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Nest box orientation affects internal temperature and nest site selection by Tree Swallows

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ABSTRACT. Orientation of nests can influence nest microclimate, particularly temperature. However, few investigators have examined orientation preference and microclimate simultaneously. We examined the possible correlation between entrance orientation of artificial nest boxes used by Tree Swallows (*Tachycineta bicolor*) and the internal temperature of boxes. Tree Swallows showed a preference for east- and south-facing boxes, but only during the first half of the breeding season (before 1 June). During the second half of the breeding season (after 1 June), Swallows selected boxes based on availability. We found that east- and south-facing boxes were warmer than north- and west-facing boxes, but only during the first half of the breeding season when those boxes were preferred. Entrance orientation and box temperature were only correlated during the morning (06:00–12:00); the temperature of all boxes was similar during the afternoon. Our results suggest that Tree Swallows show a preference for nest boxes with a certain entrance orientation only when orientation influences microclimate, suggesting that warmer nest temperatures may provide fitness benefits.

SINOPSIS. **El orientación de cajas de anidamiento afecta su temperatura interna y la selectividad por parte de *Tachycineta bicolor***

La orientación de nidos puede influir el microclima de estos, particularmente su temperatura. Sin embargo, son muy pocos los trabajos de investigación que han examinado preferencias de orientacion y aspectos microclimáticos en el mismo estudio. Examinamos la posible correlación entre preferencias en la orientacion del hueco de entrada y la temperatura interna de las cajas en la golondrina *Tachicineta bicolor*. Las aves mostraron preferencias por cajas orientadas hacia el este y hacia el sur, antes del 1 de junio. Posterior a dicha fecha, las golondrinas seleccionaron las cajas a base de la disponibilidad de estas. Encontramos que las cajas orientadas hacia el este y hacia el sur eran más calidas que las que estaban orientadas al norte y al oeste, aunque fueron utilizadas con preferencia hasta el 1 de junio. La orientación de la entrada a la caja y la temperatura se correlacionaron durante la mañana (de 06:00–12:00); en la tarde todas las temperaturas estaban equilibradas. Nuestros resultados sugieren que las golondrinas muestran una preferencia a la orientación de la entrada a la caja, cuando la misma influye en el microclima de la misma. Las más cálidas pudieran traer algún beneficio a estas.

Key words: entrance orientation, nest microclimate, *Tachycineta bicolor*, temperature, Tree Swallow

Nest microclimate can have important influences on parental costs of reproduction and offspring development in cavity nesting birds. Temperature is an important aspect of nest microclimate because conditions in nests influence egg viability (Webb 1987, Cook et al. 2003) and impact the energy balance of incubating adults (White and Kinney 1974, Vleck 1981) and developing nestlings (Webb and King 1983, Quinney et al. 1986, Visser 1998, Ardia 2005a). Warm temperatures can also lead to fewer interruptions in laying (Yom-Tov and Wright 1993) and lower incubation costs (Haftorn 1983, 1988). One way that individuals may influence nest temperature is via nest orientation (Conner 1975, Inouye 1976, Rendell and Robertson 1994, Brown and Downs 2003, Hartman and Oring 2003). Although the presumed explanation for this preference is to optimize sun exposure (Inouye 1976, Korol and Hutto 1984, Balgooyen 1990, Hooge et al. 1999), preference may also be to minimize sun exposure, depending on ambient conditions. Few investigators have explicitly examined whether nest orientation preference is actually correlated with nest temperature (Hooge et al. 1999, Wiebe 2001).

Here, we examine nest orientation preference in a population of Tree Swallows (*Tachycineta bicolor*) and compare temperatures inside nest boxes as a function of entrance orientation.

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Secondary cavity nesters are an interesting case of nest-site selection because they are likely more limited in their choice of nest sites than primary cavity nesters. Thus, nest preference can only occur within the limitations of nest site availability. For this reason, nest preferences by secondary cavity nesters may not be expressed (Nilsson 1984, Brawn 1988, Li and Martin 1991). Here, we sought to assess possible preferences in a population of Tree Swallows using an unsaturated matrix of artificial nest boxes. Tree Swallows have been found to select south- and east-facing boxes (Lumsden 1986, Rendell and Robertson 1994), but not in all studies (Peterson and Gauthier 1985). This is the first study to assess both nest orientation preference and test the relationship between box orientation and box temperature. We predicted that Tree Swallows would show nonrandom preferences for nest boxes with respect to entrance orientation, and that entrance orientation would have a significant effect on box temperature.

METHODS

Our study area was a series of open fields (81 ha) in Amherst, MA (42°22′N, 72°31′W), where we placed 153 nest boxes in April 2004. We used nest boxes (floor 7 cm ×11 cm, back 20 cm) with angled (25°), shingled, overhanging roofs placed on 1.5 m metal poles. Of these boxes, 84 (55%) were occupied by Tree Swallows from May to August 2005 (mean clutch size = 5.01). Males and females were identified by the presence or absence of a brood patch, and females were marked on the back with typewriter correction fluid. We placed a Thermochron® iButton data logger (DS1920, Maxim Semiconductor, Dallas, TX; accuracy ± 0.5°C) on a plastic key fob mounted on the left side of each settled nest box approximately 7 cm from the roof and at least 3 cm from each side. Loggers recorded temperature every 4–10 min depending on the time in the nesting season. Prior to placement in the field, we compared each logger against two independent instruments: a HOBO U12 Thermocouple thermometer (Onset Corporation, Bourne, MA) and a Roetemp TM99-A Thermometer (Roetemp, San Diego, CA). Loggers that did not record temperatures within 0.5°C of both additional thermometers were not used. Although females were incubating during temperature measurements, there was no difference in ambient temperature between adjacent unoccupied boxes of similar orientation, indicating that the presence of females did not affect internal temperatures (unpubl. data). To record ambient temperature, we placed a single data logger in the shade under a centrally located nest box. We found little evidence of among-box variation in ambient temperature (unpubl. data). We focused on temperature because wind is not an important factor for cavity nests (Wachob 1996). A compass (±0.5°) was used to determine the orientation of each nest box. Entrance orientations were recorded relative to magnetic north and corrected by 15°W to true north.

Nest boxes were checked daily from 1 May to 1 July 2005 to determine the date of clutch initiation (1 May = 1). Because Tree Swallows initiate nesting when ambient temperatures are still cool (daily average temperatures <20°C; Winkler 2000), we divided the breeding season in half (middle date = 30 May) and analyzed early- and late-nesting birds separately.

We calculated mean orientation angle using circular statistics and tested mean angle for uniform orientation using the Rayleigh test (Zar 1999). We compared mean orientation angle among groups using the Watson-Williams test (Zar 1999). We used a χ^2 test to determine nest box preferences relative to unused boxes. Correlation between box temperature and box orientation was tested using angular-linear correlation at 4-d intervals starting on day 17 (17 May) (Zar 1999). We divided days into three periods: morning (06:01–12:00 EDT), afternoon (12:01–21:00 EDT), and night (21:01–06:00 EDT). For days when a significant angular-linear correlation was calculated, we compared the mean temperature for each cardinal direction using Fisher's Least Significant Difference (SAS 1988). Differences were considered significant at $P < 0.05$.

RESULTS

Nest orientation of boxes used during the first half of the breeding season was different from uniform orientation (early: mean angle =154° SSE, $r = 0.26$, $R = 12.3$, $z = 3.2$, $P < 0.05$, $N = 48$). However, the orientation of boxes used late in the breeding season and unused boxes did not differ from uniform (late: mean angle =73°, $r = 0.16$, $R = 4.4$, $z = 0.7$, $P = 0.5$; unused boxes: mean angle =140°, $r = 0.17$, $R = 10.92$,

$z = 1.92$, $P > 0.10$, $N = 27$). Boxes used early in the breeding season differed in orientation from boxes used later in the season (Watson-Williams test $F_{1,76} = 18.4$, $P < 0.001$) and from unused boxes (Watson-Williams test, $F_{1108} = 7.5$, $P < 0.01$). The orientation of boxes used later in the breeding season did not differ from that of unused boxes (Watson-Williams test $F_{1,88} = 1.6$, $P = 0.2$). A comparison of boxes used by Tree Swallows and available unused boxes revealed that Swallows showed a preference for east- and south-facing boxes during the first half of the breeding season ($\chi^2 = 7.58$, $P = 0.04$; Fig. 1), but showed no preference during the second half of the breeding season ($\chi^2 = 0.01$, $P = 0.93$; Fig. 1).

Mean box temperature increased during the breeding season (Fig. 2 A). Boxes had the lowest temperatures during the night, followed by the morning, with the warmest temperatures during the afternoon (Fig. 2A). During most of the breeding season, there was no correlation between box temperature and box orientation. However, there was a significant angular-linear correlation between box temperature and box orientation from 6:01–12:00 during the early part of the breeding season (May 17, $\rho = 0.45$, $P < 0.01$; May 21, $\rho = 0.33$, $P < 0.01$; May 25, $\rho = 0.21$, $P < 0.05$; May 29, $\rho = 0.34$, $P < 0.01$; 2 June, $\rho = 0.17$, $P < 0.10$). On mornings when a correlation was observed, east- and south-facing boxes were warmer than north- and west-facing boxes (Fig. 3).

Ambient temperature increased during the breeding season (Fig. 2B). Daily temperature variation varied over the season, with the differences between afternoon and morning temperatures ($F_{1,55} = 4.1$, $P = 0.05$, $R^2 = 0.24$) and night and morning temperatures ($F_{1,55} = 5.4$, $P = 0.02$, $R^2 = 0.31$) decreasing during the breeding season.

DISCUSSION

Tree Swallows breeding in artificial nest boxes showed a significant preference for south- and east-facing nest boxes during the first half of the breeding season when they were warmer than

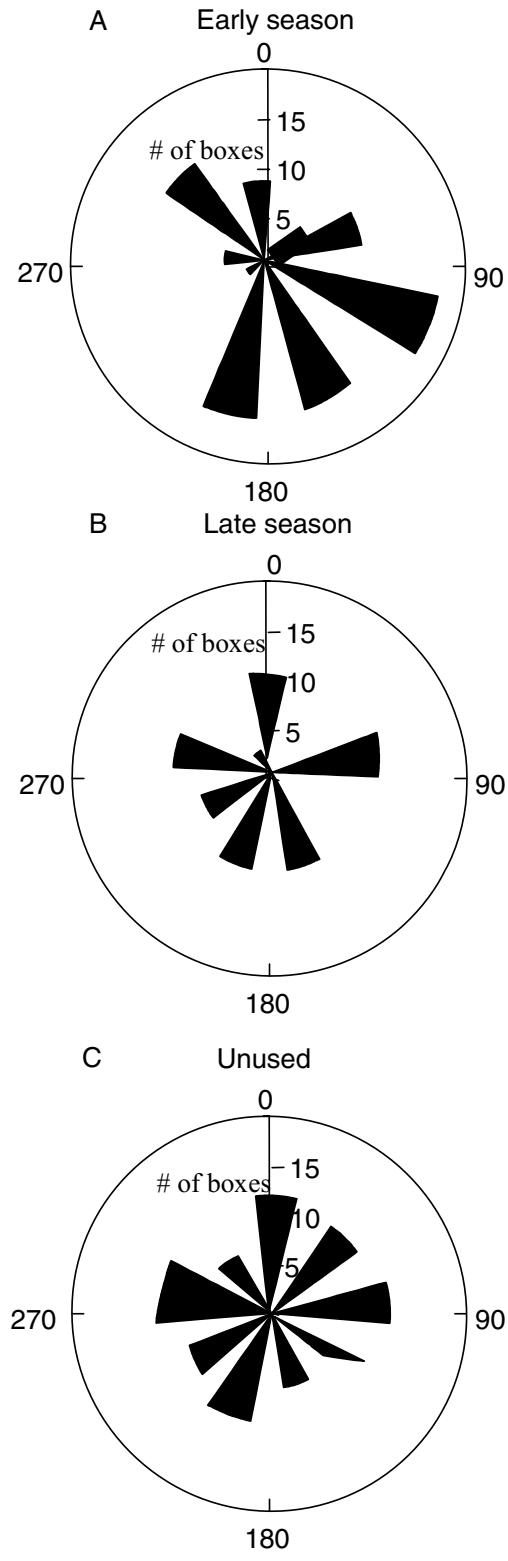

Fig. 1. Nest box orientation of early and late-breeding Tree Swallows and unused nest boxes.

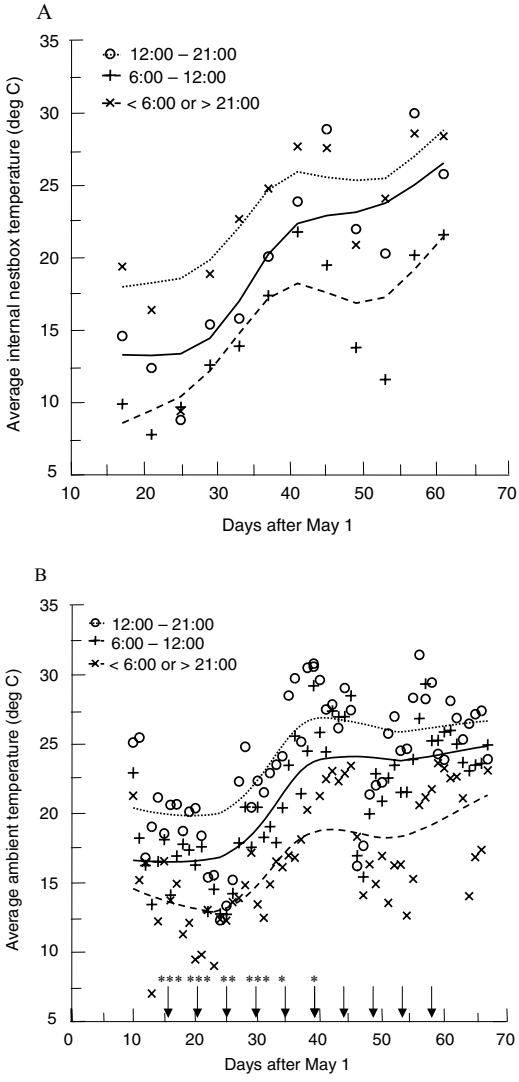

Fig. 2. Internal nest box (A) and ambient temperatures (B) at three time intervals during the breeding season. Julian day 1 = 1 May. Lines show LOESS smoothing to reflect moving average over the breeding season. Loess smoothing is a curve-fitting technique based on local regression. Arrows along *x*-axis refer to days where nest box temperature and nest box orientation were compared using angular-linear correlation; $^{***}P < 0.01$, $^{**}P < 0.05$, $^{*}P < 0.1$.

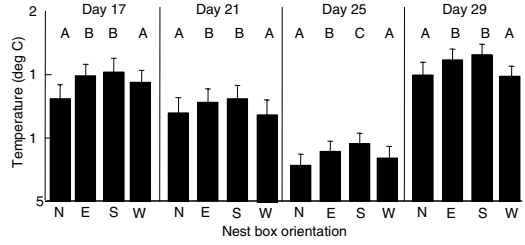

Fig. 3. Temperature differences as a function of orientation in the four cardinal directions for nest boxes on days with a significant correlation between orientation and nest temperature. Day 17 $F_{3,19} = 3.56$, $P = 0.04$, $N = 23$; Day 21 $F_{3,42} = 5.21$, $P < 0.01$, $N = 46$; Day 25, $F_{3,48} = 4.37$, $P = 0.01$, $N = 53$; Day 29, $F_{3,48} = 5.77$, $P < 0.01$, $N = 53$. Letters refer to significant differences within each day using Fisher's least significant difference. Temperatures represent average temperature during the period 6:00–12:00. Julian day 1 = 1 May.

other boxes. Similarly, Rendell and Robertson (1994) reported that Tree Swallows exhibited a preference for natural cavities with south-facing entrances. Tree Swallows showed no preference in nest-box orientation during the second half of the breeding season, and there was no correlation between nest orientation and box temperature during the second half of the breeding season. These results suggest that secondary-cavity nesters in an unsaturated habitat show a preference for entrance orientation only when orientation is actually related to temperature. Ours is the first study to compare orientation and microclimate at the same time; the pattern we report of a preference only when temperatures are warmer strongly suggests that Tree Swallows are choosing boxes based, in part, on temperature. The next step is to investigate the possible link between nest temperatures and reproduction.

The low thermal inertia of a wooden nest box is likely responsible for the temperature patterns we report. South- and east-facing boxes heat up more quickly in the morning, likely due to angled, shingled roofs absorbing more morning sunlight. However, by afternoon, temperatures in boxes equalize. Given that the coldest temperatures each day are usually during the early morning presunlight hours, the slight increase in temperature may cause birds to prefer south- and east-facing boxes. Similarly, Hooge et al. (1999) found that an east-facing box was warmer in the morning, but the differences among boxes that differed in orientation disappeared in the afternoon. The low thermal inertia and limited temperature differences of nest boxes likely causes nest site selection for nest boxes to be less constrained than for natural cavities, which

have higher thermal inertia and show greater temperature difference (du Plessis et al. 1994). Greater temperature differences among natural cavities with different orientations can lead to significant differences in reproductive success. For example, Acorn Woodpeckers (*Melanerpes formicivorus*; Hooge et al. 1999) and Northern Flickers (*Colaptes auratus*; Wiebe 2001) nesting in warmer cavities were more likely to be successful. Other investigators, however, have found no effect of orientation on reproductive success, indicating that a species-specific investigation is needed (Rendell and Robertson 1994). Limited variation in the characteristics of nest boxes may limit the effect of nest box orientation on reproductive success.

We found that nest site selection by Tree Swallows varied during the breeding season. Similarly, Prothonotary Warblers (*Protonotaria citrea*) select warm boxes for early clutches, but not for late clutches (Blem and Blem 1994). This could be due to the absence of any correlation between orientation and box temperature later in the breeding season. This is likely because the increase in temperature during morning hours relative to night time temperature is proportionally less late in the season. However, the absence of preferences in the late season may also be due to the reduced availability of quality nest sites.

Because we did not manipulate box temperatures, we cannot conclude that temperature differences are the direct cause of selection for certain orientations. Covariation with both individual quality as well as seasonal change in other variables, such as food supply, may underlie the pattern we report here. However, the fact that Tree Swallows show box preferences only when temperature and orientation were correlated suggests that temperature plays a significant role. Studies examining the influence of temperature on offspring condition have revealed that nestlings in warmer nests tend to have higher cell-mediated immune response to PHA (Ardia 2005 a, Dawson et al. 2005) and lipid levels (Ardia 2005b). Future work is needed to determine how nest orientation may influence offspring growth and parental reproductive success.

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