

EXPERIMENTS ON INDETERMINATE LAYING IN HOUSE WRENS AND EUROPEAN STARLINGS¹

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Abstract. Although long studied, determinate and indeterminate laying patterns in birds have not been related to avian ecology. House Wrens (*Troglodytes aedon*) often experience egg removal by potential nest usurpers, while European Starlings (*Sturnus vulgaris*) commonly experience both egg removal and egg addition by conspecific brood parasites. We predicted that House Wrens should respond to egg removal by laying extra eggs but should not respond to egg addition, while European Starlings should both increase clutch size in response to removal and decrease clutch size in response to addition of eggs. We manipulated clutch size at 70 House Wren and 49 European Starling nests by adding or removing two eggs during the laying period. In early wren clutches, birds altered clutch size as predicted: wrens with nests from which eggs were removed had larger clutches than did control birds, while birds with nests to which eggs were added had clutches of the same size as control birds. However, in late clutches wrens did not respond to either egg removal or addition. Starlings showed no significant response to either egg removal or addition in spite of high rates of conspecific egg removal and brood parasitism within the study population.

Key words: Clutch size; indeterminate laying; determinate laying; brood parasitism; egg removal; House Wrens; European Starlings; *Troglodytes aedon*; *Sturnus vulgaris*.

INTRODUCTION

One of the central questions of population biology is why organisms have as many offspring as they do. For more than a century, naturalists have observed that some birds, in response to egg removal, continue to lay eggs beyond their "normal" clutch size. Laying hens (*Gallus domesticus*) have been bred over centuries for this ability. Removal of eggs from nests of non-domestic species became common in the late 1800s and early 1900s as ornithologists added to egg collections. Probably the most widely cited study concerning egg removal is that of Phillips (1884, 1887), who collected 71 eggs in 73 days from a single Northern Flicker (*Colaptes auratus*) nest.

Some, but not all, birds respond to egg removal by laying additional eggs, and Cole (1917, 1930) coined the terms "indeterminate" and "determinate" to classify birds on the basis of their response to egg removal during laying. Indeterminate layers were defined as birds that laid extra eggs in response to egg removal, and determinate layers were those species that laid their normal clutch size even when eggs were removed. Davis

(1955) suggested that true indeterminate layers should be capable of responding to both removal and addition of eggs; that is, they should continue laying in response to removal of eggs but curtail laying in response to addition of eggs to the nest. Thus two types of laying were recognized in birds: (1) determinate, in which the number of eggs laid in a clutch was set at the onset of laying and could not be changed by removal or addition of eggs, and (2) indeterminate, in which the number of eggs laid in a clutch depended on stimuli received during laying, such that clutch size increased if eggs were removed and decreased if eggs were added to the clutch.

Indeterminacy, therefore, has been defined by the response to the removal or addition of eggs during laying, specifically to removal or addition by humans. However, indeterminacy has not been related to naturally occurring egg removal or addition. Here we suggest that (1) indeterminate laying should be expected to evolve only in situations in which eggs are removed or added under natural conditions, and (2) because egg removal or addition may occur independently, birds may be determinate, "removal indeterminate" only, "addition indeterminate" only, or both "removal-and-addition indeterminate."

Removal of eggs in nature most likely occurs by predation; however, predators such as raccoons, weasels, and skunks generally remove an

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entire clutch at one time, often damaging or destroying the nest. We suggest that the ability to continue laying in response to daily removal of a single egg, as occurred in most studies of egg removal by humans (Kennedy 1989), has most likely evolved in response to conspecific egg removal. This often results in removal of one egg per day (pers. observ.), usually with little or no damage to the nest, and may or may not lead to abandonment of the nest. Addition of eggs occurs by conspecific brood parasitism, and the ability to respond to the addition of eggs should be found in species in which brood parasitism occurs commonly.

House Wrens (*Troglodytes aedon*) are often subject to conspecific egg removal (Belles-Isles and Picman 1986). Between 1983 and 1986, this type of egg removal occurred at 27 of 244 active nests (11.1%) on our study sites; at 18 of these 27 nests (66.7%), removal occurred during laying. Although conspecific brood parasitism has been reported for House Wrens elsewhere (Picman and Belles-Isles 1988), no evidence of brood parasitism was found in our population. Therefore, we predicted that House Wrens should be removal indeterminate, that is, they should respond to egg removal by laying larger clutches at removal nests than at addition or control nests, but should not respond to egg addition by laying smaller clutches at addition than at control nests.

European Starlings (*Sturnus vulgaris*) in our study area are subject to both conspecific egg removal (19–23% of nests, Lombardo et al. [1989], Kennedy et al. [1989]) and conspecific brood parasitism (23–31% of nests, Kennedy et al. [1989], Lombardo et al. [1989], Romagnano et al. [1990]). Among 138 early (laying began in April) nonmanipulated nests, 15 nests (11%) were subject to egg removal only, 21 nests (15%) were subject to conspecific brood parasitism only, and 11 nests (8%) were subject to both egg removal and brood parasitism (Lombardo et al. 1989). Thus we predicted that European Starlings should be removal-and-addition indeterminate, that is, they should respond to both egg removal and egg addition. We expected starlings to lay larger clutches at removal nests than at addition or control nests and to lay smaller clutches at addition nests than at control nests.

MATERIALS AND METHODS

Both starlings and wrens were studied in central New Jersey. Starling experiments were carried

out in 50 nest boxes that were added to an existing starling nest-box trail in 1985 (see Crossner [1977] for a description of the study site). Wren experiments were carried out in boxes that were put up in either 1983 or 1984 in three old field sites in Somerset and Middlesex counties (see Kennedy [1989] for a description of the study sites).

In 1985 and 1986, EDK performed egg removal and addition experiments as follows. Nest boxes were checked daily during the laying periods, and new eggs were marked as laid. For each species, nests were divided into the following treatments: (1) removal nests, from which two eggs were removed, one each on days two and three (day one is defined as the day the first egg was laid); (2) addition nests, to which two eggs were added, one each on days two and three; and (3) control nests, at which eggs were neither removed nor added. Treatments were assigned equally with regard to initial laying date to account for any changes in clutch size that may have occurred during the laying season.

In addition, to determine how many eggs a bird might lay in response to egg removal and whether a bird would desert a nest from which all eggs were removed, EDK performed additional removal experiments at 12 wren nests and five starling nests. All removal occurred at early nests (see below). At six wren nests and all five starling nests, eggs were removed as laid beginning with the first egg, leaving no egg in the nest. At six other wren nests, eggs were removed as laid beginning with the second egg, always leaving one egg in the nest. Eggs were removed until either no new eggs were laid on two consecutive days (single-day gaps in laying were recorded and egg removal continued) or 14 eggs had been removed (the equivalent of two early wren clutches) at each nest.

European Starlings were highly synchronous in laying. In both 1985 and 1986, laying began on 19 April and 84% of nests contained at least one egg by 26 April. Only those starling nests in which laying began in April were included in this study. House Wrens were not synchronous layers. Laying began in early to mid-May and continued until late July or early August. There were usually two distinct laying peaks in each year (see Finke et al. 1987). In 1985, laying began on 9 May, and there was a gap in starting new clutches from 17–22 June. In 1986, laying began on 12 May, and there was a gap in starting new clutches

TABLE 1. Clutch-size distribution in response to treatment in House Wrens in 1985 and 1986. Host = resident female. n = total number of nests used in each treatment. Entries under host clutch sizes are the number of nests at each clutch size.

Time	Treatment	n	Host clutch size					$\bar{x} \pm SD$	
			4	5	6	7	8		9
Early	Removal	25	1	1	7	6	6	4	7.1 \pm 1.3
	Control	19	1	2	7	9			6.3 \pm 0.9
	Addition	23	1	2	10	10			6.3 \pm 0.8
Late	Removal	13	2	10	1				4.9 \pm 0.5
	Control	10	3	6	1				4.8 \pm 0.6
	Addition	9		5	4				5.4 \pm 0.5

from 8–14 June. Wren clutches started before the laying gap in each year were considered “early” and those started after the gap were considered “late.”

Distributions of clutch sizes were not significantly different between 1985 and 1986 and were pooled to increase sample sizes. All comparisons of distributions were by Mann-Whitney U -tests.

RESULTS

House Wrens behaved as predicted during the early part of the breeding season (Table 1). Birds at removal nests laid an average of almost one egg more than did those at control nests ($P < 0.025$, one-tailed). Moreover, birds at removal nests were the only ones to lay eight or nine eggs. Birds at addition and control nests did not differ in clutch size ($P > 0.10$, one-tailed). However, birds with late clutches showed no response to removal (late removal vs. late control, $P > 0.10$, one-tailed), and laid smaller clutches than birds with early nests.

Contrary to our prediction, European Starlings showed no significant response to either addition ($P > 0.10$, one-tailed) or removal ($P > 0.10$, one-tailed; Table 2), even though this population has high incidences of both brood parasitism and egg removal. Overall true host clutch size (i.e., excluding known parasite eggs) in this experimental population (4.8 ± 0.7 , $n = 70$) did not differ from that in an adjacent, control population (4.7 ± 0.9 , $n = 138$; $P > 0.10$, two-tailed).

House Wrens were capable of laying enlarged clutches in response to continuous removal of up to 14 eggs; six of 12 birds laid more than seven eggs (the size of the largest natural early clutch size recorded in this population), and three birds laid 15, 13, and 12 consecutive eggs, respectively (Table 3). There were single-day breaks in laying at four of six nests (67%) that had eggs

removed as laid but only in three of 19 control nests (16%). Starlings again showed no ability to extend their clutch size in response to egg removal (Table 3).

DISCUSSION

From these experiments, we cannot conclude that indeterminacy has evolved in response to natural addition and removal. House Wrens that nested early showed a significant response to egg removal; however, this response was not shown by every bird, and was not a one-to-one response to the number of eggs removed. Furthermore, wrens that nested late showed no response to egg removal, even though the percentage of nests destroyed by wrens did not differ between early nests (8.4%, 13 of 154 nests) and late nests (8.9%, 8 of 90 nests; $G = 0.014$, $df = 1$, $P > 0.9$). Many late nests were second broods, suggesting that egg-laying abilities may be limited late in the season, perhaps due to high temperatures (Kendeigh 1941) or hormonal changes. A similar seasonal reduction in extended laying in wrens was reported for a single bird by Cole (1917) and for seven birds by Kendeigh et al. (1956).

European Starlings showed an inability to limit clutch size when eggs were added, even though this sometimes resulted in clutches too large to rear all young (Kennedy 1989, Power et al. 1989). There may be several ways other than indeter-

TABLE 2. Clutch-size distribution in response to treatment in European Starlings in 1985 and 1986. See Table 1 for explanation.

Treatment	n	Host clutch size				$\bar{x} \pm SD$
		4	5	6	7	
Removal	23	5	14	4		5.0 \pm 0.6
Control	21	7	13	1		4.7 \pm 0.6
Addition	26	13	9	3	1	4.7 \pm 0.8

TABLE 3. Laying response of House Wrens and European Starlings to continuous egg removal. "Remove as laid" indicates that each egg was removed on the day that it was laid, and "leave one" indicates that one egg was left in the nest and each additional egg was removed as laid. Each entry is the laying history of a single female.

	House Wrens		European Starlings
	Remove as laid	Leave one	Remove as laid
	15 + 2 + 3 = 20 ^a	8 + 7 + 4 = 19	5
	12	13	4
	4 + 7 = 11	7	4
	5 + 3 = 8	6	4
	7	4	3
	5 + 1 = 6	4	
	\bar{x} (SD) = 10.7 (5.1)	8.8 (6.0)	4.0 (0.7)

^a Addition signs indicate 1-day breaks in laying.

minacy by which a bird can deal with the problems of egg removal and addition. To prevent egg addition, birds may guard their nests during laying and begin to incubate before a clutch is complete, as occurs in starlings (Romagnano et al. 1990). If parasitism is not avoided, birds may remove the added egg, although this behavior in starlings is limited to the period before the host female has begun to lay (Stouffer et al. 1987). Another response to parasitism may be to limit clutch size to avoid oversized broods, as appears to occur in starlings (Power et al. 1989).

To prevent or limit egg removal, birds may be strongly territorial and actively guard their nests during and after egg laying. In response to egg removal, birds may abandon the nest to re-nest elsewhere. However, contrary to the statement by Klomp (1970, p. 5) that one or two eggs should be left in a nest to prevent desertion, removal of all eggs as laid did not cause early desertion in either wrens ($n = 6$) or starlings ($n = 5$). Birds at all 11 nests laid at least the minimal clutch size for each respective species (Table 3). Wrens at nests in which no egg was left in the nest laid an average of 10.7 eggs, compared to 8.8 eggs in nests at which one egg was left in the nest. These values do not differ from the 8.6 eggs reported by Kendeigh et al. (1956) for a similar experiment in which one egg was left in the nest and subsequent eggs removed from seven wren nests, suggesting that in response to egg removal wrens extend their clutches by an average of two eggs.

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