of the rump, were raised and her wings were partly spread out and drooped over the young. It was later found that all but one of the eggs hatched.

On July 15, the observer entered the blind at 5 A.M., and about two hours later the female commenced to call a very faint, somewhat nasal *kunk! kunk! kunk!* This was the first time that the female had been heard to vocalize while on the nest, although 8 hours had been spent in this blind on the preceding two days (3 hours on July 13, 5 on July 14) by myself or another observer (F. McKinney), including one hour after at least some of the ducklings had hatched. The rate of calling was about one note per second, sometimes speeded up to two notes per second. Each note was very brief and quite soft. Soon the female was calling regularly while she brooded the young. The notes were often given at a steady rate but sometimes were in groups of 3 or 4 notes. There was no perceptible movement of her bill or throat as she called, but her breast and tail jerked very slightly with each *kunk!* Sometimes the female would fall silent for 5 or 10 minutes, and then she would again commence to call. Occasionally she would preen her breast.

At times the young were all beneath the female; frequently some emerged from beneath her. One or two ducklings gradually wandered as far as eight inches from the edge of the nest but maintained close contact with the mother and rest of the brood by a bridge of other ducklings in between.

At 8:18 the female became quite restless and alert, looking about repeatedly in a cautious fashion. At 8:21 A.M. the brood left the nest. To quote from the (N.C.) field notes:

> The female leaves, walking two or three feet from the nest into the grass, and while she does so, calls more *loudly* than before and *faster* (up to 3 calls per second). All of the young face her, and within 15 seconds one of them starts out after her—she continues calling, but the rest of the ducklings just crowd together in the nest and watch her, but do not follow. Within one minute the mother returns to the nest, settles down over the young, and now calls only occasionaly.
>
> Two minutes later she rises and again leaves the nest, down another of her regular "walk-ways," calling steadily and rapidly (3 calls per sec.) as she goes. The young looked toward the mother, crowded to the side of the nest nearest her, and within 5 to 10 seconds after she had stepped off the nest, they ended their hesitation and while keeping virtual contact with one another they stream out of the nest and follow after her. I can hear the hen calling as she moves off to the southeast and lose track of her after she is 15 to 20 feet away. This distance was covered in about one minute. One egg that failed to hatch is all that is left in the nest.

Although the observer remained quietly waiting in the blind for one hour, the family did not return; nor was the family on the nest when a cautious check was made at dusk of that same day.

A number of points of interest to the analysis of family integration emerged from the observation of these two families at a critical stage in their history and can be summarized as follows.

1. The female, in the case of both species, was not heard to give the attraction calls for the young until after they had hatched, although the female on her nest containing pipped eggs was observed for some hours before the young hatched. Frank McKinney informs us that he has heard a Canvasback hen on 5 well-chipped eggs emit some quiet notes sounding like "*tuc-uk-uk-uk*." McKinney has made intensive observations of incubating Mallard hens, and wrote us as follows (February 8, 1955): "No calling occurred on the nest during incubation. From the first stage of hatching (eggs chipped) the female calls frequently. At first the notes are very quiet indeed and can only just be heard as a slight squeaking from a few yards distance. As hatching proceeds, notes become louder."

2. After the first young hatched, there was a period of some 18 hours in the Blue-winged Teal brood and about 24 hours in the Canvasback brood, before the family finally left the nest. This quite prolonged period of association in the nest provided considerable opportunity for the mother and young to become conditioned to each other.

3. When the female left the nest very abruptly, as when the female Canvasback flushed directly from her nest, the young apparently made no effort to follow her.

4. The leaving of the nest by the Canvasback brood was a gradual and comparatively drawn out process, with a number of short preliminary excursions by the young in the absence of the mother and one such excursion with her; but leaving of the nest appeared to be a relatively abrupt affair with the Blue-winged Teal brood. This difference is associated with the location of the nest over water in the former species and with a land nest in the latter; however, one cannot generalize without observation of more nests and broods.

5. When a duckling (Canvasback) became separated from the rest of the brood, it gave distress calls; when it rejoined the brood, it gave contentment notes.

6. In both species the female became very alert and watchful shortly before leaving the nest.

7. In the case of the Blue-winged Teal, the female gave her attraction notes for the young more loudly and rapidly at the time the family actually left the nest. In the case of the Canvasback brood, the female was heard to give this call only at the time the family left the nest but may have given it when not observed. Milton Weller tells us that he has heard a female Redhead give the *kuk-kuk* or attraction call, after the young had hatched and before as well as after leaving the nest.

8. The young do not necessarily follow the mother immediately on her leaving the nest, even when she calls them, as was seen in the case of the Blue-winged Teal brood.

9. In both species the attraction call of the moving parent for the young, when compared with other call notes of the species, was relatively soft and low-pitched and consisted of brief, rapidly repeated monosyllabic notes of weak intensity. The broody call of the female Redhead, as described to us by Milton Weller, is quite similar to that of the female Canvasback. We have also heard the broody call of the females of the Baldpate (*Mareca americana*), Lesser Scaup (*Aythya affinis*), and Mallard (*Anas platyrhynchos*); in these species, the call resembles that of the other species in consisting of brief repetitive

notes of relatively low pitch and weak intensity. These same characteristics are found in the clucking of a broody domestic hen. In fact, it was found readily possible to attract ducklings of Canvasback, Redhead, and Mallard on the day of hatching by clucking to them.

ANALYSIS OF THE RESPONSE OF FOLLOWING

It is well known that ducklings can be readily trained to follow a human observer, and our experience resembled that of other observers in this regard.

The response of following the parent seems to be a response to sound and movement as such. If the person being followed suddenly ceases all sound and movement, a day-old duckling will at once become lost and gives its distress call, even though it happens to be perched on the shoe of the substitute parent.

In analyzing the response of following the parent by ducklings, we decided it would be best to start work with ducklings on the day of hatching. The best age for the development of the response of following comes during the first day after hatching as we had previously observed in chicks of the domestic fowl (Collias, 1950, 1952) and as Fabricius (1951) had found for the Tufted Duck (*Aythya fuligula*). In general, ducklings older than about 24 hours were likely to have developed a marked fear response, which causes them to avoid any large approaching object. Ducklings younger than about 5 hours were likely to be too weak in their legs to follow very well.

It is evident that both innate and learned factors, i.e., factors of both heredity and of individual experience, enter into the development of the response of following the parent. Innate tendencies, which will be summarized first, include responses to sound and movement.

In the field, while holding motionless and imitating the parental attraction notes of the Canvasback hen, one of us attracted a mixed brood of Canvasback and Redhead ducklings that had just left the nest, causing them to turn back and swim directly toward the observer, approaching to within a few feet of him.

Canvasback and Redhead ducklings in the first day of hatching, taken from the incubator and tested at once, were found to move toward an imitation of parental attraction notes under conditions under which they could not see the source of the sound. To an imitation of the parental alarm call played repeatedly on a commercial duck-call they were rather indifferent, or else moved away (Table 1). It should be remembered that these ducklings were in their first day after hatching and that their fear response had not yet become fully developed.

These tests were made in a runway that was three feet long and lined with cheese cloth walls. It was illuminated from within so that the observer could see the duckling, but the duckling could not see the observer. The duckling was placed in the center of the runway, and the sounds were emitted by the observer at one end of the runway. Each test lasted 30 seconds, with a 30-second interval of silence between tests. Each duckling was given 3 tests to the parental attraction notes and was then given 3 tests to the alarm call: the order of these two sounds was changed with different ducklings. Each figure in Table 1 shows the distance moved in all 3 tests taken together.

TABLE 1

CANVASBACK AND REDHEAD DUCKLINGS IN FIRST DAY AFTER HATCHING MOVE TOWARD PARENTAL ATTRACTION NOTES, AND AWAY FROM ALARM NOTES

		Distance moved in feet		
		Attraction notes	*Alarm calls*	*Difference**
Canvasback	1	0.5	−1.0	1.5
	2	0.0	−2.0	2.0
	3	10.5	0.0	10.5
	4	3.0	0.0	3.0
	5	11.0	−1.5	12.5
	6	6.5	−5.5	12.0
Redhead	1	1.5	−3.0	4.5
	2	6.0	0.0	6.0
	3	3.5	0.0	3.5
	4	6.5	0.0	6.5
	5	2.0	+0.5	1.5
	6	5.5	0.0	5.5
	7	1.0	−7.0	8.0
Average		+4.5	−1.5	6.0

* P = .0001 (Student's method for small numbers).

Another series of tests, done with Mallard ducklings, also on the day of hatching, using much the same procedure as outlined above, showed that these ducklings go much more readily to low-pitched, short notes than to high-pitched, short notes. They are also more attracted to short notes than to long notes, regardless of pitch (Table 2). The differences in each case were statistically significant.

The Mallard eggs used in this test were collected from the nests of wild birds and were not from game-farm stock. The same is true of all Mallards and other species of ducklings used in tests described in this report. The duckling was placed at one end of the runway.

TABLE 2

MALLARD DUCKLINGS, ON DAY OF HATCHING, GO MUCH MORE READILY TO LOW-PITCHED, BRIEF NOTES THAN TO HIGH-PITCHED, LONG NOTES

Duckling	*Age in hours*	*Number of feet moved toward sound*			
		Low-short	*High-short*	*Low-long*	*High-long*
1	1	17.5	16.0	0.0	0.0
2	4–5	52.0	45.0	13.0	13.0
3	6	22.0	6.5	0.5	3.0
4	7	2.5	−1.0	0.0	0.0
5	7	45.0	30.0	9.0	15.0
6	7	35.0	12.0	12.0	1.0
7	8	43.0	20.0	6.0	8.0
8	10	15.0	6.0	6.0	1.0
9	4	21.0	17.0	7.5	12.0
10	10	8.0	7.0	2.0	4.0
11	11	19.5	15.0	0.0	0.0
Average		25.5	15.5*	5.0	5.0

* Probability of chance difference between low, short and high, short notes = .002 (Student's small numbers formula).

The observer, at the other end of the runway, sounded the notes on a pitch-pipe. Each test lasted one minute, with a 30-second interval of silence between tests; each duckling was given 3 to 5 tests for each type of sound. For low notes, the E below Middle C was used; for high notes the E in the second octave above Middle C was used. Short notes were as brief as the observer could make them (a fraction of a second long). Long notes were about 3 seconds long. All notes were played repetitively, with only a fraction of a second between notes. The four sounds tested were low-short, high-short, low-long, and high-long. The sequence of the different sounds was changed systematically with different ducklings.

Another series of tests with Mallard ducklings was conducted, and although the same general procedure was used, the *rate* of these notes was varied in different tests. Only low-short notes were used. Each duckling was tested to notes delivered at the rate of 3 per second, 1 per second, and 1 every 3 seconds. An interval of 30 seconds was maintained between tests. The results in Table 3 show that Mallard ducklings on the day of hatching go much more readily to high than to low rates of artificial sound repetition.

The preceding tests showed that ducklings can be attracted to appropriate sounds when they cannot see the source of the sound. It was also demonstrated in the laboratory that ducklings on the day of hatching may follow a *moving* object in the absence of sound

TABLE 3

MALLARD DUCKLINGS, ON DAY OF HATCHING, GO MUCH MORE READILY TO HIGH THAN TO LOW RATES OF ARTIFICIAL SOUND REPETITION. ONLY LOW-PITCHED, BRIEF NOTES WERE USED

Duckling	*Age in hours*	*Feet moved toward sounds of indicated rate* *3 per sec.*	*1 per sec.*	*1 per 3 sec.*
1	4–5	74	37	3
2	6	39	1	3
3	7	29	15	3
4	8	47	0	0
5	10	24	0	0
6	4	10	3	0
7	10	18	3	6
8	11	30	0	13
9	9	27	18	11
10	1–2	7	3	3
Average		30	7	5

orientation. The moving object consisted of a man (N.C.) walking slowly away from or toward the duckling. To muffle any sound of walking he wore heavy wool socks, and as an additional safeguard against extraneous noises sometimes turned on a ventilator to provide a continuous background noise that apparently was not disturbing to the duckling being tested.

An attempt was made to standardize these tests. Redhead ducklings were taken individually from the incubator, given a few minutes to adapt to the light, and placed at the feet of the substitute parent, who then proceeded over a standard course, moving slowly and steadily away from the duckling at the rate of about one step per second to a distance of 15 feet, and back again. Each trip of 15 feet was considered to be one trial, and the number of feet that the duckling moved toward the leader was recorded for each trial by another observer (E.C.). The trials continued until the duckling followed regularly, the arbitrary criterion being ten successive trials of perfect following. The response of following improved progressively until the duckling followed regularly (Table 4), apparently as a result merely of the experience of following.

If, in addition to walking in front of the duckling, the human observer imitated the parental attraction notes (*kuks*) for the young, the response of following improved at a significantly greater rate than was true if the observer remained silent (Table 5). In fact,

TABLE 4

REDHEAD DUCKLINGS ON DAY OF HATCHING FOLLOW A MOVING OBJECT IN ABSENCE OF SOUND ORIENTATION

		Number of trial in which follows		
Duckling	*Age in hours*	*Starts*	*Goes full distance*	*Regularly (10 successive trials)*
1	11–15	1	13	50*
2	12–15	21	32	63
3	15–18	1	10	9
4	15–18	11	25	41
5	15–16	9	18	57
6	15–16	15	20	20
7	16–19	3	15	15
8	16–19	7	10	10
9	17–20	19	55	55
10	16–22	10	28	47
Average		10	23	37

* Only nine successive trials for this duckling.

TABLE 5

REDHEAD DUCKLINGS FOLLOWED SOUND PLUS MOVEMENT BETTER THAN THEY FOLLOWED MOVEMENT ALONE

	Movement alone (10 birds)	*Movement + sound (12 birds)*	*Probability**
First trial in which follows	9.7	6.6	0.37
First trial follows full distance	22.6	10.3	0.025
Follows regularly (10 successive trials)	36.7	18.2	0.020

* Fisher's formula for small numbers.

TABLE 6

REDHEAD DUCKLINGS FOLLOWED MOVEMENT PLUS SOUND MUCH BETTER WHEN RETESTED 1 TO 6.5 HOURS AFTER THE INITIAL TEST. AVERAGES OF TEN BIRDS

	Initial test	*Retest*	*Probability* of chance difference*
First trial in which follows	7.5	1.0	0.072
First trial follows full distance	13.1	1.4	0.053
Follows regularly (10 successive trials)	25.9	4.8	0.003

* Student's method of paired comparisons for small numbers.

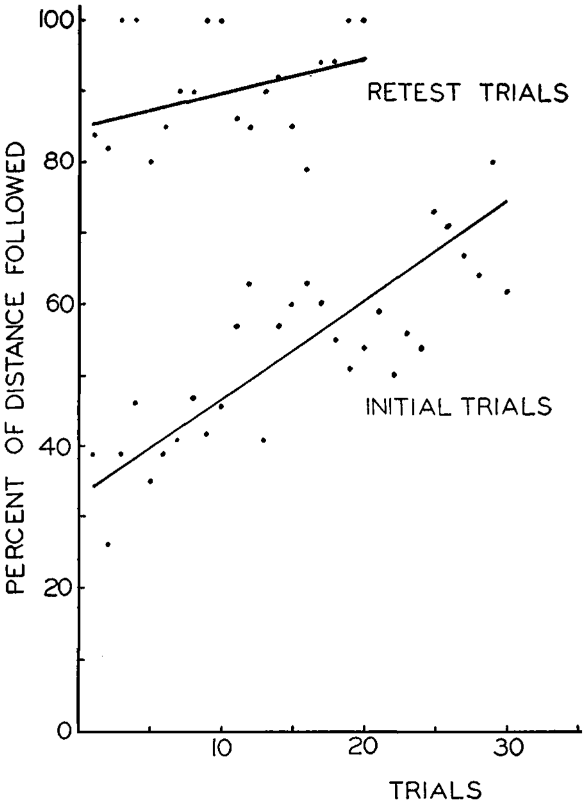

Figure 1. Redhead ducklings follow a human observer much more readily when retested 1 to 6.5 hours after the initial test. This graph illustrates the variability of the data. Each dot represents the per cent of the distance followed over a standard course on any given trial, and is the average of ten different ducklings.

the ducklings followed nearly twice as well as a result of this intersensory summation.

Another series of tests confirmed the idea that learning quickly strengthens the response of following. A duckling taken from the incubator at an appropriate age, as a rule, does not immediately follow a person but may do so after only a few minutes. If a duckling was retested within a few hours, we found that the duckling, as a rule, followed immediately and consistently (Table 6).

Figure 1 shows the same results in another way to bring out the variability of the data. Each dot on the graph represents the percentage of the distance followed on any given trial and is the average for all 10 Redhead ducklings for that trial. It will be seen that, despite the wide scatter of dots, there are two distinct and well separated groups of dots representing the initial and retest trials, respectively.

The period of time (1 to 6.5 hours) between the first tests and the retests seems too long for the difference to be accounted for by conventional ideas of physiological temporal summation. Maturation, in the sense of innately determined growth changes, might enter in but would seem to be unimportant in this experiment, because the improvement in following on retesting was not closely associated with the age of the birds.

Learning is further important to the attachment of ducklings to their specific mother. Thus, the ducklings belonging to a Mallard hen within an outdoor flight pen, on the day of leaving the nest, were seen often to follow older ducklings in the pen as well as their mother. This often resulted in their being attacked and bitten by these ducklings; and within a few days, they had learned not to follow the older ducklings.

Learning has its limitations. We gathered some evidence indicating that it is very difficult if not impossible for training to reverse the normal preference of a duckling for sound stimuli having certain specific properties, for example, low pitch, if the duckling has had the opportunity to hear the sound it prefers. During the first 5 days after hatching, two Redhead ducklings were each exposed repeatedly to a series of low-short notes alternating with a series of high-short notes, each series of notes being continued for 10 seconds. This was done for more than one-half hour daily for each duckling. One duckling was consistently "rewarded" only while the high notes were sounded, the reward being physical contact with and sight of repeated movements of the human observer, as substitute-parent. The other duckling was rewarded only while low-pitched notes were being sounded. Both ducklings, when tested in the cheesecloth runway on the fourth, fifth, and sixth days after hatching, continued to prefer low-pitched to high-pitched notes. It is possible that repeated exposure to the former but not the latter notes functioned as its own reward. Such selective and innate responsiveness to appropriate stimuli with disregard of inappropriate stimuli must play an important role in limiting and channeling the development of the response of following the parent.

Another important factor in the development of the response of following the parent is the social facilitation of this response through the presence of other members of the brood. We were able to induce two three-day-old Redhead ducklings (old enough to have a marked fear response) to follow us, by placing with them two other ducklings that had previously been trained to follow us. This suggests an important role of leadership among ducklings in nature. The first ducklings to hatch are not only older but probably have developed a stronger tendency to follow the mother than is true of the last ducklings to hatch. The attachment of the ducklings to one another will, therefore, help the laggards to maintain contact with the mother through the intermediacy of the better followers, until the response of following has become fully developed in these youngest ducklings.

The brood shows a strong tendency to keep together, whether or not a parent is present. Thus, it was often observed that ducklings hatched in the incubator, when separated from the other ducklings, gave loud and repeated distress calls until they were able to rejoin the group. One downy Mallard duckling, removed from the company of other ducklings in the incubator and introduced on the day of hatching into a box containing two five-day-old Redhead ducklings, was attacked persistently by the Redheads; but every time it was rescued by the observer and isolated, it gave distress calls until it was returned to the company of its tormentors.

TABLE 7

REDHEAD AND CANVASBACK DUCKLINGS MOVE MORE READILY TOWARD CONTENTMENT NOTES THAN TOWARD DISTRESS CALLS OF OTHER DUCKLINGS OF THESE SPECIES. DUCKLINGS WERE TESTED INDIVIDUALLY 15–30 HOURS AFTER HATCHING

	Number of ducklings tested	*Latent (seconds)*	*Time required to reach source of sound (seconds)*
Contentment notes	12	26	29
Distress calls	10	61	59
Probability of chance difference*		0.03	0.06

* Fisher's formula for small numbers.

The brood is kept together in part by means of the contentment notes, which therefore function as contact notes. A series of tests with Redhead and Canvasback ducklings in the cheesecloth runway showed that ducklings are more attracted by contentment notes than by distress calls (Table 7). This suggests that a lost duckling is more likely to go to the intact brood in preference to joining another lost duckling. This difference in attractive power was tested by our observing the response of Canvasback and Redhead ducklings placed individually in a runway about 2½ to 3 feet from one end where there was a compartment screened with paper and wire behind which other ducklings could be placed without being seen by the test duckling. When a group of ducklings was placed in the end compartment, the ducklings generally kept up a continual twitter of contentment notes. When a single duckling was placed in the end compartment, it gave distress calls more or less continuously until the end of the test. Each test lasted four minutes, and the observer recorded the latent time before the test duckling started to move toward the source of sound and also the time required to reach the screen, once the test duckling started to move. Generally, the test duckling remained at the screen when a group of ducklings emitting contentment notes was behind the screen. If, instead, there was another duckling giving distress calls behind the screen, the test duckling, as a rule, did not remain very long before leaving, moving back and forth in the runway while giving its own distress calls.

The response of following the mother is made possible by the tolerance of the mother for the brood and of the various members of the brood for each other. A brood of young ducklings in the flight pen was attacked not only by the older ducklings but also by all of the five adults in the pen, with the exception of their mother and another broody female Mallard. At the same time, the mother frequently attacked and drove other ducklings away from her brood. Aggressiveness between ducklings reared together in the incubator was rarely observed before the third or fourth day after hatching; it would seem, therefore, that this delay in the development of aggression within a brood would permit the members of the brood to remain together until they had developed a strong attraction for one another.

The aggression of ducklings and their mother toward other ducks and ducklings probably helps to maintain the family size within manageable limits. When reinforced by the aid or presence of the mother, ducklings of the brood readily attack much older and larger ducklings. In fact, one downy Mallard duckling, in the second day after hatching, was seen to chase an adult female Mallard.

DEVELOPMENT OF SPECIES RECOGNITION

An important part of the study of family life in ducks concerns the relationship of family life to species recognition.

Objective evidence for species recognition in ducks comes from the obvious tendency of ducks of different species to mate and to aggregate with their own kind and to be more or less segregated from other species. This species segregation prior to the period of sexual activity could result from one or any combination of three groups of responses: (1) the responses of the parent to the young, (2) the responses of the young to the parent, and (3) the responses of the young to other ducklings.

To test the responses of the mother to ducklings of strange species, experiments were conducted in a large flight pen. The eggs were removed from an incubating Baldpate and from an incubating Mallard hen, and eggs of other species were substituted. In the case of the Baldpate these eggs were Mallard eggs, and three of them hatched. The young were tolerated, brooded, and defended, as were ducklings of three other species—2 Redheads, 2 Canvasback, and one Blue-winged Teal—ranging in age from 1 to 4 days, which were added to the brood on the day after the first young hatched.

The substitute brood of the Mallard hen included 4 Redheads and 2 Mallard ducklings, all of which were hatched beneath the hen. This brood provided a somewhat better test of species recognition of ducklings by the mother than did the Baldpate brood mentioned above, since the Mallard hen had a choice between her own and a strange species. Nevertheless, this Mallard hen tolerated, brooded, and defended the Redhead ducklings just as well as she did the Mallard ducklings.

After 5 days a strange Mallard duckling of the same age as the ducklings of the brood was introduced into the pen near the family and at once was attacked by various older ducklings that did not belong to the family. The mother Mallard, on hearing its distress cries, swam to its aid, drove off the older ducklings, and then herself bit the downy duckling she had rescued until it managed to escape from her. Still this Mallard hen continued to tolerate, defend, and care for the 4 Redheads of her mixed brood, in addition to her own 2 Mallard young.

No completely satisfactory data were secured regarding the preference of ducklings for a parent of their own species, but it was noticed that the various species of ducklings in the mixed brood of the Baldpate hen followed her as a more or less coherent group. In the mixed brood of the Mallard hen, the Redhead ducklings followed the Mallard hen just as well as did the Mallard ducklings. However, Redhead ducklings due to the parasitic habits of the species might conceivably have a relatively strong tendency to follow a mother of another species. In another case, a brood of Mallards was hatched beneath a Ring-necked Duck (*Aythya collaris*) female, and the ducklings were adjudged to follow their foster mother poorly and to be more scattered than we have observed to be normal for young Mallard broods. This Ring-necked mother was broody, defended, called, and persistently followed her straying and scattered brood. This last case suggests that at least in some species of ducks the normal family integration and species segregation may depend partly on inherited tendencies of the young to prefer a mother of their own species, perhaps related to inter-locking behavior patterns of mother and young.

Ducklings may be hatched with or develop some degree of attraction to specific call notes of broody birds of certain other species, and their attraction to some call notes may develop much sooner than does their attraction to other calls. For example, six Mallard ducklings hatched beneath a broody domestic fowl would go to her clucking, which was given in response to the distress calls of the isolated duckling, within six hours of hatching, even when the hen was screened from the view of the duckling. But the daily tests showed that it was not until their second week that the ducklings began to come promptly and regularly to the food calls of the hen, whether they could see her or not. It seems probable that normally ducklings are capable of learned reinforcements to the parental call-notes of their own as well as those of some other species.

Attention was next turned to the study of the tolerance of ducklings for other ducklings. It has often been observed in the course of routine work at the Delta hatchery that the different species eventually tend to segregate out from each other to some extent, although raised in the hatchery together, often from the same incubator tray, and without the complication of a parent. Evidence was secured suggesting that specific intolerance between ducklings of different species helps to account for this tendency toward species segregation. For example, when a mixed group of 3-weeks-old Mallard and Pintail (*Anas acuta*) ducklings was driven out of the hatchery into a pond through a door that had been left open for some days, the Pintails promptly reëntered, being driven back in by other Mallard ducklings which had been resting outdoors near the door. The result was a neat separation of Pintails indoors from Mallards outdoors.

The aggressive-submissive interactions in a mixed group containing 22 Mallards and 22 Pintails, hatched together and kept together in the same brooder, were observed and tabulated during their first 11 days after hatching. It was found that the Mallard ducklings dominated and were intolerant of the Pintail ducklings (Table 8). Pintail ducklings are much grayer than are Mallard ducklings. During the period of observation there seemed to be some tendency toward species segregation, but it was not very marked or definite.

TABLE 8

MALLARD DUCKLINGS DOMINATED AND WERE INTOLERANT OF PINTAIL DUCKLINGS OF THE SAME HATCH, WHEN REARED TOGETHER

Group composition	22 Mallards: 22 Pintails
Age of birds	9–11 days
Time observed	4 hours, 30 minutes
Dominant/subordinate interactions	
Mallard/Mallard	22
Pintail/Pintail	6
Mallard/Pintail	125
Pintail/Mallard	14
Mallard dominance; chance probability* P < .0001	
Intolerance of Pintails; chance probability* P < .0001	

* Chi Square test.

TABLE 9

REDHEAD AND CANVASBACK DUCKLINGS DOMINATED AND WERE INTOLERANT OF MALLARD AND PINTAIL DUCKLINGS OF THE SAME HATCH, WHEN REARED TOGETHER

	Group A	*Group B*
Group composition	37R + C: 9M: 4P	41R + C: 5M: 2P
Age of birds	5–6 days	1 week
Time observed	2 hours	2 hours, 40 min.
Dominant/subordinate interactions		
Redhead or Canvasback/Redhead or Canvasback	0	10
Mallard or Pintail/Mallard or Pintail	0	2
Redhead or Canvasback/Mallard	15	176
Redhead or Canvasback/Pintail	31	49
Mallard or Pintail/Redhead or Canvasback	1	0
Chance probability*		
Dominance by Redhead and Canvasback	P = .03	P < .0001
Intolerance by Redhead or Canvasback of Mallard or Pintail	P < .0001	P < .0001

* Chi Square test.

Similar observations were made on two large groups of ducklings, each of which contained a majority of Redhead and Canvasback ducklings, and a minority of Mallard and Pintail ducklings. All of the ducklings within each group came from the same hatch and were reared together. It was found in each group that the Redhead and Canvasback ducklings dominated and were intolerant of the

Mallard and Pintail ducklings. These results were also statistically significant (Table 9). We have also observed an instance in which a lone Canvasback duckling was kept in a group of Mallard and Pintail ducklings, all of which were somewhat older and larger than was the Canvasback. Nevertheless, this greatly outnumbered little Canvasback duckling consistently dominated these other species, with the exception of one Pintail about three times its size.

Resident Mallard ducklings may dominate strange Redhead ducklings introduced into their living quarters and attack the latter much more often than they attack strange individuals of their own species. Thus when we introduced 2 Redheads, about 3 weeks old, and 3 Mallard ducklings, 15 to 17 days old, into a yard containing six resident Mallard ducklings, also 3 weeks old, the resident Mallards attacked the Redheads several times as often as they attacked the introduced Mallards (Table 10). Eventually, all of the introduced birds were driven into hiding in various places in the yard. During succeeding days there followed a period of gradually increasing toleration by the resident birds for the newcomers.

TABLE 10

MALLARD DUCKLINGS ATTACKED STRANGE DUCKLINGS OF THE SAME SPECIES LESS FREQUENTLY THAN THEY ATTACKED STRANGERS OF ANOTHER SPECIES

	Species introduced	
	Mallard	*Redhead*
Number of birds introduced	3	2
Attacks by six resident Mallards		
First 5 minutes	28	96
Second 5 minutes	33	134
Total attacks	61	230
Probability of chance difference between attacks on Redheads and on Mallards*	P < .0001	

* Chi Square test.

One might inquire as to the significant cues in this *interspecific intolerance*, and an experiment was arranged to help answer this question. It happens that Canvasback and Redhead ducklings, like the young of diving ducks (Aythyinae) in general, lack the conspicuous eye-stripe of ducklings of the Mallard, Pintail, and most other surface-feeding ducks or Anatinae (Hochbaum, 1944: 101). Twenty Redhead ducklings were painted with black eyestripes, and 20 other Redhead ducklings of the same hatch and raised in the same brooder were left with faces unpainted. Observations were made almost daily during the first two weeks after the ducklings had hatched, for a total time of 8½ hours, and we saw twice as many attacks on ducklings with artificial face-stripes as on the normal, plain-faced ducklings. The difference was statistically significant (Table 11). Actually, the rate of aggression was so low, compared, for example, with the frequency of attacks by Redhead ducklings on Mallard ducklings reared with them, that it seems probable that other cues to species recognition, possibly involving voice and other differences in behavior are also important.

Some confirmation of this supposition was obtained, when it was observed that 8 Redheads and 7 Mallards reared together and then tested individually in the cheesecloth runway when about a week old, moved toward individuals of their own species under conditions where they could hear but not see other ducklings. A group of ducklings of each of the two species was hidden at either end of the runway within a special compartment. Interestingly enough, each duckling group in the end compartments would answer the distress calls of the lone test duckling of its own species but was either silent or called much less often in response to the test duckling of the other species.

TABLE 11

REDHEAD DUCKLINGS PAINTED WITH EYE-STRIPES WERE ATTACKED MORE OFTEN THAN UNPAINTED REDHEAD DUCKLINGS, BY OTHER REDHEAD DUCKLINGS

	Bird attacked	
	Striped face	*Unpainted face*
Aggressor		
Striped face	23	11
Unpainted face	19	8
Total reactions	42	19
Probability of chance difference*	P = .003	

* Chi Square test.

During our third summer of study it seemed desirable to check more closely the inter-individual relations of ducklings with respect to dominance and grouping behavior. Accordingly, a group of 7 Redheads (5 female: 2 male) and 9 Canvasback (6 female: 3 male) of the same hatch were individually color-banded, raised together, and watched for a total of about 16 hours when they were from 2 weeks to 2 months of age. A total of 675 aggressive-submissive interactions was observed, and 104 of the 120 possible paired relationships between different individuals, i.e., permutations (combinations) as determined by the formula, $n(n - 1)/2$, were observed. In only 11 out of 86 combinations in which more than one interaction was seen, was a reversal of dominance involved, i.e., one bird dominated another bird and was in turn dominated by this same bird at a later date. Furthermore, in 23 combinations, a given individual dominated the same subordinate bird on 10 or more different occasions and was never seen to be dominated by this subordinate. These results indicate that even among these young birds dominance relationships were consistent between different individuals most of the time.

Each of the 7 Redheads was seen to dominate all or all but one of the 9 Canvasbacks, whereas none of the Canvasbacks ever dominated more than one or two of the Redheads, and only one Canvasback consistently dominated a Redhead (the smallest one). The Redheads dominated the Canvasbacks in 12 times as many encounters as the reverse. The dominance order, regardless of species, showed no consistent parallel to differences in sex or weight. The average weight of the Redheads near the close of the observation period was 611 grams, that of the Canvasbacks was quite similar, 669 grams.

The sensory cues involved in the species recognition were not established, although it was noted that the Canvasbacks almost from the start had a more sloping profile, a lower-pitched voice, and more often used a rolling alarm call than did the Redheads.

The Redheads were relatively intolerant of Canvasbacks, and on the average, the Redhead ducklings dominated each of their Canvasback subordinates almost twice as often as they dominated each of their Redhead subordinates. A point of some interest was the fact that the Redheads showed more intraspecific tolerance than did the Canvasbacks, which belonged to the subordinate species. On the average, each Redhead dominated its Redhead subordinates much less frequently (ratio of 7 to 12) than each Canvasback dominated its Canvasback subordinates.

In general, aggression did not occur in relation to food competition but was often observed when one bird was moving about and disturbing resting birds, and aggressions could readily be provoked by moderately crowding the birds. We often observed that the more wary Canvasbacks would quickly crowd into the corner farthest from the observer, but the Redheads would then preëmpt this corner and would repeatedly drive away the Canvasbacks, thus gradually resulting in a segregation of the two species with the dominant Redheads in the preferred location. A quite typical grouping pattern when the birds were undisturbed was with a group of Redheads in one place surrounded by a scattering of Canvasbacks on the periphery of the Redhead group.

However, dominance relations and differences in wariness were only part of the mechanism of species segregation. Partial species segregation began to be noticeable at about the second week after hatching, but species segregation was never complete under the conditions of study. At times it seemed evident that individuals would walk over and form a group with other members of their own species, although no threatening or driving by the other species was involved. It was as if an actual species preference existed; to what extent this phenomenon might depend on conditioning is conjectural.

SUMMARY AND CONCLUSIONS

In concluding this report on the analysis of family integration in ducks, we think that our evidence could and should be made still more objective by the consistent use of mechanical sound recordings and of mechanical movement, in an appropriate way. But such devices often lack much of the flexibility so important to the initial stages of any investigation. In the present analysis we have attempted to indicate what we believe to be some of the more profitable lines for further investigations and to contribute some convincing evidence for these conclusions.

The following conclusions seem justified for at least some species of ducks. Ducklings on the day of hatching have a strong tendency to follow a moving object, particularly if this object emits soft monosyllabic sounds of low pitch at a rapid rate. Intersensory summation of the visual and auditory cues greatly enhance the response of following, as does the mere experience of following the parent. Other factors that facilitate the response of following the parent by ducklings are the absence of a strong fear response during the first day after hatching, contagious behavior and leadership by other members of the brood, toleration within the family, and probably increased social attachment with repeated satisfaction of any inherited response tendency related to social life.

Species recognition in some ducks depends in part on intolerance by ducklings of color differences and perhaps of voice and other behavioral differences in other species of ducklings. The most basic of these color differences may be the general color pattern that characteristically distinguishes ducklings of most surface-feeding species (Anatinae) from those of most diving ducks (Aythyinae), i.e., the presence of a conspicuous eye-stripe in the former and its absence in the latter. Tolerance of the parent bird for ducklings of the same species as the parent and attraction of ducklings to a parent bird of their own species, rather than of some other species, depend in large part on the circumstance that ducklings are normally reared by a parent of their own species. However, evidence was also secured suggesting that there may be some inherited preference by ducklings for parents of their own species.

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