

TREE SWALLOWS CANNOT BE CLASSIFIED AS DETERMINATE OR INDETERMINATE LAYERS¹

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Abstract. We used egg removals, additions, and swaps (controls) to determine whether Tree Swallows (*Tachycineta bicolor*) are determinate or indeterminate layers. Since Tree Swallows modify their clutch size in response to their environments, and since egg additions and removals occur naturally in this species, we predicted full indeterminacy. Females laid more eggs in response to the removal of their third and fourth laid eggs but did not lay clutches outside the normal range. Females did not lay fewer eggs when an egg was added on each of the second and third days of laying. From this we conclude that Tree Swallows have limited removal indeterminacy but are determinate with respect to egg addition. When daily egg removal was used to keep females at 1 or 0 eggs, which led to abandonment of the nesting attempt followed by relaying, the second clutch was much larger, on average, than the first. This suggests that the first clutch had been terminated early. Thus Tree Swallows, although addition determinate, were capable of early cessation of laying. Although removal indeterminate, they were not capable of laying abnormally large clutches. We therefore argue that determinate and indeterminate laying patterns cannot be used to infer a female's ability to modify clutch size in response to other stimuli, and that strict categorization of Tree Swallows as determinate or indeterminate is not appropriate.

Key words: Tree Swallow; clutch size; determinate laying; indeterminate laying.

INTRODUCTION

Laying determinacy has been assessed for many species (reviews in Davis 1955, Lehrman 1959, Klomp 1970, Kennedy 1991). Determinate layers are birds which do not respond to egg removal or addition during laying by altering the number of eggs laid (Cole 1917, Davis 1955). In some species, the lack of response may occur because only a limited number of follicles develop (Eisner 1960, Barry 1962). In other species, more follicles may develop than eggs are ovulated and ovulation is not influenced by the number of eggs in the nest (Klomp 1970). In contrast, indeterminate layers respond to egg removal by laying more eggs or respond to egg addition by reducing the number of eggs laid. Kennedy and Power (1990) define these two responses as removal and addition indeterminacy, respectively. Species exhibiting both responses are removal-and-addition indeterminate. This refines Davis' (1955) definition, in which responses to both manipulations are required for a species to be classified as indeterminate. An anecdotal definition of removal indeterminacy is provided by Phillips (1887), who induced a Northern Flicker (*Co-*

lptes auratus) to lay 71 eggs in 73 days by removing an egg daily, leaving a single egg in the nest. Undisturbed, Northern Flickers lay clutches of 6-8 eggs (Bent 1939).

Some authors treat interspecific variation in laying determinacy as variation only in the proximate control of clutch size (e.g., Lehrman 1959, Dunham and Clapp 1962, Kendra et al. 1988). That is, for indeterminate layers, the number of eggs in the nest may be a visual or tactile cue influencing when laying stops (Witschi 1935). For determinate layers, this cue may not be involved and time of laying cessation has been fixed prior to clutch initiation by the number of follicles developing or by a hormonal set-point (Eisner 1960). (Especially for species in which more follicles develop than eggs are laid, clutch size is set by when laying stops [Hamann et al. 1986, Kennedy 1991].)

If determinate and indeterminate laying reflect differences in proximate processes, determinate layers may be constrained in their ability to adaptively modify clutch size in response to local conditions. Kennedy and Power (1990) define determinate layers as species "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." This is a two-part definition. The second half, regarding egg removal and ad-

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dition, is the traditional definition. The first half is more restrictive, stating that no change in final clutch size is possible after clutch initiation regardless of the stimulus. The definition reflects the perception that determinate laying, while it may be assessed using clutch manipulations, reflects fundamental differences in internal processes involved in egg formation. Similarly, Arnold (1992) interpreted determinate as meaning that limited follicular development prevents a response to egg removal. He therefore argues that failure to observe a response to egg removal, while it indicates that eggs in the nest is not a cue controlling laying, does not necessarily demonstrate that a species is a determinate layer, in the sense that "the number of eggs laid in a clutch was set at the onset of laying." If the concept that determinate laying reflects the time at which final clutch size is set is appropriate, then it has implications for the understanding of intraspecific clutch size variation. For example, Anderson (1989) concludes that House Sparrows (*Passer domesticus*) are removal-determinate and predicts that females for whom food availability increases following the onset of laying will, because their clutch size has already been determined, be incapable of laying more eggs in response to the new circumstances.

Indeterminate laying has also been examined from an ultimate perspective, as an adaptive response to naturally occurring egg removal and addition, particularly to conspecific nest parasitism (Kennedy and Power 1990). Kendra et al. (1988) argue that indeterminate laying is a precondition for conspecific nest parasitism, rather than an adaptive response to it. Rothstein (1990) and Kennedy (1991) note that this explanation is inconsistent with the high levels of conspecific nest parasitism found in European Starlings (*Sturnus vulgaris*), which are determinate layers (Power et al. 1989). If removal and addition indeterminacy have evolved in response to naturally occurring egg removal and addition, then a prerequisite should be the natural occurrence of such changes in egg number. This need not be through nest parasitism. Further, the number of eggs in the nest should be considered a possible additional cue to a laying female, rather than as the exclusive cue.

The status of Tree Swallows (*Tachycineta bicolor*) as determinate or indeterminate has not been assessed. Tree swallows are secondary hole-nesters which readily use nest boxes. This has

led to their widespread use in studies of breeding biology (reviewed in Robertson et al. 1992). Observations of two eggs appearing in a nest on one day suggest that there may be a very low level of intraspecific brood parasitism in some local populations (Lombardo 1988), but DNA fingerprinting has not revealed evidence of brood parasitism in our study population (Lifjeld et al. 1993). Nevertheless, both egg removal and addition do occur even in the absence of brood parasitism. House Wrens (*Troglodytes aedon*) have broken eggs in nests in this same population near forest edge (Rendell and Robertson 1990). Egg addition occurs following resident turnover at a nest. The new female may bury old eggs under new nesting material, roll eggs out of the nest cup, or lay new eggs directly on top of the old clutch. Eggs removed from the nest cup or buried may be returned to the cup, apparently by the nesting female, during laying or incubation (pers. observ.). Eggs from previous clutches are often still viable (this study). Where eggs are unburied and returned to the cup during laying, they have, effectively, been "added." Less commonly, egg addition of sorts occurs when two females lay in the same nest (Quinney 1983). Thus, even if intraspecific brood parasitism does not occur in this population of Tree Swallows, both removal and addition indeterminacy could be adaptive.

Clutch size in Tree Swallows varies from 2–8 eggs, more commonly 4–7 (Paynter 1954, Robertson et al. 1992), and is influenced by environmental conditions. Second-year females lay smaller clutches than older females (DeSteven 1978, Stutchbury and Robertson 1988). Later laying females also lay smaller clutches (Stutchbury and Robertson 1988). Clutch sizes of local populations are correlated with laying season food abundance (Hussel and Quinney 1987). Reduction of box volume midway through nest building (mean 7–8 days prelaying) through the addition of false walls also reduces clutch size (Rendell and Robertson, in press). These are all responses to prelaying conditions. Kuerzi (1941) reports pauses mid-laying (after the first or second egg) of 1–7 days in response to cold weather and/or reduced sunlight with pre-pause eggs retaining viability. Thus, Tree Swallow clutch sizes track changes in internal and external environments, and some control of laying is retained into the laying period. Again, if a female's ability to modify her clutch size is related to an indeter-

minate laying pattern, then we predict Tree Swallows to be indeterminate layers.

To assess the Tree Swallow's status as determinate or indeterminate layers and to assess implications for clutch size variation, we used a modified version of the protocol recommended by Kennedy (1991). We addressed the following questions.

- (1.) Are Tree Swallows removal- or addition-indeterminate? Given that both egg removal and addition occur naturally in Tree Swallows, and that individuals do respond to environmental change by altering clutch size, we predicted that Tree Swallows would lay more eggs when eggs were removed and that they would stop laying sooner when eggs were added. We further hypothesized, based on Kuerzi's (1941) observations, that Tree Swallows abandoning a nesting attempt as a result of clutch manipulation would be able to cease laying prior to completion of a normal clutch.
- (2.) Does the timing of the manipulation influence its effect? Davis (1955) and Kennedy (1991) state that an indeterminate response, if present, is more likely to be observed if manipulations are performed early in the laying sequence. Eisner (1960) suggests that species initiating incubation prior to clutch completion, as do Tree Swallows (Robertson et al. 1992), cannot modify clutch size after incubation has begun. We predicted that an indeterminate response, if present, would be more likely to manifest itself when clutch size was altered early in the laying attempt.
- (3.) Given that eggs from previous clutches appear to be the chief source of natural egg addition, how viable are such eggs? Based on Kuerzi's (1941) findings, we expected some viability of old eggs. Partial clutch removal induced some females to abandon the laying attempt. Hatch of the remaining eggs at nests which were reused allowed us to assess old egg viability.

STUDY AREA AND METHODS

The study was conducted May–July 1992, using Tree Swallows breeding in nest boxes in and around hayfields near the Queen's University Biological Station in Leed's County, 50 km north

of Kingston, Ontario. Nest boxes were mounted on aluminum poles or on fence posts at heights of 1–2 m. All nests were checked twice weekly during nest building, incubation, and nestling periods, and daily during laying and expected hatch periods. Nests were checked and clutch manipulations performed in the late morning or early afternoon.

We conducted two experiments. In the first, we removed the third and fourth eggs as laid at 11 nests. At another 11 nests we added two eggs, 1 each on the day of laying of the second and third eggs. Finally, at 11 control nests, eggs were swapped: The third and fourth eggs laid were removed as laid and were replaced with eggs no more than a day old taken from nests at which the female was not yet incubating. Nests were grouped into triplets according to laying date. Where clutches were initiated at more than three nests on the same day, grouping was done randomly. Within each triplet, one nest was used as a removal, one as a swap, and one as an egg addition. Results could then be analyzed using paired sample (sign) tests. When nests grouped together did not initiate laying on the same day, an effort was made to do egg removals at the later laying nest, so that the seasonal decline in clutch size (Stutchbury and Robertson 1988) minimized rather than exaggerated any increase in clutch size due to egg removal. Female age (second year or older), determined using plumage differences (Hussel 1983), did not differ markedly between treatment groups (two second year females in the removal group, one each in the control and addition groups). Eggs were numbered lightly with pencil as laid, allowing movement of the correct egg and an assessment of the effect of egg movement on viability.

In the second experiment, eggs were removed daily starting with the first (4 nests), second (13 nests), or third (5 nests) egg laid until the female stopped laying. Thus nests were kept at zero, one, and two eggs respectively. We did not use egg additions in this experiment. Unfortunately, eggs in this experiment were not marked as laid. However, during the pause between clutches, the eggs left in the "kept at 1" nests were marked. Thus, when a second clutch was laid in the nest, the old egg could be identified, but it could not be aged exactly as its position in the laying cycle of the first clutch was unknown. Female age was not recorded at several of the nests used in experiment 2, so we cannot assess its impact.

TABLE 1. Distribution of clutch sizes (number of eggs laid) and percent hatching in response to removal of two eggs, replacement of two eggs (control), and addition of two eggs during laying. Sample size for percent hatching varies because of desertion and predation, and is given below.

Treatment	Clutch size distribution					SE	(n)	Percent hatch		
	4	5	6	7	\bar{x}			\bar{x}	SE	(n)
Removal		2	8	1	5.9	0.16	(11)	91.7	4.2	(9)
Control	1	5	5		5.4	0.2	(11)	98.5	1.5	(11)
Addition	1	3	7		5.6	0.21	(11)	94.4	2.3	(10)

RESULTS

At nests where two eggs were removed, females laid more eggs than at controls (one-tailed sign test, $n = 5$, $C = 0$, $P = 0.03$) (Table 1). Addition of two eggs did not cause females to reduce the number of eggs laid (one-tailed sign test, $n = 6$, $C = 4$, $P = 0.89$). By Kennedy's (1991) definitions, Tree Swallows therefore exhibit a modest degree of removal indeterminacy but they are addition-determinate. However, no female laid a clutch outside the normal range for the species.

Eggs moved between nests remained viable. Only one of 42 eggs moved between nests did not hatch (97.6% hatch), which is comparable to the five of 126 eggs left where laid which failed to hatch (96.0% hatch). At two removal nests, the female deserted midway through incubation. At one addition nest, the nest was depredated during incubation. These three nests are excluded in assessing hatching success. An egg was missing following hatching at one control and one addition nest. We treat these eggs as having failed to hatch, but cannot identify them as moved or original and therefore exclude them in calculating hatching success. At no nest did more than one egg fail to hatch. Three of nine removal nests, six of 10 addition nests, and one of 11 control nests contained an unhatched egg. The probability of removal and addition nests containing an unhatched egg did not differ significantly from that for control nests (two-tailed Fisher exact probability tests, $P = 0.5$ and $P = 0.15$ respectively). However, in the case of egg addition the difference was not significant. Hatch occurred over 1–3 days. The degree of asynchrony was independent of treatment group (log-likelihood ratio, $df = 4$, $G = 0.64$, $0.975 > P > 0.95$).

In experiment 2 (continuous egg removal) the five females kept at two eggs laid apparently complete clutches (4–7 eggs) and incubated the 2 eggs not taken (Table 2). One female kept at a single

egg incubated that egg after laying five. This female was also the last to lay. The other 12 females laid 2–5 eggs and did not incubate the remaining egg. At least 8 of these 12 relaid (second clutches: 4–6 eggs). In these cases the female was either positively identified for both nesting attempts or was assumed to have laid both clutches because of the short time period between laying attempts and the lack of any change in nest structure between clutches.

At the four nests where all eggs were taken, the females also relaid. First clutches ranged from 3–5, second clutches from 2–7. Second clutches were larger than first clutches for the eight "kept at 1" females (one-tailed sign test, $n = 6$, $C = 1$, $P = 0.11$) and were significantly larger for "kept at 1" and "kept at 0" nests combined (one-tailed sign test, $n = 8$, $C = 1$, $P = 0.04$). Sample size was insufficient for comparisons of "kept at 0" nests alone. For Tree Swallows, re-nest clutch sizes are generally equal to (Kuerzi 1941) or smaller than (Paynter 1954) those of complete first clutches. This indicates that at least some "kept at 1" and "kept at 0" females stopped laying prior to completion of the first clutch.

At 7 "kept at 1" nests, a second clutch was laid by the original or a new female and eggs were incubated to hatching, allowing the viability of the egg remaining from the first clutch to be assessed (Table 2). The old egg hatched at four nests (57%), despite pauses of 4–11 days between laying periods. In one case, the old egg had been laid by a different female.

DISCUSSION

Using the anecdotal definition of indeterminacy provided by Phillips' (1887) for the Northern Flicker, Tree Swallows are determinate layers. They cannot be induced to lay clutches outside the normal range. In fact, when kept at 0 or 1 egg (experiment 2), fewer eggs were laid rather than more. However, when 2 eggs were removed,

TABLE 2. Laying pattern for nests where an egg was removed daily until laying stopped. Kept at 2/1/0: eggs removed starting on the third/second/first day of laying, leaving 2/1/0 eggs in the nest; pause: # of days between successive laying periods during which no eggs were laid. For "kept at 1" nests at which a second clutch was laid, hatch of the old egg is given as yes (Y) or no (N) except at nests G and I, which were deserted, and nest K, which was relaid in a different nest. At nests J, L, P, and Q the female was not observed relaying so no second clutch is given. Nests J and L were reused by different females, who initiated laying after the pause indicated. The nest R female incubated a single egg.

Treatment Nest Box	Kept at 2										Kept at 1										Kept at 0						
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	x	SE	S	T	U	V	x	SE	
No. eggs in	4	4	6	6	7	5.4	0.6	2	2	2	3	4	5	5	5	5	5	5	5	4.1	0.37	3	4	4	5	4.0	0.41
1st clutch						4	4	5	4	-	4	-	5	5	6	-	-	-	4.6	0.26	4	4	5	5	4.5	0.29	
2nd clutch						11	13	4	6	12	7	7	6	6	6	-	-	-	7.4	1.1	7	5	2	3	4.2	1.1	
Pause						Y	-	Y	-	N	-	Y	N	N	Y	-	-	-	-	-	-	-	-	-	-	-	-
Old egg hatch?																											

the number of eggs laid was, on average, slightly greater than at control nests (experiment 1), as expected for an indeterminate layer. We saw no response to egg addition. Thus, Tree Swallows have limited removal indeterminacy but are addition determinate. This is based on a limited sample size, but we feel this makes the significance of our results more noteworthy, as it highlights the consistency of the responses observed.

Since females kept with a single egg or from whom all eggs were taken abandoned the nesting attempt, we cannot assess whether the limited extent of the response observed is related to when in the laying period eggs were removed. Consequently, we cannot answer the second question posed, regarding the timing of the manipulation. This abandonment in response to egg removal is consistent with Klomp's (1970) comment that one or more eggs should be left in the nest to prevent desertion, but contrasts with Kennedy and Power's (1990) finding that in both House Wrens and European Starlings, removal of all eggs as laid did not lead to early desertion.

Hamilton and Orians (1965) gave coloniality and limits on breeding opportunities as two factors predisposing a species to interspecific brood parasitism. Similar criteria seem reasonable for the evolution of conspecific brood parasitism, and are met by Tree Swallows (Robertson et al. 1992). However, DNA fingerprinting studies examining patterns of paternity have not found nestlings unrelated to the resident female at any nests, indicating that conspecific nest parasitism is rare in this population (Lifjeld et al., 1993). If indeterminate laying is exclusively a response to nest parasitism, it should not be expected in Tree Swallows.

However, egg removal and addition do occur naturally in Tree Swallows. Egg depredation by House Wrens was not observed at nests used during this study but was not uncommon in the area (pers. observ.). Egg addition occurred when females relaid in nests which had been kept at a single egg. These eggs had some viability even after being left untended in the nest for up to 11 days. The old egg and the new clutch were not necessarily laid by the same female. Addition indeterminacy could therefore be adaptive if either costs of nestling care or of incubation limit clutch size. DeSteven (1980) found no evidence that Tree Swallow clutch size was limited by ability to feed additional nestlings. Our first experiment led to artificially reduced and enlarged

clutches ranging from 3–8 eggs. There was some suggestion of reduced percent hatching in nests to which eggs were added, suggesting limits on the number of eggs which can be successfully incubated. However, since only one egg failed to hatch in any one nest, brood sizes at egg addition nests were still larger than at controls. Incubation ability, then, should not limit clutch size. Briskie and Sealy (1989) noted a similar pattern in the Least Flycatcher (*Empidonax minimus*). However, sample sizes in both DeSteven's (1980) study and in our own limit the probability of detecting differences in nestling or adult survival or in estimating percent hatching. Further, we do not assess differences in post-hatching success associated with differences in clutch size. Wiggins (1990) found that nestlings from experimentally enlarged broods weighed less, on average, than controls but was unable to assess subsequent survival.

In the second experiment, Tree Swallows abandoning their first nesting effort in response to egg removal generally tried again. Thus, Tree Swallows could be induced to lay large numbers of eggs, as expected for an indeterminate layer. Unlike Phillips' (1887) Northern Flicker, these eggs were laid in discrete sets, separated by delays ranging from three days to two weeks. Kuerzi (1941) reported intervals of 6–7 days between laying periods, roughly similar to our observations. Lombardo (1983) observed a single female laying three clutches, totalling 14 eggs, with 8–10 days between laying periods. The rapid growth phase of follicular development lasts 2–5 days in passerines (Ojanen 1983). If Tree Swallows fall within this range, then the two laying periods truly are separate, rather than being equivalent to the pauses of one or more days occasionally observed in the laying of a single clutch. That is, follicular development for the second clutch need not have begun until after the first attempt was abandoned. Laying of a series of clutches in response to egg removal, with no clutch exceeding the normal upper limit, can be confused with removal indeterminacy. Thus, Kendra et al. (1988) conclude that House Sparrows are removal indeterminate because they lay additional eggs when eggs are taken, while Anderson (1989) argues that they are determinate because the extra eggs are laid as a second clutch, not as part of the original clutch.

An interesting effect of continuous, daily egg removal (experiment 2) was that first clutches at

some nests were smaller than renests, suggesting that females abandoned the first nesting attempt prior to clutch completion. While it is possible that females abandoned and then "dumped" their remaining eggs, we did not find these dumped eggs. Early cessation of laying, the expected response to egg addition, was instead a response to egg removal which left fewer than two eggs in the nest. Superficially, the effect is similar to the temporary pause in laying in response to bad weather (Kuerzi 1941), in that a female apparently expected to lay but fails to do so. Kuerzi's females, of course, laid but a single clutch, while our females laid two.

The difference in the response, when two eggs or one egg was left in the nest, may indicate that two eggs are worth incubating while one is not, at least if relaying is possible. This observation is consistent with the hypothesis that females use expected benefits, rather than past investment (costs) in making parental investment decisions (Dawkins and Carlisle 1976). The only female to incubate a single egg was also the last female to lay, thus her expected benefits from relaying would likely have been lower.

Determinate and indeterminate laying patterns do not appear to be reliable indicators of a species' ability to alter clutch size in response to other stimuli. Tree Swallows are addition determinate but nevertheless capable of indeterminate responses, namely terminating laying early or altering their laying cycle by delaying laying. Tree Swallows' addition determinacy cannot be used to infer response capabilities during laying to other stimuli known to be prelaying cues, such as food supply (Hussel and Quinney 1987) and nest box volume (Rendell and Robertson, in press). The broader definition of determinacy as reflecting the time at which clutch size is fixed (Kennedy and Power 1990), rather than solely as absence of response to clutch manipulation as a proximate cue, is misleading. Using the example of Anderson (1989), House Sparrows may not respond to changes in food availability during laying, but this need not be because a determinate laying pattern constrains them. Determinate laying should be used only as a description of a response to a specific manipulation, not as indicative of a more generalized constraint on clutch size.

We also feel the distinct categorization of Tree Swallows as determinate or indeterminate may be inappropriate given the response we observed

to removal of two eggs, as opposed to continuous removal. Resulting clutch sizes were larger, indicating that eggs in the nest are, to some extent, a proximate cue to cessation of laying. However, the response was far from one-to-one and did not result in clutches outside a normal range. Kennedy and Power (1990) found that while House Wrens could be induced to lay clutches outside the normal range in response to egg removal, and were therefore removal indeterminate, the relationship between number of eggs removed and number of additional eggs laid was not one-to-one.

Dichotomous classifications are generally more useful as means of identifying continua through definition of their endpoints than they are as reflections of reality. If researchers recognize that the variables used are continuous, not discrete, reference to the dichotomy is useful. (For a critical examination of classifications, see Peters [1991:Ch. 4].) The determinate/indeterminate dichotomy, however, has been treated as a discontinuous variable, without considering the complexity underlying it. This is evident from current ornithology texts, which either treat laying determinacy as a simple dichotomy (e.g., Welty and Baptista 1988:329–330) or recognize the variation but downplay it (e.g., Faaborg and Chaplin 1988:289). We have demonstrated that Tree Swallows cannot be neatly categorized as determinate or indeterminate layers. Any definition of “determinate” which allows unambiguous classification ignores the variation present in responses to clutch manipulations and prevents understanding that variation. We suggest that extent of a response to clutch manipulation is a more useful measure than discrete categorization, and a measure more likely to shed light on the proximate and ultimate control of clutch size.

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