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THE POTENTIAL TO LAY REPLACEMENT CLUTCHES BY TREE SWALLOWS[1]

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Abstract: To determine the factors that influence a female's decision of whether or not to re-lay, we removed first clutches from 17 marked female Tree Swallows (*Tachycineta bicolor*) in a nest-box population in eastern Ontario, Canada. Females and nests were then monitored to determine whether a replacement clutch was laid. Forty-one percent of females laid replacement clutches. First clutches of those females that laid replacement clutches were significantly larger than those of females that did not re-lay. This suggests that female quality, indicated by having higher levels of expendable energy or greater foraging skill or efficiency, is the determining factor as to whether or not a replacement clutch will be laid. For birds that re-laid, the replacement clutch was significantly smaller than the first clutch. This suggests either a depletion of energy reserves with each subsequent nesting attempt, or an individual female's energetic tradeoffs to ensure her own survival to the next breeding season.

Key words: *replacement clutch, re-lay, Tree Swallow,* Tachycineta bicolor.

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The re-laying potential of passerines, that is, the proportion of females that will lay a replacement clutch, has seldom been described in detail. Based on recent accounts of 47 species in *The Birds of North America* series (Gill and Poole, Eds., 1992–1996), 32 of 47 (68%) species of single-brooded passerines are capable of laying replacement clutches. However, only a handful of these accounts report the proportions of females in the populations that re-lay upon the loss of the first clutch.

Tree Swallows (*Tachycineta bicolor*) are widely distributed throughout much of North America; they are socially monogamous passerines that arrive in Ontario in late March or early April and begin breeding in early to mid-May. They are secondary cavity nesters which readily accept nest boxes. Females are usually single-brooded, with occasional double broods in the southern parts of their range (Chapman 1955, Hussell 1983). In an effort to determine the factors that influence a female's decision of whether or not to re-lay, we used an experimental approach to determine what proportion of female Tree Swallows will lay replacement clutches.

METHODS

The study was conducted on grids of nest boxes at the Queen's University Biological Station at Lake Opinicon, Ontario, Canada (44°33′N, 76°19′W) between 2 May and 15 July, 1994. A grid of forty-five nest boxes which had been in place for over 10 years was used in this study (some boxes were reused to cross-foster eggs).

All birds ($n = 40$ pairs) settling on the study grid were individually marked using a numbered aluminum band on the right leg and a unique pattern of acrylic paint on the right wing. This allowed for individual identification from a distance without recapture.

Each morning, we surveyed the study grid for newly settled pairs and monitored nest-building activity. Tree Swallows lay one egg per day, producing a final clutch of 4–7 eggs (Robertson et al. 1992). As each new egg was laid we numbered it with either a pencil or an indelible fine-tipped marker.

To simulate loss of a clutch to predation, a situation in which a female might re-lay, we removed the female's first clutch. Tree Swallows exhibit some degree of indeterminacy (that is, egg removals during laying may affect the number of eggs laid by that female; Mitchell and Robertson 1993), so we did not remove any eggs until after clutch completion. Clutches were defined as complete when no new eggs had been laid for two consecutive days. On this second day post-laying, the entire clutch was removed from the nest. We removed the completed first clutches of 17 females. These females were closely monitored to see if they laid replacement clutches and, if so, replacement clutches were subsequently removed (using the same scheme). Only females that laid first clutches during the peak period of laying, from 12 May–3 June, were used in this study (Table 1).

This study was done in conjunction with another study which required large family groups (multiple broods) from individual females, so removed clutches were cross-fostered to other nests for incubation. This provided a good opportunity to study re-laying capacity in this species.

RESULTS

Seven (41%) of 17 females laid replacement clutches after their first clutches were removed, and two of these 7 (12% of experimental females, or 29% of those laying replacement clutches) laid third clutches. Those females that re-laid ($n = 7$) had significantly larger first clutches (mean = 6.0 ± 0.39) than those individuals ($n = 10$) that did not re-lay (mean ± SE = 5.1 ± 0.28) (t-test, $t_{15} = -2.14$, $P < 0.05$; Table 1). Every female that laid seven eggs in her first clutch re-laid ($n = 2$), whereas 43% of those with six eggs in their first clutch re-laid ($n = 7$), 40% of those with five eggs in their first clutch re-laid ($n = 5$), and no individuals with four eggs in their first clutch re-laid ($n = 3$). First clutches were significantly larger than second clutches in those birds that re-laid (paired t-test, $t_6 = 6.0$, $P = 0.001$; Table 1).

Re-laying was unrelated to the date of egg removal (Kolmogorov-Smirnov two-tailed, two-sample test, $\chi^2_1 = 0.7$, $P = 0.7$). However, it is noteworthy that the last two experimental removals did not result in females re-laying. The experimental nests chosen for this study were representative of the study population, because the distributions of first egg dates of the experimental nests do not differ significantly from the study population (total of 46 nests) (Kolmogorov-Smirnov test, $\chi^2_2 = 2.79$, $P = 0.40$).

DISCUSSION

Although Tree Swallows usually are single-brooded, they have been known to lay a second or even a third clutch in a single breeding season in response to nest failure (Hussell 1983, Lombardo 1983). However, the proportion of a Tree Swallow population capable of laying replacement clutches has heretofore been unknown. Almost half of the experimental females in this study laid one replacement clutch and 12% laid two replacement clutches in response to simulated predation. Thus, a large proportion of Tree Swallows that lose clutches during incubation are able to lay at least one replacement clutch. It was not feasible to follow the individual birds that left the study area following nest failure, and because they were not observed, these females were assumed not to have laid replacement clutches. Therefore, our data represent a conservative estimate of the re-laying capacity for this population.

Females responding to clutch loss through predation or other factors must weigh the costs and benefits of re-laying. Three main factors represent the bulk of energetic expenditures that female Tree Swallows must consider in a reproductive season. First, offspring require parental care for approximately 40 days after laying, which puts a relatively high energetic demand on the parents (Robertson et al. 1992). If a female loses her first clutch, she must invest energy into the laying of a replacement clutch, which may affect the female's survivorship. Second, adults must conserve energy for migration and their young must develop sufficiently to undergo migration, and time is limited. The later in the season that a clutch

TABLE 1. Nest records of experimental Tree Swallows which underwent clutch removals.

Nest #	1st clutch nest box	1st egg date 1st clutch	# of eggs in 1st clutch	2nd clutch nest box	1st egg date 2nd clutch	# of eggs in 2nd clutch	3rd clutch nest box	1st egg date 3rd clutch	# of eggs in 3rd clutch
1	BGD2	May 15	7	BGD2	June 1	6			
2	SPD2	May 17	7	SPC1	June 4	6	SPD2	June 21	4
3	BGE5	May 13	6	BGH2	May 23	5	BGE5	June 11	5
4	SPC3	May 13	6						
5	BGI7	May 15	6						
6	BGE1	May 16	6						
7	BGG5	May 16	6	BGG5	June 1	6			
8	BGF2	May 22	6	BGF2	June 7	5			
9	BGC5	May 26	6						
10	BGI1	May 12	5						
11	BGC3	May 13	5	BGC3	June 3	4			
12	BGD6	May 14	5	BGC7	June 2	4			
13	BGJ4	May 14	5						
14	BGI3	May 29	5						
15	BGH4	May 13	4						
16	BGI5	May 15	4						
17	BGJ6	June 3	4						

is laid, the closer to the time of fall migration the young will fledge, and thus replacement clutches will have later fledge dates. Late-fledging broods can reduce both offspring and adult survivorship (Perrins 1970, Askenmo 1979, Bryant 1979), and delaying migration too long (until temperatures drop substantially) may be fatal (Weatherhead and Sealy 1985), especially in the case of an early winter. Third, adult Tree Swallows molt after the young have fledged but prior to migration. Molting is an energy-expensive process that reduces flight ability and thus foraging efficiency due to loss and regrowth of the primaries (Hussell 1983). This energy expenditure could be important in the case of a female that is still feeding her fledglings while molting and preparing for migration. The weighing of these factors becomes important when a predation event occurs and a female is in a position to lay a replacement clutch, or wait until the following breeding season to try again.

The seasonal decline in first clutch size which regularly occurs in this population (Stutchbury and Robertson 1988) was controlled for in this study by limiting experimental clutches to the beginning of the breeding season (13 out of 17 first clutches were laid between May 12–May 17); hence the data are not confounded by seasonal variation in first clutch size. Within this brief window of time, the date of first clutch loss did not affect whether or not experimental females laid replacement clutches because we effectively eliminated this variable.

It is possible that only those females which are in better condition or are of higher quality than others have the potential to lay replacement clutches. First clutch size often has been used as an indicator of both a female's energy levels upon entering the breeding season and her overall quality (Nur 1986, 1987). In this study, females that laid a replacement clutch had significantly larger first clutches than those that did not re-lay, suggesting that the re-layers had higher levels of expendable energy (i.e., were not as energy-limited), or had greater foraging skill or efficiency during the breeding season. Furthermore, replacement clutches of the same individuals were significantly smaller than first clutches, suggesting a depletion of energy reserves with each subsequent nesting attempt. This is supported by the finding that only two of the seven re-laying females laid third clutches. Alternatively, decreasing clutch size later in the breeding season may reflect an individual's tradeoffs in ensuring maintenance of energy levels above a critical level, and thus their own survival to the next breeding season (Hussell 1972).

Laying a smaller replacement clutch may allow a female to conserve energy by producing fewer eggs and energetically expensive egg shells (Romanoff and Romanoff 1949). In addition, smaller clutches produce smaller broods, which require less food. Decreasing clutch size also may enable a female to increase her chance of survival to the next breeding season by decreasing the incubation time (per day) that a larger clutch would require (Hussell 1972), thus allowing her to forage and to conserve more energy than if she had a larger clutch to incubate.

This study shows that about half (41%) of female

Tree Swallows will re-lay upon the loss of their first clutch, and about one third (29%) of those that re-lay will lay a second replacement (i.e., third) clutch. Although the ability to re-lay is likely molded by natural selection and influenced by many factors, such as adult survivorship, length of breeding season, food abundance, and frequency of nest loss, further study will be required to determine the decision rules used by females in deciding whether or not to re-lay.

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A TECHNIQUE FOR DORSAL SUBCUTANEOUS IMPLANTATION OF HEART RATE BIOTELEMETRY TRANSMITTERS IN BLACK DUCKS: APPLICATION IN AN AIRCRAFT NOISE RESPONSE STUDY[1]

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Abstract: A technique for heart rate biotelemetry transmitter implantation was developed to monitor heart rate fluctuations of Black Ducks (*Anas rubripes*) in response to simulated aircraft noise in a large outdoor enclosure. A dorsal subcutaneous approach, with subcutaneous tunneling of lead wires, was employed for placement of the 32 g transmitters. A base-apex lead configuration, with leads anchored at the dorsal cervico-thoracic junction and the caudal keel, yielded the maximal ECG wave-form

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