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DO NEST BUILDING AND FIRST EGG DATES REFLECT SETTLEMENT PATTERNS OF FEMALES?[1]

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Abstract. The order in which females settle on territories likely reflects patterns of female choice of territory and/or mates. Yet in most studies of female choice, settlement dates are usually only inferred from dates of nest initiation or first egg date. To test whether there is a close correlation between the order of female settlement and the initiation of nest building or egg laying, we determined the settlement date of female Tree Swallows (*Tachycineta bicolor*) through direct observation. The order of female settlement on territories was not significantly correlated with either the initiation of nest building or first egg date. The interval between settlement and egg laying shortened as settlement date advanced, and females began egg laying during a short period in May, regardless of when they had settled. Some females that we experimentally prevented from settling until early May began egg laying at the same time as females that settled in early April. We suggest that female Tree Swallows are under pressure to settle early due to intense competition for limited nesting sites, but then time their egg laying for mid-May to benefit from synchronous breeding and favorable environmental conditions. We predict that the order of settlement is not closely correlated with initiation of nesting activities by females in other species in which females breed synchronously and have a long interval between settlement and egg laying.

Key words: Tree Swallow; Tachycineta bicolor; *mate choice; settlement pattern; nest building; first egg date.*

INTRODUCTION

The order in which females become established on territories can be an important indicator of territory and/or mate quality as measured by female choice (Pleszczynska 1978, Wittenberger 1978, Yasukawa 1981, Alatalo et al. 1984, Nagata 1986). The order of female settlement is also important in the study of mating systems, since the polygyny threshold model predicts the order in which females should settle as primary vs. secondary females on a territory (Verner and Willson 1966, Orians 1969, Lenington 1980, Garson et al. 1981). Although settlement patterns of females can reveal much about mate choice and mating systems, relatively few studies have determined female settlement directly (e.g., Pleszczynska 1978, Wittenberger 1978, Carey and Nolan 1979, Lenington 1980, Alatalo et al. 1984). However, it is often not clear exactly how female establishment dates were determined and whether systematic observations were conducted. Instead, most studies of female mate choice use some measure of the initiation of nesting activities to infer the order of female settlement (e.g., Crawford 1977, Orians 1980, Yasukawa 1981, Roskaft and Jarvi 1983, Catchpole et al. 1985, Muldal et al. 1985, Wooten et al. 1986). These studies assume that settlement date is closely correlated with nest building or egg laying, although this critical assumption has rarely been tested (Lenington 1983, Alatalo et al. 1984).

The purpose of this study was to test the assumption that nest building and first egg dates are correlated with settlement date in female Tree Swallows (*Tachycineta bicolor*). Tree Swallows are secondary cavity nesters, and readily breed in nest boxes. Thus, they are easily observed during settlement, and the initiation of nesting activities can be closely monitored.

METHODS

This study was conducted during the summers of 1985 and 1986 at the Queen's University Biological Station on Lake Opinicon, 50 km north of Kingston, Ontario. The population studied has been established for 10 years, and has remained at a relatively constant size (55 to 65 pairs) since 1982. Tree Swallows breed in nest boxes mounted on aluminum posts 1.5 m high, which are distributed throughout four hayfields that cover

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a total area of about 5 ha. In late March of both years, nest boxes were placed on every other post of a rectangular grid (20-m spacing), such that the interbox distance was 40 m along a row and 28 m across the diagonal. The four fields (NB, BG, SP, HU) contained 11, 22, 8, and 18 nest boxes respectively during the settlement period. Some nest sites were not settled early in the season because they were defended by neighboring Tree Swallows (Harris 1979, Robertson and Gibbs 1982, Muldal et al. 1985), or occupied by Eastern Bluebirds (*Sialia sialis*). Nest sites where there had been a definite change of female residency were excluded from the analysis.

To determine when females were established at a nest site, we scanned each field for 20 min, every day between 06:30 and 10:00, except during inclement weather. Observations were made only in the NB field in 1985, but in all four fields in 1986. Scans were done from 8 April to 1 May in 1985, and from 2 to 24 April in 1986. Each observation period consisted of 20 1-min scans of a field during which we sequentially and momentarily focused on each nest box. During each 1-min scan, we recorded the number of birds perched on or within 5 m of each nest site at that instant. For each nest site, on a particular day, we had 20 instantaneous observations of the number of birds occupying the site. Adult Tree Swallows are sexually monochromatic, so we could not identify the sex of the birds at a box. Single birds were often seen at a nest site before pair formation. We assumed that these lone birds were males, and therefore the date of female settlement was the date on which pair formation occurred at the nest site. A nest site was defined as being defended by a pair if we saw two birds on the box for at least five observations out of 20. The settlement date of the female was defined as the first day that a pair was seen at a box, provided that the box was defended by a pair on at least one of the next five days on which scans were done.

In order to experimentally delay the settlement of some females in 1986, we waited until early May, when most other nest boxes were already defended, to erect 16 nest boxes that were evenly distributed in the regular grid pattern. The boxes were erected four per day between 5 and 8 May, with 2, 12, and 2 respectively in the NB, BG, and SP fields. Immediately following the erection of a nest site we recorded all activity around the site for 1 hr to determine whether a pair became established. A ½-hr watch was done the following day to confirm the status of the nest site. Six of these nest sites were defended by a neighboring pair, and were not included in the analysis.

Beginning in mid-April, we recorded the amount of nesting material in each nest box every other day. Nest checks were done in the afternoon to minimize the disturbance to resident females. Since females add small amounts of material to their boxes in early April, we defined the date of initiation of nest building as the first day that the depth of the nesting material was 3 cm. A complete nest had an average depth of 6 cm. Beginning in early May, we checked the boxes each afternoon to determine the date on which the first egg was laid.

To ensure that females which eventually laid eggs in a nest site were the same individuals that were seen during the settlement period, we caught females during April and May using mist nets and nest traps (Stutchbury and Robertson 1986). Each captured bird was banded with a Canadian Wildlife Service numbered leg band, and uniquely marked on the wings or tail with different colors of acrylic paint.

We used nonparametric statistics because some variables (settlement date) were not normally distributed, and we were interested in the relative ranking of females. All correlations are Spearman's rank correlations.

RESULTS

The initiation of nest building was not significantly correlated with the order of female settlement in April 1986 (Fig. 1; $r_s = 0.22$, $n = 43$, $P > 0.10$). Females settling on 2 or 3 April had nest building dates ranging over 16 days. Some females, which settled as much as two weeks later, started nest building as early as the first settling females. In 1985, there was also no significant correlation between the order of nest building and settlement (Fig. 2; $r_s = 0.48$, $n = 8$, $P > 0.20$). To assess whether this lack of correlation was due to a poor estimate of pairing (a pair seen in five of 20 scans), a more conservative measure of settlement date was obtained by defining pairing as two birds seen at a box in 10 of 20 scans. With this definition of settlement date, nest building was still not significantly correlated with settlement (1986: $r_s = 0.16$, $n = 43$, $P > 0.30$; 1985: $r_s = 0.10$, $n = 8$, $P > 0.80$).

When the females that were forced to delay settlement until early May were included in the

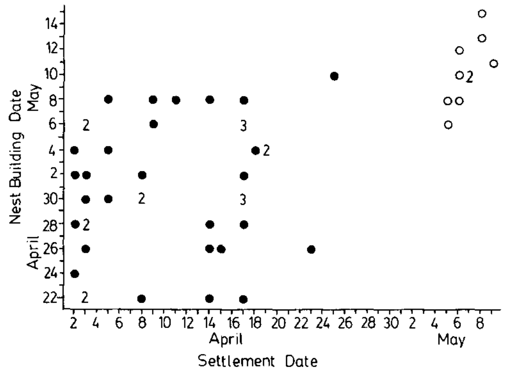

FIGURE 1. Date of nest-building initiation and settlement date of early settling females (April; closed circles) and late settling females (May; open circles) in 1986. Numbers represent multiple observations at that point.

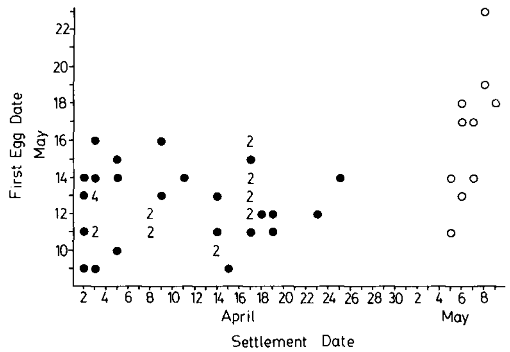

FIGURE 3. First egg date and settlement date of early settling females (April; closed circles) and late settling females (May; open circles) in 1986. Numbers represent multiple observations at that point.

analysis, initiation of nest building was significantly correlated with settlement (Fig. 1; r_s = 0.56, n = 53, P < 0.001). The long delay in settlement also forced a delay in nest building, since these females could not begin nest building before 5 May.

First egg date was not significantly correlated with settlement date of early settling females in 1986 (Fig. 3; r_s = 0.09, n = 43, P > 0.50), or 1985 (Fig. 4; r_s = 0.25, n = 8, P > 0.50). In 1986, females that laid their first egg on 11 or 12 May had settlement dates ranging from 2 to 23 April. All females in this sample began egg laying over 8 days, whereas settlement dates spanned 23 days. First egg date was also not correlated with the more conservative measure of settlement (1986: r_s = 0.11, n = 43, P > 0.40; 1985: r_s = −0.10, n = 8, P > 0.80).

When late settling females were included, first egg date was significantly correlated with settlement date (Fig. 3; r_s = 0.39, n = 53, P < 0.01). However, four of the late settling females had first egg dates that were in the same range as the early settling females.

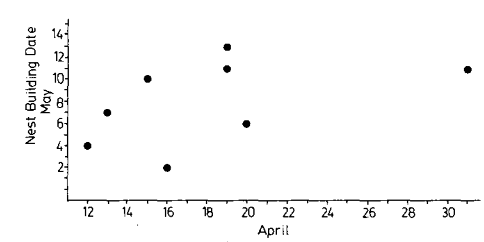

FIGURE 2. Date of nest-building initiation and settlement date of females in 1985.

Although neither initiation of nest building nor egg laying by early settling females were significantly correlated with the order of female settlement, first egg date was significantly correlated with initiation of nest building (r_s = 0.39, n = 43, P < 0.01). When a less rigorous criterion for nest-building initiation was used (i.e., light covering of nesting material), there was no longer a significant correlation between first egg date and nest building (r_s = 0.23, n = 43, P > 0.10), and nest building was still not correlated with settlement date (r_s = 0.08, n = 43, P > 0.60).

The settlement to nest building interval decreased significantly with advancing settlement date (Fig. 5; Early females: r_s = −0.72, n = 43, P < 0.001; All females: r_s = −0.83, n = 53, P< 0.001). Females that settled in early April waited 19 to 36 days to build nests, whereas females settling in early May waited only 1 to 5 days. The correlation of the nest-building to egg-laying interval with settlement date was not significant for early settling females (r_s = −0.23, n = 43, P > 0.01), but was significant when late settling females were included (r_s = −0.48, n = 53, P < 0.001). The interval between settlement and first egg date decreased significantly with settlement date (Early females: r_s = −0.92, n = 43, P < 0.001; All females: r_s = −0.95, n = 53, P < 0.001). Early settling females laid eggs 35 to 43 days after settlement, whereas late settling females laid eggs after only 6 to 15 days. The high correlation coefficient of the settlement to egg-laying interval and settlement date, relative to

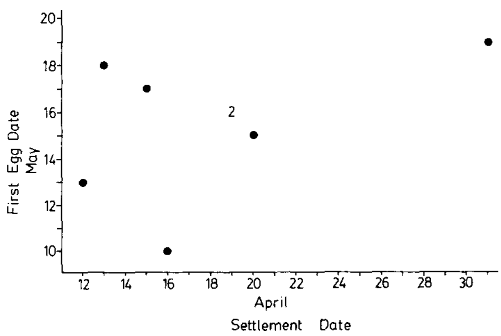

FIGURE 4. First egg date and settlement date of females in 1985. Numbers represent multiple observations at that point.

the settlement to nest-building interval, indicates that for a given settlement date, females that had a relatively short delay between settlement and nest building tended to have a relatively long delay between nest building and egg laying.

To interpret why there was no correlation of egg laying and nest building with settlement date, it is important to know whether the same individual females were involved from settlement through egg laying. Of the females that eventually laid eggs in a nest site that was available during the early settlement period in 1986 ($n = 43$), 61% were first captured at that nest site before initiation of nest building, and 20% were first captured between nest building and first egg date. Clearly, in most cases, the female first settling at a nest site was the one which eventually laid eggs there.

Capturing females before nest building or egg laying did not appear to affect their nest building or first egg dates. For a given settlement date, females first caught before nest building did not have a longer settlement to nest-building interval than females first caught after initiating nest building. Likewise, females first caught between nest building and egg laying did not have a longer nest-building to egg-laying interval than females first caught after egg laying.

DISCUSSION

The order in which female Tree Swallows initiated nest building and egg laying was not correlated with the order in which they settled on territories in early spring in either 1985 or 1986. Although some females settled up to 2 weeks before other females, they did not begin their nesting activities any earlier. The consistent results in both years suggest that this lack of correlation between nesting activities and settlement date was not simply a year effect.

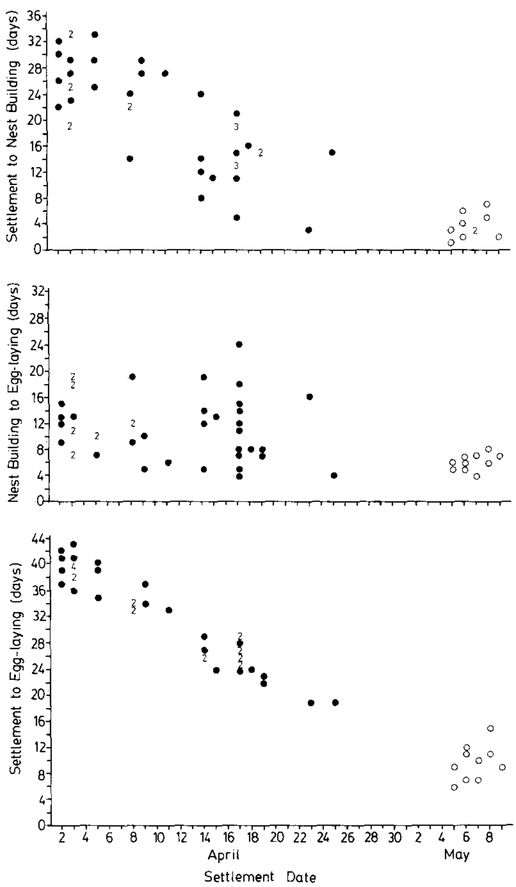

FIGURE 5. The interval between settlement date, nest building date, and first egg date vs. settlement date of early settling females (April; closed circles) and late settling females (May; open circles) in 1986. Numbers represent multiple observations at that point.

The lack of correlation between nesting activities and settlement date could result from the criteria that we used to define settlement and nest building. We assumed that lone birds defending a nest site were males, and defined female settlement as the date of pairing at a nest site. This assumption is supported by our own observations of the behavior of lone birds, and those of Cohen (1984). A more conservative definition of pairing date did not result in a stronger correlation between nesting activities and settlement. The definition of nest building based on 3 cm of nesting material is relatively conservative because the average completed nest is about 6 cm in depth. We found that a less rigorous measure (i.e., a light covering of nesting material) was still not significantly correlated with settlement. We therefore feel that our criteria for defining settlement and nest-building date are accurate.

Another factor which could influence the strength of the correlation between nesting activities and settlement date is undetected changes in female residency at a nest site between settlement and egg laying. A large proportion (81%) of the females that were known to lay eggs in their nest site were first caught at their nest site before initiation of nest building or between nest building and egg laying. Therefore, it is unlikely that there was a high frequency of evictions of resident females before egg laying.

If females that settle very early do not necessarily breed earlier, what are the benefits to females that settle early in April? Tree Swallows are obligate cavity nesters, and nest sites are severely limited (Holroyd 1975). We have found large floating populations of females in our study area (Stutchbury and Robertson 1985). There is intense competition among females for breeding opportunities, which often results in fights and injuries (Leffelaar and Robertson 1985, Lombardo 1986a, Robertson et al. 1986). The earliest arriving females likely have a higher probability of securing a nesting site, and therefore breeding, than females which arrive later in the spring.

Why do females that obtain a nest site very early in the season have such a long delay before egg laying? Females that settle relatively early may delay their nesting activities because of the high costs of early settlement. Early in April, overnight temperatures are often below freezing, which can result in mortality (Weatherhead et al. 1985, Lombardo 1986b). Females may be further energetically stressed because food abundance is relatively low during poor weather conditions early in the season (Taylor 1963). Finally, because of the intense competition for breeding resources, females that settle early likely expend time and energy defending their nest site from females that arrive later.

Another reason that early settling females might delay their nesting activities is because there may be benefits to breeding synchronously. Tree Swallows mob potential predators (Kuerzi 1941), so synchronous breeding could enhance an individual's breeding success by taking advantage of more effective predator mobbing (Hoogland and Sherman 1976). Synchronous breeding may also result in a swamping effect on predators, so that there is a lower probability of individual females having their nest depredated (Robertson 1973, Hoogland and Sherman 1976, Wittenberger and Hunt 1985).

Females may also be delaying egg laying until mid-May so that egg production, incubation, and the feeding of nestlings occur under conditions of relatively favorable weather and food abundance (Zach and Mayoh 1982). Females that do not obtain a nest site until May or June are under pressure to breed as soon as possible, because those that breed late in the season have a lower reproductive success (DeSteven 1978). Tree Swallows molt before they migrate south in September (Dwight 1900), so nestlings that fledge from late nests in July (rather than June) may have a lower survival rate because they must face the energetic costs of molt and migration in very close succession.

The length of time females delay nesting activities after settling depends on when in the season they became established at a nest site (Fig. 5). Females that settled relatively late reduced the interval between settlement and egg laying primarily by shortening the interval between settlement and nest building, rather than the interval between nest building and egg laying. Interestingly, females that built nests relatively early for a given settlement date tended to have a relatively long nest-building to egg-laying interval, and conversely, those that built nests relatively late had a short nest-building to egg-laying interval. This suggests that females are timing their egg laying to benefit from breeding synchronously and/or breeding when conditions are most favorable, rather than being forced to delay breeding because of the high costs of early settlement.

In Tree Swallows there are floating populations of females, and some of these females breed in nest sites that become available in May or early June through abandonment, predation, or decreased territorial defense by neighboring Tree Swallows (Stutchbury and Robertson 1985). To what extent do nest-building and egg-laying dates that range over the entire season reflect the settlement pattern of female Tree Swallows? The females that we experimentally prevented from settling until early May are comparable to females that naturally settle late. Nest building was significantly correlated with settlement when late settling females were included (Fig. 1). However, the experimental females settled at empty boxes that were erected after most early settling females had begun nest building, so they were forced to have relatively late nest building dates. When late settling females were included, first egg date was also significantly correlated with settlement date, but some of the females that did not settle until early May were still able to begin egg laying at the same time as the females that settled in April (Fig. 3). Clearly, even first egg dates that range over a long period cannot be used to accurately rank the order of female settlement. However, females with first egg dates well after the initial peak of egg laying in mid-May most likely settled after the initial period of settlement in April. Therefore, first egg dates that differ by several weeks likely do reflect differences in settlement date.

Muldal et al. (1985) examined the preferred spacing pattern of Tree Swallows when provided with a wide range of internest-site distances. They found that Tree Swallows did not show spacing preferences when nearest neighbors were more than 36 m away. They also found that when more than one pair settled in boxes that were within 18 m of each other, the pairs nested as far away as possible, and tended to be temporally spaced. This study used first egg date as a measure of which nest site was chosen first. They argued that since egg laying was correlated with nest building, then it was likely correlated with settlement date. However, we found that neither egg laying nor nest building were correlated with settlement, even when using a similar definition of nest-building initiation (first appearance of nesting material). In their sample, most females (68%) laid their first eggs within 3 days of the mean for the population. Their interpretation of nest site preferences over the entire grid of available sites is not valid because the assumption that first egg date is correlated with settlement date does not hold over such narrow ranges of first egg date. However, their general conclusion, that within relatively short distances Tree Swallows prefer to space their nests as far away from conspecifics as possible, is not strongly affected by our results. They rarely found more than two pairs settled in boxes that were clumped within 18 m of each other. If Tree Swallows preferred close neighbors, then there should have been many pairs nesting in each cluster of boxes. When there were two pairs, the first egg dates of the two females were, on average, 13 days apart. Their interpretation that the settlement of the two pairs was temporally spaced is likely correct because first egg dates that differ by well over a week likely reflect differences in settlement date.

Since it is important to determine the sequence of female settlement to evaluate nest site and mate choice decisions by females, our study points out the need to determine settlement date directly, or verify the relationship between settlement date and other nesting parameters such as nest building or egg laying. In many species it may be very difficult to test the assumption that nest building or first egg date are correlated with settlement date, because females are relatively cryptic before they begin nesting activities. We predict that this assumption does not necessarily hold in species in which females breed synchronously but settle on territories long before egg laying. Lenington (1980) found that the first egg date of female Red-winged Blackbirds (*Agelaius phoeniceus*) was not closely correlated with the order of female settlement. In this species, as in Tree Swallows, females settle on territories several weeks before the initiation of breeding activities, and females breed fairly synchronously (Robertson 1973). In contrast, the order of egg laying in female Pied Flycatchers (*Ficedula hypoleuca*) was closely correlated with settlement date (Alatalo et al. 1984). Here, females did not breed synchronously, and the interval between settlement and egg laying was only about 10 days. These studies provide some support for our prediction.

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