



## The hatching and nest-exodus behaviour of Mallard

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### Introduction

In laboratory investigations on the early ontogeny of behaviour in nidifugous birds, Mallard ducklings *Anas platyrhynchos* have been the commonest subjects apart from the chicks of domestic fowl. As a result, much information has been obtained about the principles of the learning process known as imprinting and the so-called following-response of this species. Briefly, the experiments have consisted of a period of isolation from hatching up to a certain age, a subsequent training to a specific object (and/or sound) and finally a test to that object. The response of the duckling in the test has been considered as a measure of imprinting. The imprinting process is thought to be initiated by the following-response during training and to result in a gradually increased preference for the training object. In this way it has been shown that the strongest and most complete imprinting is restricted to a short period, usually called the critical period, which in Mallard occurs between 13 and 16 hours of age (Ramsay and Hess 1954, Hess 1959).

Our knowledge of how these laboratory results relate to events in the real nest,

after the eggs hatch, is very limited. In his work on 'the law of effort' Hess (1959) obtained results indicating that the degree of imprinting may be directly proportional to the physical effort expended during training. This suggested that imprinting under natural conditions might be linked to the actual departure of duck and ducklings from the nest, and provided part of the background for the present study.

### PART I. DETERMINATION OF HATCHING AND DEPARTURE

#### Methods

Some of the methods used have already been described (Björvall 1967), but a few remain to be defined.

The time of hatching was determined by visits to the nest and, when necessary, flushing the female. The use of a conducting paint described in Salter and Vince (1966) would probably be as disturbing, since the method requires a long stay at the nest after the eggs have pipped; moreover it is extremely expensive for natural clutches, containing normally 9 and 10 eggs. The time of hatching was ascertained as precisely as possible usually by visiting the nest twice

during the hatching process and then using the following score-system. An egg found on the point of hatching was scored 1 to that hour. A dry duckling was considered to be older than 2 hours, determined in accordance with data presented by Low (1945) for the Redhead *Aythya americana*. Thus a wet duckling of unknown age gave the score  $\frac{1}{2}$  to each of the 2 preceding hours. A dry duckling in a nest that 5 hours earlier contained unhatched eggs, thus gave the score  $\frac{1}{2}$  to each of the 3 hours following the time of the first control, and so on. In this way figures up to and including 8 have been used as divisors (the longest interval of inspection being 10 hours).

The time of departure from the nest was determined by close inspection, with the aid of an electric temperature-recorder or by long-distance visual control at irregular intervals by means of field glasses. The last method has in a later analysis also given rise to a score system. When the interval was for instance 3 hours, each of the hours has been given the score  $\frac{1}{3}$ .

It is obvious that by these methods it was impossible to know the exact age of more than a few ducklings. Therefore they are described as being 'older than' and 'younger than' (Table I).

### Observations and results

#### *Length of stay in the nest*

In 1964 and 1965 the age of ducklings at the time of departure from 21 nests was determined. Twelve of these were situated on the ground and nine in baskets or boxes, the latter being referred to as hole-nests in the following text. The results have been published already

(Björvall 1967). In 1966 observations were made of a further 29 nests, 20 of which were on the ground. The combined results are shown in Table I.

The available values, for 50 nests over three years, do not give a simple figure for the age of ducklings at the time of departure. The variation is from less than 9 to more than 46 hours. In the earlier study it was shown that the ducklings, to a large extent, spent the first 16 hours of their lives (the supposed upper limit of the critical period) in the nest. Some further notes can now be added. At 13 hours, referred to as a lower limit of the critical period, 75% (27 out of 36) of the observed broods were still in the nest, and if the oldest duckling of each brood is considered alone, the corresponding figure was 94% (47 out of 50). The youngest duckling of the brood was younger than 13 hours in only 14% of the observed broods (6 out of 42).

It is very rare that every duckling of the brood is younger than 16 hours at the time of departure. This was observed in 8% only (2 out of 26) of the broods and on both occasions every duckling was less than 11 hours old.

Summarizing these results, it is found that, although the majority of ducklings are older than 16 hours on leaving the nest, it is quite common for the younger ducklings of the brood to be below this age. Most of them, however, are older than 13 hours. Consequently Mallard ducklings, with very few exceptions, spend at least part of the critical period in the nest.

Some comparison has been made already between ducklings from different nest sites (Björvall 1967). It was suggested that Mallard broods hatched in holes stay

**Table I. Age in hours of Mallard ducklings at the time of departure: 50 nests from 1964, 1965 and 1966. Also given are results of rank-sum tests for difference between hole- and ground-nests.**

	Hole-nests			Ground-nests		
	No.	Average	Range	No.	Average	Range
<i>Oldest duckling is older than</i>	18	25 $\frac{3}{4}$ $T^1=623.5$	16 $\frac{1}{2}$ -46 $\frac{1}{4}$ $z=3.34$	32	19 $\frac{3}{4}$ $P<0.001$	9 $\frac{3}{4}$ -34 $\frac{3}{4}$
<i>Youngest duckling is younger than</i>	14	21 $\frac{3}{4}$ $T^1=408.0$	14 $\frac{1}{2}$ -46 $z=2.86$	28	16 $\frac{1}{4}$ $P<0.001$	8 $\frac{3}{4}$ -27 $\frac{3}{4}$
<i>All ducklings are older than</i>	13	20 $T^1=317.5$	13 $\frac{1}{2}$ -35 $\frac{1}{2}$ $z=2.55$	25	14 $\frac{1}{2}$ $0.01<P<0.001$	4-22 $\frac{3}{4}$
<i>All ducklings are younger than</i>	8	25 $\frac{1}{2}$ $T^1=142.5$	20 $\frac{1}{4}$ -30 $\frac{1}{2}$ $z=1.94$	18	21 $\frac{1}{4}$ $0.1<P<0.05$	10 $\frac{3}{4}$ -36 $\frac{3}{4}$

longer in the nest than those hatched on the ground. The conclusion was based on limited data but results from 1966 have now been added and rank-sum tests (Dixon and Massey 1957) are shown in Table I. For three of the four age-groups the difference is significant at the 0.001 level and the group in which no difference is found is that with the least material. The results essentially confirm the original conclusion, that ducklings from hole-nests are older at the time of departure than those from ground-nests.

It should be possible to establish a reason for this difference and, to this end, the processes of hatching and the departure from the nest have been subjected to a more detailed analysis.

#### *The chronology of hatching*

Material collected on the chronology of hatching and presented in Figure 1, shows that although Mallard eggs can hatch at any time of the day or night, most seem to hatch during the day. Indeed, more than 35% of the eggs hatched between 09.00 and 15.00 hours. The purpose of this part of the study is to see whether the difference in age at the time of departure from different nest types could be caused by differences in the hour of hatching. Besides the peak at the middle of the day, Figure 1 seems to indicate a

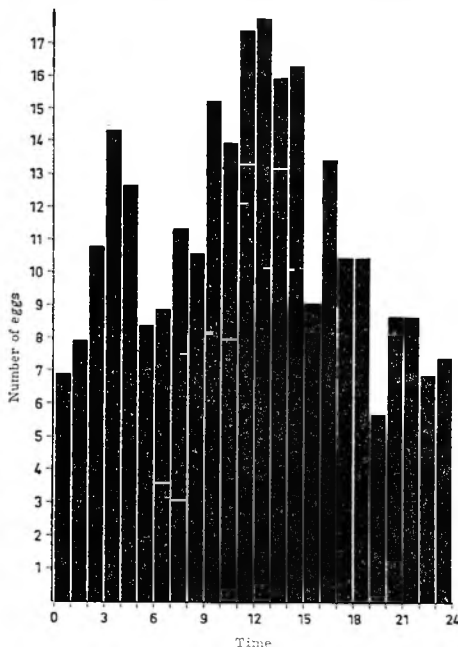


Figure 1. The distribution of hatching of 269 eggs in 43 different Mallard nests.

lesser peak between 02.00 and 06.00. Is it possible that either peak is represented mainly by hole- or ground-nests? To examine this, the median-values of 35 known cases have been analysed in respect of their distribution around 06.00. The result, shown in Table II, clearly indicates that there is no difference between the two types of nest in this respect.

#### *Hour of departure*

The time of departure of the female and brood from the nest is shown graphically in Figure 2.

Every departure from a nest has occurred during daylight although a departure after 17.00 has never been recorded. The figure shows a distinct peak in the forenoon and more than 60% of nests were quitted between 04.00 and 10.00. During the afternoon there is an indication of a second lower peak. The material in Figure 2 has been re-analysed to see whether the greater part of either peak might be caused by departures from nests of a particular type. Certain departures that occurred at about noon, without the precise time being recorded, have been excluded, plus one nest that was situated in an old Magpie nest in a low bush (because of the difficulty of classifying it

Table II. Distribution of the median values of the hatching times.

Nest site	Hatching time	
	Before 06.00	After 06.00
Hole	1	10
Ground	7	17
<b>Total</b>	<b>8</b>	<b>27</b>

$\chi^2=0.752$   $f=1$   $0.5 > P > 0.3$

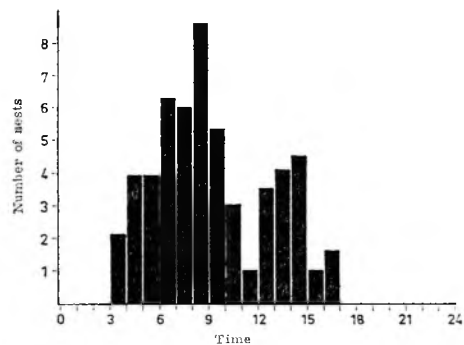


Figure 2. The time of departure of the female and brood from 54 Mallard nests. Note that daylength runs from approximately 02.00 hours to 22.00 hours.

as a real hole-nest). The remaining cases have been categorized as ground- or hole-nests and the distribution of exodus in relation to noon analysed. The result given in Table III shows that the second peak in Figure 2 is probably related to late departure from hole-nests.

The material has also been examined with a rank-sum test. Only nests of which the precise time of departure is known, have been used and in those cases where the whole brood has not left the nest simultaneously, the time of the first duckling has been used. The result ( $T^1 = 209.5$ ,  $z = 2.11$ ,  $P < 0.05$ ) showed very good accordance with that in Table III.

**Table III.** Distribution of the time of departure.

Nest site	Departure time	
	Before 12.00	After 12.00
Hole	8	7
Ground	29	5
Total	37	12

$$\chi^2=4.15 \quad f=1 \quad P<0.05$$

**The possible influence of hatching success upon length of stay in the nest**

Thus data have been obtained indicating that ducklings hatched in hole-nests are older at the time of departure than those hatched on the ground. This does not seem to depend on any difference in the actual hour of hatching, but on a delay in the time of departure from the hole.

It is well known that many female birds continue to incubate much longer than normal if the eggs fail to hatch (Sowls 1955). This has been described, for instance, for domestic fowl (Manson-Bahr 1946) and Mallard (Wheeler 1966) and has been observed occasionally in this study. One might suppose, therefore, that the presence of unhatched eggs stimulates the female to stay longer than normal, even if the nest also contains ducklings capable of leaving. If the hatching success was found to differ between the two nest types, this might explain the delayed departure such as that observed in hole-nesters.

The normal manner of describing hatching success is to present the clutch-size and the hatch as a percentage of this, for example Hunt and Naylor (1955). In the present study, however, the percentage figure is considered to be of less interest and instead a distinction has been made between clutches which have hatched completely and those that have

contained at least one unhatched egg after departure of the brood. (There was no significant difference in clutch-size between hole- and ground-nests.) In the three earliest nests in 1966, egg-laying occurred between 6th and 18th April when the night temperature was as low as  $-10^\circ\text{C}$ . on several occasions. The hatching success in these nests, which were all situated on the ground, was exceptionally poor. Since comparative material from early hole-sites is not available, these three nests have been excluded from Table IV in which the hatching success of 77 later nests is shown. About 50% contained unhatched eggs and these seemed commoner in hole-nests than in ground-nests.

**Table IV.** Hatching success in 77 nests in relation to site.

Nest site	Hatching success	
	Complete	Incomplete
Hole	5	15
Ground	31	26
Total	36	41

$$\chi^2=4.02 \quad f=1 \quad P<0.05$$

Data from nests in which hatching was incomplete have been analysed once more with reference to the number of unhatched eggs. One nest has been excluded because the precise number was not recorded. The result from 40 others can be seen in Table V, which shows that if a nest contains 2 or more eggs at the time of departure, it is likely to be a hole-nest.

**Table V.** Hatching success in 40 nests containing at least one unhatched egg.

Nest site	Number of unhatched eggs	
	1	$\geq 2$
Hole	2	12
Ground	16	10
Total	18	22

$$\chi^2=6.41 \quad f=1 \quad P<0.05$$

To test whether the presence of a small number of unhatched eggs stimulates the female to stay longer on the nest after hatching and thus cause the ducklings to be older at the time of departure, the material in Table I has been further analysed by a rank-sum test. For all age-categories and for both hole- and ground-nests no differences were found (at the 0.05 significance level) between nests which hatched completely and those con-

taining unhatched eggs. This conclusion is also confirmed by consideration of the afternoon peak in Figure 2. If the females were influenced by a small number of unhatched eggs this peak should be, to a great extent, composed of nests containing such eggs, but from Table VI it can be seen that this is not the case.

**Table VI. Time of departure compared with presence of unhatched eggs.**

Hatching success	Number of departures	
	Before 12.00	After 12.00
No unhatched egg		
Hole-nests	3	2
Ground-nests	16	3
Unhatched egg(s)		
Hole-nests	4	4
Ground-nests	12	2

## PART II. THE BEHAVIOUR OF THE FEMALE AND THE DUCKLINGS DURING THE STAY IN THE NEST: THE PERIODS OF ACTIVITY

It has been demonstrated that most Mallard ducklings spend at least part of the age-period 13 to 16 hours in the nest; and from laboratory experiments it is known that the greatest possibilities for strong and complete visual imprinting exist during this period. Preliminary observations during the present study indicated that while the ducklings are in the nest they behave in such a way that they are exposed to visual and auditory stimuli of the kind that induce imprinting (Björvall 1967). This hypothesis has been investigated further by observations, from a hide, of the behaviour of female and ducklings in the nest.

Besides visual imprinting, the existence of auditory imprinting has also been recognised. This is considered to be of great importance in holding the members of the brood together during the later period of growth. Such imprinting is said to occur during the ducklings' stay in the nest when the females of several duck species have been found to utter sounds (Collias and Collias 1956, Collias 1962, Gottlieb 1963a, 1963b). A closer investigation of this call in the Mallard was made by using a tape recorder in conjunction with visual observations.

### Methods and results

Gottlieb (1963a, 1963b, 1965a) studied the vocal activity at nests of Mallard and North American Wood Duck *Aix sponsa* from the pipping of the first egg to

exodus. He found that the female started vocalizing during the hatching of the young and continued to do so through to departure, that the amplitude (intensity) and calling rate rose during this period, and that the rate of the hole-nester (Wood Duck) was higher than that of the ground-nester (Mallard).

In view of Gottlieb's results, the initial plan was not to make continuous sound-recordings, but to take samples of vocal activity at intervals. Thus tape-recordings of half-hour lengths and at four hour intervals were made. Contrary to Gottlieb's findings, these showed that although many sounds came from female and ducklings there were also long periods of complete silence. Since other lengths and intervals gave the same result, recordings were later combined with simultaneous observation from the hide.

No extensive study of the behaviour of the female and nidifugous young at the nest seems to have been made. Collias and Collias (1956) reported observations from one nest of Blue-winged Teal *Anas discors* that suggested that the ducklings were not covered by the female the whole time, but later Gottlieb (1965a) indicated that ducklings of both Wood Duck and Mallard were covered by the body of the mother during the period in the nest. Observations in the present study, however, have given a considerably more varied picture of events between hatching and exodus.

After hatching, the wet ducklings are covered by the female for a couple of hours. When they are dry they appear beside her and start moving around the nest. Within a short time, a pattern of activity is set up; the ducklings behave in a synchronised manner and periods of high activity alternate with periods of rest when the ducklings lie still, usually under the female but sometimes in warm weather wholly or partly outside her plumage.

The early movements are very stumbling and at first physical contact between the ducklings and the female is seldom broken. The ducklings then show a rapidly increasing mobility and, during periods of activity near the end of their stay in the nest, normally leave the female and make short excursions. They usually go 10-20 cm. away but, in a few cases, walks up to 1 m. have been noted. These observations refer to nests situated on the ground, but for ducklings hatched in hole-nests the possibility of movement must be considerably restricted.

During periods of activity, when the ducklings move around in the nest, they

utter continuous 'contentment-notes' the normal function of which is to keep the brood together (Collias 1962). Sometimes, for example when only a single duckling is outside the female's plumage, 'distress calls' can be heard. These attract the female to a duckling temporarily out of contact (Collias 1962). During periods of inactivity the ducklings are almost completely silent although sometimes short series of sounds can be heard.

The female regularly utters her maternal call during periods of activity and, without exception, also answers distress calls from the ducklings. On the other hand during inactivity the female, as well as the ducklings, is almost completely silent. It is thus obvious that her vocal performance reflects both the physical and vocal state of her offspring. This fact has been of great importance in collecting information on the distribution of activity and rest in the Mallard nest.

The determination of activity and rest cycles, as registered from a hide, must to some extent be subjective. It is obvious that an alternation occurs and, while both activity and quiescence in their most pronounced forms are easy to characterize by ear or eye, difficulties lie in defining the limits particularly, for instance, when a single duckling shows movement during an otherwise idle period. The following principles were employed: a period of activity was considered to begin when more than one duckling came out from under the female. Thus the appearance of only one duckling was discounted. The period terminated when the last duckling disappeared beneath the parent. A short pause was not counted if most of the ducklings were actually outside. The vocal activity in the nest also helped in defining the limits of different periods.

As a result of the discovery of activity cycles different techniques of vocal recording were employed. The intention now was to give a general description of the distribution of activity and rest, and thus in 1966 the sound-recordings were taken in two lengthy sessions at each nest, one just after hatching and the other at the end of the ducklings' stay. Eleven nests were observed from hides for a total of 58 hours, during which time the sounds produced in most of the active periods were recorded. Five of these nests were observed for a period shortly after hatching (in the afternoon and evening of the day of hatching) and for a second period before and including the exodus (in the morning of the day after hatching). The remaining six nests were observed only before and through the exodus.

In order to give a general description of events in the Mallard nest, material from all nests has been treated together. This assumes that no major differences exist between different types of nests and that the pattern of activity does not show any regular change such as a decrease in interval length as the ducklings grow older. No statistical tests have been made but, in general, data confirm the validity of these assumptions. From the results shown in Figures 3 and 4, it can be seen that the interval between the start of one period of activity and the beginning of the next has been usually 30-50 minutes, and that each period of activity has lasted 3-12 minutes.

The sounds produced by female and ducklings were recorded in 53 out of the 73 active periods studied. In 7 out of 11 nests studied, the vocal activity before and through the departure was taped and

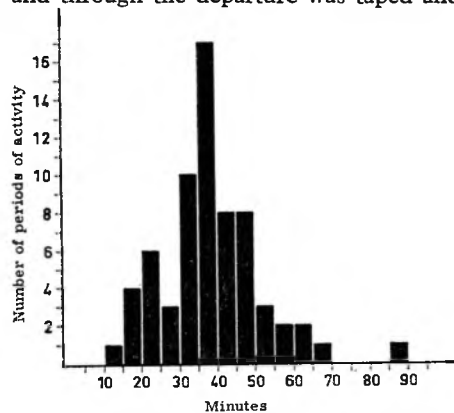


Figure 3. The time between two consecutive periods of activity. The time is taken from the beginning of one period to the beginning of the next.

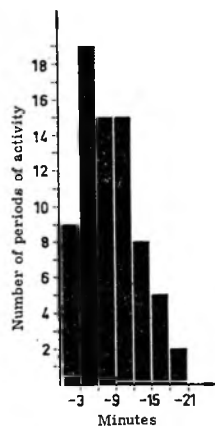


Figure 4. The length of 73 periods of activity studied in 11 different Mallard nests.

thus recordings from 60 periods of activity are available for analysis. The rate of the female's vocalizations has been determined as the average number of calls per minute and the figures have been rounded to the nearest whole number. The result is given in Table VII, which shows that, although the rate of female vocalization shows great fluctuation, it very obviously increases as the time of exodus approaches. During the period that included the departure from the nest, vocal activity was very high, in the range of 66-200 calls per minute.

figure for Goldeneye *Bucephala clangula* is 24-37½ hours (Siren 1953) while the ducklings of Wood Duck are found to leave the nest on the day after hatching (Leopold 1951), presumably about 24 hours old. For Canada Geese *Branta canadensis*, 24 hours has been reported by both Kossack (1950) and Brakhage (1965).

Of the values presented, many are notably multiples of 12, and since the methods used in determination are not described, it seems likely that some are very approximate. Nevertheless, it is reasonable to assume that the ducklings

**Table VII. The vocal activity of the female during periods of activity in seven different nests.**

Number of calls/minute from the female during periods of activity					
20-10 hours before exodus			7.5-0 hours before exodus		
Periods	Mean	Range	Periods	Mean	Range
14	8	0-46	46	40	0-219

### Discussion

The laboratory experiments on imprinting and following in artificially-hatched nidifugous birds have been fully summarized by, for instance, Bateson (1966). Records of the length of the ducklings' stay in the natural nest, however, seem rather scattered. For the Mallard, the age of the ducklings at the time of departure from the nests has been reported as 6-12 hours (Raitasuo 1964) and 10-12 hours (Girard 1941, Weidmann 1956). Kear (1965) found that Mallard ducklings leave the nest 10-12 hours after the last duckling has dried, but that the time varies according to the time of day and weather conditions. Kear's results show the closest agreement with those of the present study. For other *Anas* species, the age of ducklings of Blue-winged Teal has been found to be 18 hours (Collias and Collias 1956) and less than 12 hours (Bennet 1938, Glover 1956), and of Pintail *A. acuta* less than 24 hours (Sowls 1955). Ducklings of Cape Shoveler *A. smithii* were observed to depart from the nest in one study as soon as they were dry (Brand 1961) which should mean at an age of only a couple of hours, and in another before 48 hours old (Siegfried 1965). For ground-nesting diving ducks the figures reported for Canvasback *Aythya valisineria* are about 24 hours (Collias and Collias 1956), for Tufted Duck *A. fuligula* often more than 24 hours (Fabricius 1964) and about 48 hours (Nordberg 1950), for Redhead 3-18 hours (Low 1945) and for Eider *Somateria mollissima* less than 24 hours (Flint 1955) and about 48 hours (Nordberg 1950). For hole-nesting ducks the corresponding

of many species are older than 16 hours when leaving the nest.

Weller (1964) reports of ducks in general that if the weather is bad departure can take place 2-3 days after hatching, and 3 days has been mentioned for Eider (Gerasimova and Barabanova 1960) in a similar situation. Leopold (1951) was also of the opinion that departure can be delayed in bad weather, but for a few hours only and in any case for less than half a day. In the present study no obvious correlation with weather has been observed, although detailed measurements of temperature, precipitation, etc., were not taken. Nevertheless, broods were sometimes seen to leave the nest during heavy rain, apparently ignoring it. Temperature might be of greater importance since, in chicks of domestic fowl, it has been found that cold slows the appearance of the following response due to its physiological effect on general motor activity (Salzen and Tomlin 1963).

In the course of the present study the possibility of the ducklings becoming imprinted on the female during the stay in the nest was examined. Of special importance was the length of time the ducklings must be exposed to the female and her calls for imprinting to be established. An approximate idea might be obtained from some of the laboratory experiments previously mentioned in which, at ages ranging from just a few hours to 50 hours, Mallard ducklings were exposed to synchronous visual and auditory stimuli in a training situation (Ramsay and Hess 1954, Klopfer 1957, 1959, Gottlieb 1961, Klopfer and Gottlieb 1962a, 1962b).

Tests have shown that exposure to the object for 10-30 minutes was sufficient for imprinting to be established, although to a varying extent in different age-classes. Weidmann (1956) considered that some of the results presented by Ramsay and Hess (1954) indicated that 10 minutes might be too short. He devised an experiment in which the ducklings were first exposed to an object emitting a sound and then tested in a choice-situation of the same object without sound and another object with that sound. In this test only a small fraction of the ducklings chose the silent training object. This might be caused by a conflict between visual and auditory stimuli.

Gottlieb (1961, 1965b) has used only visual stimuli and exposed ducklings, all less than 27 hours old, to an object for 20 minutes. The following-reaction during the training in this case was less intensive, but a fairly high percentage of the ducklings that followed also became visually imprinted. Finally, Klopfer (1959) used solely auditory stimuli, with the total exposure time of 30 minutes. Here also a following-reaction was observed during training. It was less intensive, however, than that in experiments with combined visual and auditory stimuli, and in a later test imprinting on sound only was not observed. Gottlieb (1965b) also reported that newly-hatched Mallard ducklings seem to have an unlearned preference for the maternal call of their own species and that this preference was highly resistant to change through experience.

It is probably impossible to establish from a hide the length of time that ducklings in any nest are exposed to stimuli that might result in imprinting on their mother. Some generalizations must be made and to begin with it will be assumed that imprinting only occurs when the ducklings are 13-16 hours old. From Figure 3 it can be calculated that, on average, 38 minutes pass from the beginning of one period of activity to the beginning of the next. There were no observations indicating exceptional activity of the birds during the period 13-16 hours as compared to that during the adjacent periods on either side, so four bouts of activity usually occurred during this, as in any other 3 hour period (except perhaps in the first hour or two). The standard deviation of intervals between activity bouts amounted to 13 minutes and thus it was quite common for three or five active periods to occur in the same 13-16 hour period. The duration of active periods was 9 minutes on average and the standard deviation 4.6 minutes. Although

every duckling does not spend all periods of activity completely outside the female, these figures suggest that it must be quite common for most of the brood to spend at least 30 minutes of the 13-16 hour period outside, and it is very unlikely that each duckling has been outside her plumage for less than 10 minutes of the period. These figures correspond with the 10-30 minutes that, in laboratory experiments with visual or combined visual and acoustic stimuli, were sufficient for imprinting to occur. Hence, it is concluded that visual imprinting in natural conditions can occur during the Mallard ducklings' stay in the nest. Further evidence for this is provided by experiments where a degree of imprinting has been observed even earlier than the critical period (Fabricius 1951, Ramsay and Hess 1954, Gottlieb 1961). These, and the present observations that the behaviour of the birds during the 13-16 hour period does not differ from that during the rest of their nest-life, indicate that the critical period is much less limited in time than Ramsay and Hess (1954) postulated. The appearance of escape-reactions, for instance, has often been said to define the upper limits of the age when imprinting can occur. Ramsay and Hess (1954) did not observe escape-reactions in the laboratory until their ducklings were over 24 hours of age, but under natural conditions these can be seen much earlier, even before the ducklings are 10 hours old. In a laboratory test at Oster-Malma 32% of the ducklings aged 13-16 hours showed escape-reaction when confronted with an object after previous visual isolation (Fabricius, Bjärvall and Fält unpubl.).

Little information seems to have been published about the chronology of egg hatching. Among certain Central American passerines, Skutch (1952) described the eggs of flycatchers *Myiozetetes* hatching at the end of the night or in the morning but almost never in the afternoon, *Ramphocelus passerinii* in the morning but almost never at night and many other species in the afternoon. One Mallard and three Blue-winged Teal nests (Girard 1941, Glover 1956) were reported to hatch during the day. The reason for the tendency to hatch at some times of the day rather than others was supposed by Skutch to result partly from a very constant incubation-period combined with egg-laying at the same time every day and partly from an innate daily rhythm in the embryos. Klopfer (1957, 1959), in studying incubator-hatched eggs of several species of waterfowl including Mallard, stated that hatching at night was less



common than hatching during the day. In an incubator the light, temperature and humidity are more or less constant, so a difference in hatching time could be caused either by a circadian rhythm or by auditory stimulation between the unhatched eggs, as Vince (1964, 1966a, 1966b) has described for some Quail species *Coturnix*. Such auditory stimulation might occur when the number of eggs is small, as in Klopfer's study, for large numbers of Mallard eggs have been artificially hatched at Oster-Malma without any difference between day and night being observed. It seems more probable that the difference between day and night hatching in natural clutches (Figure 1) is caused by the activity of the female. Her excursions from the nest take place almost exclusively during the day (Girard 1941) and on her return she brings moisture which is of very great importance for the actual hatching (Baerends 1959, Collias 1962).

Departures of duck and ducklings from the nest observed in this study have occurred during the day, with an obvious concentration in the morning hours (Figure 2). Information in the literature on the time at which broods leave for the first time after hatching, is rather scattered; for Mallard, Robinson (1940) and Girard (1941) have reported that, on single occasions, it occurred at 11.00 and before 08.00 respectively. Single broods of Blue-winged Teal, Canvasback and Canada Goose have been observed leaving their nests at 08.21 (Collias and Collias 1956), 09.01 (Collias and Collias 1956) and 08.00 (Craighead and Stockstad 1958) respectively. For Goldeneye, Siren (1952) stated that departures always occurred between 07.36 and 10.51. For Wood Duck and the Canada Goose respectively, Leopold (1951) and Brakhage (1965) reported departure to take place in the morning. Apart from the old concept that 'the night must be the calmest and most peaceful time for such an undertaking' (Merikallio 1916), previous findings are in good accord with the results of the present study. The only divergence seems to be in the departure of Mallard from hole-nests, where to a certain extent (Table III) a delay is to be found and departure takes place in the afternoon.

The difference in hatching success between ground- and hole-nests (Tables IV and V) could be the cause of this delay if unhatched eggs in the nest stimulated the female to stay longer. Table VI, however, indicates that this is not the case. At present it seems more probable that the difference lies in the behaviour of the

ducklings. The actual departure from the nest has occurred, in every case observed, in the course of a period of activity and although the initiative is taken by the female it is apparently released by the behaviour of the ducklings.

The structure of a hole-nest reduces the light and restricts the movements of the ducklings. This might reduce the possibilities for visual, and even also for auditory imprinting, during the nest stage. Furthermore, the ducklings' actual departure from a hole seems to be solely in response to an auditory signal from the mother on the water below, while departure from an ordinary ground-nest is directed by both auditory and visual stimuli (a heterogeneous summation). In an earlier paper (Björvall 1967) these factors were thought to contribute to the delay and some observations of holdups in departures from hole-nests were related.

Kear (1967), in studying the behaviour of young nidifugous birds on a visual cliff, obtained some results of interest here. She found that young of ground-nesting species avoided the drop side of the visual cliff, while those of hole-nesting species chose equally the drop and the shallow side. The Mallard, which nests principally on the ground but on occasions also in trees, gave an intermediate score. Partial avoidance of the drop, therefore, may also contribute to the observed delay.

On two occasions holdups like those earlier seen at hole-nests were observed at ground-nests. In the first case the female tried to leave the nest at 11.32 at which time every duckling of the brood was younger than  $9\frac{3}{4}$  hours and the youngest less than  $7\frac{3}{4}$  hours. When none of the ducklings showed the least sign of following her she returned to the nest. About an hour later, at 12.38, she made a second attempt and this time the whole brood followed immediately. In the second case the female tried to leave the nest at 08.25. At that time the eldest duckling was older than  $23\frac{3}{4}$  hours but the youngest less than 14 hours. The female stopped about 1 metre away, with the ducklings spread out in a line between her and the nest, and then returned. At 09.00 she made a second attempt and this time all but two ducklings followed but these stayed in the nest giving vigorous distress-calls. At the third attempt at 09.35 the whole brood except one duckling followed the female about 3 m. away from the nest. The final departure, when all ducklings followed, did not occur until the fourth attempt at 10.13.

In these two nests the ducklings' initial refusals to follow the female could not

depend on any 'visual-cliff' effect, since the nests were situated on flat ground, but the events show obvious similarity to those observed several times at hole-nests. It is suggested that the reduced possibilities for imprinting that occur in the hole, the fact that the exodus is largely in response to auditory stimuli only and, perhaps, an avoidance of the drop, are the factors contributing to the delay found in leaving nest-sites that are elevated and enclosed.

### Summary

Under experimental conditions the strongest and most complete imprinting by Mallard ducklings has been found to occur at the age of 13-16 hours. This interval has been called the critical period.

A study was made of the chronology of hatching and exodus from Mallard nests under natural conditions. It was found that the ducklings normally spend the critical period in the nest and that ducklings hatched in nests situated above ground (hole-nests) are older at exodus than are ducklings from an ordinary ground-nest.

The hatching success, expressed as the number of unhatched eggs left in the nest, was lower in hole-nests than in ground-nests. The female Mallard can, if all eggs of her clutch fail to hatch, continue the incubation for much longer than normal. The delay did not however seem to be correlated to the presence of a small number of unhatched eggs in the nest.

Observations were made on the behaviour of female and ducklings in the nest. The ducklings spent periods of activity outside the female's plumage and periods of rest, usually under the female. During the periods of activity the ducklings utter 'contentment notes' and the female 'maternal calls'. A description of the female's vocal activity is given.

A comparison between the pattern of activity of the ducklings in the nest and results of laboratory experiments suggests that the ducklings under natural conditions spend enough time outside the female's plumage to make imprinting possible.

The delay found in hole-nests is discussed. Contributory factors to the delay may include reduced possibilities for imprinting in hole-nests, the exodus being in response solely to auditory stimuli, and the effect of the 'visual cliff'.

### References

- BAERENDS, G. P. 1959. The ethological analysis of incubation behaviour. *Ibis* 101 : 357-67.
- BATESON, P. P. G. 1966. The characteristics and context of imprinting. *Biol. Rev.* 41 : 177-220.
- BENNETT, L. J. 1938. *The Blue-winged Teal, its ecology and management*. Ames, Iowa: Collegiate Press Inc.
- BJARVALL, A. 1967. The critical period and the interval between hatching and exodus in Mallard ducklings. *Behaviour* 28 : 141-8.
- BRAKHAGE, G. K. 1965. Biology and behaviour of tub-nesting Canada Geese. *J. Wildl. Mgmt.* 29 : 751-71.
- BRAND, D. J. 1961. A comparative study of the Cape Teal (*Anas capensis*) and the Cape Shoveler (*Spatula capensis*), with special reference to breeding biology, development and food requirements. Unpubl. Ph.D. thesis, Dept. Zoo., Univ. S. Africa.
- COLLIAS, N. E. 1962. The behaviour of ducks. In *The Behaviour of Domestic Animals* by E. S. E. Hafez. London: Baillière, Tindall and Cox.
- COLLIAS, N. E. and E. C. COLLIAS. 1956. Some mechanisms of family integration in ducks. *Auk* 73 : 378-400.
- CRAIGHEAD, J. J. and D. S. STOCKSTAD. 1958. Goslings descend from aerial nest. *J. Wildl. Mgmt.* 22 : 206-7.
- DIXON, W. J. and F. J. MASSEY. 1957. *Introduction to Statistical Analysis*. London: McGraw-Hill.
- FABRICIUS, E. 1951. Zur ethologie junger Anatiden. *Acta Zool. Fenn.* 68 : 1-178.
- FABRICIUS, E. 1964. Crucial periods in the development of the following response in young nidifugous birds. *Z. Tierpsychol.* 21 : 326-37.
- FLINT, W. E. 1955. Zur Biologie der gewöhnlichen Eiderente. *Bull. d. Moskvaer Naturforscher Gesellschaft, abt. Biologie*, Bd. 50 : 53 (In Russian.)
- GERASIMOWA, I. D. and Z. U. BARABANOWA. 1960. Die Oekologie des gewöhnlichen Eiders (*Somateria mollissima*) im Kandalakschen Schutzgebiet. *Arb. des Kand. Schutzg.* 3 : 8-90.
- GIRARD, G. L. 1941. The Mallard: its management in western Montana. *J. Wildl. Mgmt.* 5 : 233-59.

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- GLOVER, F.A. 1956. Nesting and production of the Blue-winged Teal (*Anas discors*) in north-west Iowa. *J. Wildl. Mgmt.* 20 : 28-46.
- GOTTLIEB, G. 1961. The following-response and imprinting in wild and domestic ducklings of the same species (*Anas platyrhynchos*). *Behaviour* 18 : 205-28.
- GOTTLIEB, G. 1963a. A naturalistic study of imprinting in Wood ducklings (*Aix sponsa*). *J. Comp. Physiol. Psychol.* 56 : 86-91.
- GOTTLIEB, G. 1963b. "Imprinting" in Nature. *Science* 139 : 497-8.
- GOTTLIEB, G. 1965a. Components of recognition in ducklings. Auditory cues help develop familial bond. *Natural History* 25 : 12-19.
- GOTTLIEB, G. 1965b. Imprinting in relation to parental and species identification by avian neonates. *J. Comp. Physiol. Psychol.* 59 : 345-56.
- HESS, E. H. 1957. Effects of meprobamate on imprinting in waterfowl. *Ann. N. Y. Acad. Sci.* 67 : 724-39.
- HESS, E. H. 1959. Imprinting. *Science* 130 : 133-41.
- HUNT, E. G. and A. E. NAYLOR. 1955. Nesting studies of ducks and coots in Honey Lake Valley. *Calif. Fish and Game* 41 : 295-314.
- KEAR, J. 1965. The internal food reserves of hatching Mallard ducklings. *J. Wildl. Mgmt.* 29 : 523-8.
- KEAR, J. 1967. Experiments with young nidifugous birds on a visual cliff. *Wildfowl Trust Ann. Rep.* 18 : 122-4.
- KLOPFER, P. H. 1957. An analysis of learning in young Anatidae. Unpubl. Ph.D. thesis, Yale Univ.
- KLOPFER, P. H. . 1959. An analysis of learning in young Anatidae. *Ecology* 40 : 90-102.
- KLOPFER, P. H. and G. GOTTLIEB. 1962a. Learning ability and behavioral polymorphism within individual clutches of wild ducklings (*Anas platyrhynchos*). *Z. Tierpsychol.* 19 : 183-90.
- KLOPFER, P. H. and G. GOTTLIEB. 1962b. Imprinting and behavioral polymorphism: Auditory and visual imprinting in domestic ducks (*Anas platyrhynchos*) and the involvement of the critical period. *J. Comp. Physiol. Psychol.* 55 : 126-30.
- KOSSACK, C. W. 1950. Breeding habits of Canada Geese under refuge conditions. *Amer. Midl. Nat.* 43 : 627-49.
- LEOPOLD, F. 1951. A study of nesting Wood Ducks in Iowa. *Condor* 53 : 209-20.
- LOW, J. B. 1945. Ecology and management of the Redhead in Iowa. *Ecol. Monogr.* 15 : 35-69.
- MANSON-BAHR, P. 1946. Delayed hatching of eggs. *Brit. Birds* 39 : 160.
- MERIKALLIO, E. 1916. Om de i hule traer rugende aenders oekologie. *Dansk Ornith. Foren. Tidsskr.* 11 : 85-96.
- NORDBERG, S. 1950. Researches on the bird fauna of the marine zone on the Åland archipelago. *Acta Zool. Fenn.* 63 : 1-62.
- RAITASUO, K. 1964. Social behaviour of the Mallard, *Anas platyrhynchos*, in the course of the annual cycle. *Pap. Game Res.* 24 : 1-72.
- RAMSAY, A. O. and E. H. HESS. 1954. A laboratory approach to the study of imprinting. *Wilson Bull.* 66 : 196-206.
- ROBINSON, H. A. 1940. Mallard ducklings descent from nest in tree. *Brit. Birds* 34 : 47.
- SALTER, S. H. and M. A. VINCE. 1966. The use of conducting paint for recording hatching times. *Med. & Biol. Engng.* 4 : 283-5.
- SALZEN, E. A. and F. J. TOMLIN. 1963. The effect of cold on the following response of domestic fowl. *Anim. Behav.* 11 : 62-65.
- SIEGFRIED, W. R. 1965. The Cape Shoveler, *Anas smithii*, in southern Africa. *Ostrich* 36 : 155-98.
- SIREN, M. 1952. Undersökningar över knipans, *Bucephala clangula*, fortplantningsbiologi. *Pap. Game Res.* 8 : 101-111.
- SKUTCH, A. F. 1952. On the hour of laying and hatching of birds' eggs. *Ibis* 94 : 49-61.
- SOWLS, L. K. 1955. *Prairie Ducks*. Harrisburg: The Stackpole Co.
- VINCE, M. A. 1964. Synchronization of hatching in American Bobwhite Quail (*Colinus virginianus*). *Nature* 203 : 1192-3.
- VINCE, M. A. 1966a. Potential stimulation produced by avian embryos. *Anim. Behav.* 14 : 34-40.
- VINCE, M. A. 1966b. Artificial acceleration of hatching in Quail embryos. *Anim. Behav.* 14 : 389-94.
- WEIDMANN, U. 1956. Verhaltenstudien an der Stockente (*Anas platyrhynchos*). I. Das Aktions-system. *Z. Tierpsychol.* 13 : 208-71.
- WELLER, M. 1964. In *The Waterfowl of the World* by J. Delacour, Vol. 4. London: Country Life.
- WHEELER, R. J. 1966. An unusually long incubation period of the Mallard. *Condor* 68 : 301.