

## DETERMINATE LAYING IN BARN SWALLOWS AND BLACK-BILLED MAGPIES

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The problem of the mechanisms controlling cessation of laying eggs has intrigued ornithologists for years. Some birds continue to lay eggs even though the eggs are continually removed but other species lay a definite number irrespective of removals. The first type has been called indeterminate (Cole, 1917, 1930) and apparently occurs in gallinaceous birds and some woodpeckers. The second type is called determinate and has been found (Davis, 1942a) in Herring Gulls (*Larus argentatus*), which lay three eggs, except in rare instances. But many birds, especially passerines, lay a variable number of eggs, three to five for example, and some of these species may be indeterminate layers. The procedure for testing this hypothesis is to add eggs to the nest and also to remove eggs from the nest. If the species is an indeterminate layer the addition of eggs should result in a reduction of clutch size and the removal should result in an increase. If the species is determinate, the clutch size should not differ significantly from the reference clutches. A species will be considered determinate if during laying the addition of eggs to some nests and the removal of eggs from others both fail to produce a difference between the number of eggs laid consecutively in such nests and the number laid consecutively in an unmolested clutch. Series of eggs with gaps in the daily sequence are assumed to consist of several clutches.

By this standard no species is known to be indeterminate. It is recognized that this standard may be too rigid and that eventually evidence may show that a species may be indeterminate in the sense that removal results in an increased number of eggs but that addition has no effect. However, for the present it seems best to use the more stringent definition. No systematic experiment on chickens is reported in the literature although anecdotes about cessation of laying are common. Craig (1913) contrasts the determinate laying of pigeons with the indeterminate laying of the domestic fowl but does not cite specific experiments.

A likely candidate for indeterminate laying is a species that lays a variable and large number of eggs. Variability may indicate that external stimuli control ovulation. A large number permits more time for experimentation in each clutch.

Barn Swallows (*Hirundo rustica*) were chosen because this species nests colonially in readily accessible places. The particular barn used in this study, from 1952 to 1954, was about 16 miles northwest of Baltimore, Maryland, and was a conventional cowbarn with ample nesting sites on the rafters. The procedure was simply to remove eggs as laid from certain nests and to add them to other nests. Some nests were undisturbed to serve as reference nests. In the "removal" nests the second and subsequent eggs were taken, thus always leaving one egg. To the "addition" nests a number (4-5) of eggs was added on the day the first egg was laid. The reason that the removals and additions were done at the start of laying is that several days are required for the hormonal mechanisms to act upon ovulation; hence manipulations on the next to last day of laying could have no effect on the number of eggs laid.

Data for Black-billed Magpies (*Pica pica*) were obtained by the Montana Fish and Game Commission as part of a study of the control of magpies. The raw data were printed in the Quarterly Report for April-June, 1950. Permission to use these data was generously granted by Mr. Wynn Freeman.

The results of the experiments are given in table 1 for both species. It requires no

elaborate analysis to show that the removal of eggs did not stimulate laying in either species. It is true that in both species less than the normal number of eggs was laid in the nests to which eggs were added, thus suggesting that the addition of eggs inhibited laying. However, a detailed consideration of the record for each nest suggests that loss of eggs or interference by the observer may be responsible for the reduced number. At any rate, without a clear demonstration of a continuation of laying when eggs are removed, these species cannot be called indeterminate.

Table 1

Number of Eggs Laid per Clutch by Barn Swallows and Magpies under Normal and Experimental Conditions

Number of Barn Swallow nests				Number of Magpie nests				
Eggs laid	Normal	Eggs removed	Eggs added	Eggs laid	Normal	All eggs removed daily	1-2 eggs left daily	Eggs added
2	0	1	0	4	0	0	1	1
3	0	1	0	5	0	1	0	3
4	3	4	4	6	2	3	4	3
5	7	5	6	7	14	6	4	2
6	3	4	0	8	6	5	4	1
	—	—	—	9	0	0	1	0
Total nests	13	15	10	Total nests	22	15	14	10
Mean size of clutch	5.0	4.7	4.6	Mean size of clutch	7.2	7.0	6.9	5.9
Standard deviation	0.67	1.21	0.63	Standard deviation	0.58	1.07	1.14	

Since these species are determinate layers, the variability in clutch size found must be explained by appealing to varying physiological conditions due to age, nutrition, temperature, or other factors. For Barn Swallows in this particular cowbarn, the clutch-size for 80 normal clutches (1949 to 1953) averaged 4.64 (standard deviation = 1.00) with a range of 2 to 6. While possibly the 2- and 3-egg clutches had lost some eggs, there were 15 4-egg clutches, 42 5-egg clutches and 12 6-egg clutches. This variation may be considered normal. In other barns near Baltimore, 45 nests averaged 4.55 eggs (standard deviation = .76).

It seems desirable to bring together as many data as possible concerning the topic of determinate laying, for the literature is widely scattered and often located in old or obscure journals. Some data were presented in tabular form by Laven (1940*b*). The papers mentioned by Laven have been checked in the original (except Altum, 1869, and Eisenhut and Lutz, 1936). Unfortunately, Laven did not clearly distinguish between laying of eggs daily and laying of several clutches in the same nest.

Apparently some species may be shown to be indeterminate. The Yellow-shafted Flicker (*Colaptes auratus*) may actually lay up to 71 eggs (Phillips, 1887) consecutively. Burns (1900) compiled a list of seven cases in which the eggs were taken daily and the total number of eggs laid varied from 17 to 71. Burns also listed 11 cases in which the eggs were collected in sets; these varied from 15 to 48 eggs per nest. For the Wryneck (*Jynx torquilla*), Alderson (1897) reported a case of 62 eggs laid consecutively, Warga (1925) reported 33, and Hanke (see Jull, 1940), reported 48. Witschi (1935) reported that House Sparrows (*Passer domesticus*) laid up to 50 eggs, in some

cases 12 to 19 being consecutive. Puhlman (1914) did not state clearly that he removed eggs consecutively but found that *Passer domesticus* and *Passer montanus* never went above twice the "clutch-size." Kreymborg (1911) found 16 eggs in a House Sparrow nest but no proof of consecutive laying. Bisshop (1923) reported a sparrow that laid 29 eggs in 7 clutches and Wenzel (see Jull, 1940) got 51 eggs from a sparrow. Roberts (1940b) stated that the Gentoo Penguin (*Pygoscelis papua*) can replace eggs that are taken from the nest, but he gave no data. Gwynn (1953) found that the Gentoo Penguin laid a third egg in 4 out of 8 cases when the 2 eggs were removed as laid. Also, when only the first egg was removed, 2 more eggs were laid in 2 out of 8 cases. But when only the second egg was removed no more eggs were laid in 10 cases. These data suggest that this species is indeterminate. Thus far the species mentioned are the only ones for which data actually suggest indeterminate laying. But in no case was the addition of eggs tried.

In many instances it is clear that several sets were laid in the same nest but usually there is no proof that the same bird laid the various sets. For this type of work banded birds must be used. Burns (1900) quoted C. L. Rawson's observations that in 14 species the seasonal total when eggs were removed as laid was no more than 2 to 4 sets, except a Sharp-shinned Hawk (*Accipiter striatus*) which laid 17 eggs in one nest in 5 sets. Riviere (1897) reported that a Starling (*Sturnus vulgaris*) laid 2 sets with an interval of 5 days between. Kreymborg (1911) reported a magpie laying 20 eggs but said nothing about consecutiveness. Grabham (1897) took 28 eggs from a nest of a Dipper (*Cinclus cinclus*) but said nothing about the details. Miller (1910) took 36 eggs from a Gallinule (*Gallinula chloropus*) nest in 3 visits. Groebbels (1937:243) listed several observations that appear to be consecutive laying of sets rather than continual laying. Burrows (1945:40) quoted a statement in an old book by Jesse that the Long-tailed Tit (*Aegithalos caudatus*) laid 30 eggs in succession as the set was depleted.

Some species have been tested a few times by regular removal. Puhlman (1914) stated that the European Coot (*Fulica atra*) lays only 4 eggs. Bankes (1897) found that a Redshank (*Totanus totanus*) laid 5 clutches of 4 eggs. Roberts (1940a) reported that the Wilson Petrel (*Oceanites oceanicus*), and all known procellariiform birds, do not replace their egg after destruction. Laven (1940a) found that the Ringed Plover (*Charadrius hiaticula*) laid only 4 when an egg was removed daily. The same was true for *Vanellus vanellus* (Laven, 1940a). Nash (1942) found that an Eastern Bluebird (*Sialia sialis*) laid only 5 eggs. A cuckoo (*Guirra guirra*) mentioned by Farley (1924) probably laid several clutches. Nice (1937) commented that the addition of Cowbird (*Molothrus ater*) eggs to sets of the Song Sparrow (*Melospiza melodia*) did not inhibit the latter from laying the usual complement of eggs. Howell (1942:561) removed eggs from nests of three American Robins (*Turdus migratorius*) without any increase in number laid. He commented that the ovaries of several birds that had laid full clutches contained ova with large yolk. Berndt (1943) merely stated that the addition or removal of eggs from the nest of the Pied Flycatcher (*Muscicapa hypoleuca*) had hardly any effect on the number of eggs laid. A number of miscellaneous experiments have been done by the author over a period of years on five species of passerine birds with no indication of indeterminacy. From this review of the literature it is obvious that very few species have received the detailed study of many nests that is necessary to determine the results in respect to determinacy.

The problem of determinacy naturally arises for the domestic fowl, but no series of experiments has been found reported and consequently a series has been started. Craig (1913) merely stated that hens continue to lay. There are many studies of the time

interval between eggs which show that 24 to 28 hours may separate layings. The number of consecutive days of laying comprises a cycle whose length depends upon the separation of eggs in hours. Birds that have 28 hours between eggs perform lay only 2 in a cycle because darkness interrupts a sequence, whereas birds with a 24-hour separation may lay as many as 69 (Heywang, 1938). Unfortunately, the cycle is often confused with a clutch. The latter term should be used to refer to the number of eggs laid up to the time of brooding, whether they are laid daily or not. Thus, some passerine birds have been known to miss a day in the laying of a clutch and many non-passerine birds regularly lay at two-day intervals. The number of hours between eggs may be an important aspect in the control of clutch size since in some species the cycle length may determine the clutch size.

Domesticated ducks apparently are similar to domesticated fowls such as chickens and turkeys. An old report (see Jull, 1940:292) states that a wild Mallard lays 80 to 100 eggs if one is removed daily.

Stieve (1918:557) showed that a hen has a series of ova of decreasing size in the ovary while she is laying in contrast to the situation in the Jackdaw (*Corvus monedula*) (Stieve, 1919), which has only a certain number of ova that reach large size.

The problem of determinacy in gulls has been studied by several persons. Salomonson (1939) reported that Herring Gulls may lay as many as 16 eggs in a season. In some cases 4 eggs were laid consecutively in one nest. Spear (1942) found up to 12 eggs in some nests. Goethe (1937:51) stated that if eggs are added to a gull's nest, it will continue laying even though 5 or 6 eggs are in the nest. Davis (1942a) performed apparently the first experiment designed to test the determinacy of laying. He added eggs and removed eggs and found that Herring Gulls laid only 3. Von Torne (1940) reported 5 eggs for one *Larus canus*, which species normally lays 3.

Cowbirds, although social parasites, apparently lay eggs in clutches. Davis (1942b) examined the ovaries histologically and found that the old follicles were in chronological groups of 4 or 5. Nice (1949), from her observations on Cowbird eggs in Song Sparrow nests and from Walkinshaw's (1949) data, concluded that Cowbirds lay in clutches. The communistic cuckoos of the subfamily Crotophaginae must be determinate layers (Davis, 1942c) because several females lay in one nest but each female lays 5 to 7 eggs.

Lack (1933) called attention to the fact that variations in local conditions may affect the maturing of the eggs in the ovary. Indeed, laying may actually be suspended as was found by Pitt (1929) for *Turdus filaris*, by Timmerman (1932) for *Phylloscopus collybita*, and by Weydemeyer (1934) for Tree Swallows (*Iridoprocne bicolor*). Rowan's (1918) report of apparent suspension may be a case of two birds laying in the same nest. This suspension of laying certainly raises questions about the changes in the ovary during these days.

Frances Hammerstrom kindly permitted the use of some unpublished data on House Wrens (*Troglodytes aëdon*). In 1913 L. J. Cole removed eggs as laid by a wren. This bird laid 13 eggs, rested 4 days, laid 7, rested 4 days, laid 5, rested 5 days, laid 5, and stopped. In a subsequent experiment the addition of 7 eggs on the day that the first egg was laid did not prevent the laying of 7 eggs. Recently Hammerstrom removed eggs daily from the nests of 13 females. The average of 20 clutches was 6.2 eggs (range 4 to 9). Kendeigh (MS) summarizes this work and adds some data of his own. He suggests the interesting possibility that wrens are indeterminate in the early part of the season but not in the late part, because when eggs were removed there were more large clutches (8-9 eggs) in the early part of the season than in the late part. However, the normal seasonal decline in clutch size is perhaps a factor.

## SUMMARY

The problem of determinate laying has been investigated for two species that lay a variable number of eggs in the nest: Barn Swallows (*Hirundo rustica*) and Black-billed Magpies (*Pica pica*). A species may be considered an indeterminate layer if the addition of eggs to the nest at the start of laying results in a reduction of clutch size and if the daily removal of eggs results in an increase. For Barn Swallows the normal (unmolested) clutch size was 5.0. Nests from which eggs were removed averaged 4.7 while nests to which eggs were added averaged 4.6. The corresponding values for magpies were 7.2, 7.0 and 5.9. It is concluded that these species are determinate layers.

A thorough review of the literature shows no clear proof that any species is indeterminate by these standards, although flickers, Wrynecks, House Sparrows, and the domestic fowl may be.

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