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TEMPERATURE DOES NOT AFFECT THE TIMING OF FIRST NEST DEPARTURE IN ORANGE-CROWNED WARBLERS

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ABSTRACT.—Organisms often respond to variation in temperature by altering their behavior, but the sensitivity of each behavioral trait depends on the degree to which temperature affects its costs and benefits. Here, we tested whether a little-studied trait, the timing of the first nest departure in the morning, varied in response to ambient temperature at sunrise, sunrise time, and nesting stage (incubation vs. nestling) in female Orange-crowned Warblers breeding on Santa Catalina Island, California. We found that the time of first nest departure was significantly correlated with sunrise time but was not affected by ambient temperature at sunrise. Compared with the nestling period, first nest departure times tended to be later and more variable during incubation, but the causes of these patterns remain to be explored in future studies of avian early-morning behavior.

RESUMEN.—Los organismos suelen responder a las variaciones de temperatura alterando su conducta, la modificación de cada aspecto de dicho comportamiento depende del grado en que la temperatura afecte los costos y beneficios. En este estudio analizamos si una característica poco estudiada, el momento de la primera partida del nido durante la mañana, se modificó en función de la temperatura al amanecer, en el horario del amanecer y en la etapa de anidación (incubación versus salida del cascarón) en las crías femeninas de la especie *Oreothlypis celata* en la Isla Santa Catalina, California. Encontramos que el momento de la primera partida del nido tiene una estrecha relación con el horario del amanecer, pero no era afectado por la temperatura ambiental al amanecer. En comparación con el período de crecimiento de los pollos en el nido, los momentos de la primera partida del nido fueron posteriores y más variables durante la incubación. Sin embargo, todavía se deben investigar las causas por las cuales esta especie sigue estos patrones en futuros estudios sobre el comportamiento matutino de las aves.

Understanding behavioral and physiological responses to variation in temperature is critical for predicting organisms' responses to environmental variation and global climate change. In birds, ambient temperature influences a range of behaviors by altering their energetic costs and benefits. For example, parents of altricial birds face a trade-off between keeping their eggs warm and leaving the nest to forage for the energy needed for incubation (Drent et al. 1985, Conway and Martin 2000a, Cresswell et al. 2003, Ardia et al. 2009). This trade-off is exaggerated under colder temperatures, when birds may be forced to expend more energy on incubation (Williams 1996, Tinbergen and Williams 2002) and decrease the length of off-bouts (Lofaldli 1985, Haftorn 1988, Conway and Martin 2000a); a similar trade-off likely applies during the early nestling period because altricial nestlings hatch without the ability to thermoregulate (Visser 1998). Yet, despite recognition that temperature often shapes the parental behavior of temperate breeding birds, little is known about the sensitivity of some behavioral traits, namely early-morning behavior.

Although the coldest temperatures at which breeding birds are active generally occur in the early morning, the effects of ambient temperature on the timing of first nest departure has received little study. To date, most research on the timing of first morning activity either has focused on the importance of light levels (Nice 1943, Davis and Lussenhop 1970, Swingland 1976) or has evaluated the effects of temperature during the nonbreeding season. For example, several studies have shown that cold temperatures increase time spent at roost sites (Brodsky and Weatherhead 1984, Reebs 1986, Warkentin 1986, Everding and Jones 2006, Xu et al. 2008; but see Doucette and Reebs 1994). However, patterns observed during winter may not be maintained during the breeding season, when the activity patterns of nesting birds depend on both parental

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and offspring energetics. Indeed, Kluijver (1950) found that Great Tits (*Parus major*) became active later on warmer winter days, an effect partly attributable to cloudy weather, but in a detailed study of a single breeding female's behavior, he found no relationship between climatic variables and the time of first nest departure. Similarly, Nolan (1978) found no effect of temperature on the time of first nest departure in incubating Prairie Warblers (*Dendroica discolor*). Finally, the timing of first morning activity can differ between breeding and nonbreeding individuals and can also depend on the stage and age of the young (Maxson 1977). Although these studies are decades old and largely qualitative, they remain representative of our understanding of climatic effects on the timing of first nest departure and stand in striking contrast to the large body of research on how temperature affects other aspects of avian parental behavior.

We studied how ambient temperature affected the timing of first nest departure in female Orange-crowned Warblers (*Oreothlypis celata*), controlling for variation in sunrise time. This species has been shown to increase the length of each incubation on-bout and to decrease the length of each off-bout in lower ambient temperatures (Conway and Martin 2000b). Females could respond to lower ambient temperatures by either remaining on the nest longer to thermoregulate their young or leaving the nest sooner to forage and support their own metabolic needs and those of the nestlings. We also tested for effects of nesting stage (incubation vs. nestling), which could reflect the difference between providing only warmth during the incubation stage versus providing both warmth and nutrition during the nestling stage. Despite a long scientific interest in geographic variation in avian activity patterns (Lack 1947, Karplus 1952, Weeden 1966, King 1986, Sanz 1999), very few studies have evaluated how temperature, nesting stage, and sunrise time affect the precise timing of first activity in a breeding bird.

METHODS

We studied Orange-crowned Warblers breeding in Bulrush Canyon (2003–2009; 33°20′N, 118°26′W) on Santa Catalina Island, California, in April–May 2009. This insular population has no visually oriented nest predators (Peluc et al. 2008, Sofaer et al. 2013), so first nest departure times in the morning were unlikely to be affected by spatial or temporal variation in perceived predation risk. We videotaped nests for a 24-h period starting at midday via small camouflaged video cameras (Swann Inc.) placed beside the nest site and video recorders (Archos Inc.) with custom battery packs (Batteries Plus Inc.) placed 10–20 m away. During the nestling period, birds in this study population were active for an average of 13.4 h (SD 0.5) during each 24-h period (Sofaer 2012). Video cameras were not infrared but did function under low-light conditions. We analyzed 32 video recordings from 25 nests during the incubation ($n = 23$ videos) and nestling ($n = 9$ videos) stages. We transcribed videos to record parental behavior, including the time of the female's first departure from the nest in the morning. The female's nest departure represented the first daily activity, as only females incubate and brood young in this species, and in all nestling-stage videos the female left the nest before the male arrived with food. Nestling videos were recorded 6 or 7 days after hatching.

We obtained the sunrise temperature (°C) and overnight low temperature (°C) for each video date from the Western Regional Climate Center's weather station in Hayfield, California (http://www.wrcc.dri.edu/catalina/). Due to a strong positive correlation (Pearson correlation coefficient: $r = 0.79$) between the overnight low and sunrise temperatures, we used only sunrise temperature in our analysis. An analysis with only overnight low temperatures yielded similar results. Mean sunrise temperature was 10.7 °C (SD 3.1, range 6.1–19.6 °C). We determined the sunrise time for each video date based on the online database of the Astronomical Applications Department of the U.S. Naval Observatory (http://aa.usno.navy.mil/).

We analyzed the time of first activity using a linear mixed model (Pinheiro and Bates 2000). Our model included 3 fixed effects: sunrise temperature, sunrise time, and nesting stage. We included a random effect of nest identity because we videotaped 5 nests on more than one day, including 2 that we recorded on 3 days. To create numeric variables, we calculated both sunrise time and the time of first activity as the number of minutes after 6:00 (earlier values were negative). Our model was run in the lme4 package of R version

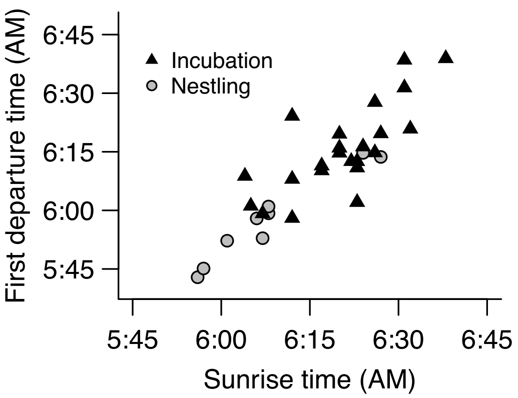

Fig. 1. Timing of first nest departure of female Orange-crowned Warblers versus sunrise time. A positive linear relationship is observed during both the incubation and nestling periods; sunrise occurred earlier during the nestling period.

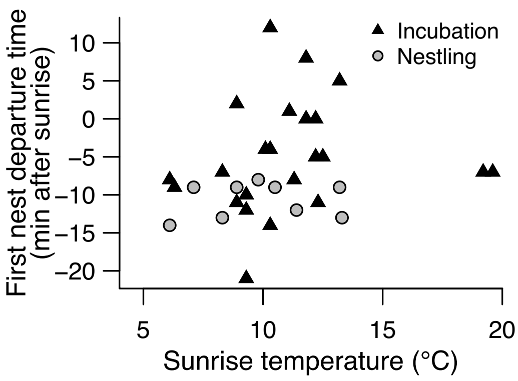

Fig. 2. Timing of first nest departure of female Orange-crowned Warblers versus temperature at sunrise. Departure times are shown relative to sunrise, with negative values representing times before sunrise; temperature had no effect on the time of first nest departure during either the incubation or nestling stage.

2.15.1 (Bates et al. 2012, R Development Core Team 2012). Because calculation of the degrees of freedom in mixed models is not straightforward, lme4 does not provide this output or *P* values. We used the languageR package to estimate *P* values using Markov chain Monte Carlo methods (Baayen 2011). In a separate analysis, we used the Brown–Forsythe modification of Levene's test to test for a difference in the variance in nest departure time relative to sunrise between the incubation and nestling periods.

RESULTS

Females departed from the nest earlier on days with an earlier sunrise (Fig. 1; $t = 5.89$, $P = 0.0001$), but temperature did not affect the time of first nest departure (Fig. 2; $t = 1.30$, $P = 0.43$). During the incubation period, mean first nest departure occurred 5 min (SD 7) before sunrise, whereas during the nestling period mean first nest departure occurred 11 min (SD 2) before sunrise. The difference in the mean between the incubation and the nestling stages showed a tendency toward statistical significance ($t = –1.63$, $P = 0.09$). The difference in the variance of relative nest departure times (i.e., minutes before or after sunrise) between the incubation and the nestling stages bordered on significance ($F_{1,30} = 4.13$, $P = 0.051$), with more variability during incubation (Fig. 2). Our mixed model estimated the standard deviation of the random nest effect as 5.9 min (the model assumed that the nests in our study were a sample drawn from a broader population of nests, and the estimated standard deviation quantified the magnitude of variation between nests in that population).

DISCUSSION

Although variation in ambient temperature can often lead to behavioral variation in breeding birds, we found that the time of first nest departure was not affected by temperature (Fig. 2). Instead, females' first nest departure times were strongly correlated only with sunrise time (Fig. 1), with a tendency for birds brooding young to depart the nest earlier than those incubating eggs (Fig. 2). Our results are somewhat surprising because adult energetic requirements and embryonic and nestling development are known to be sensitive to ambient temperature (Vleck 1981, Haftorn and Reinertsen 1985, Williams 1996, Hoset et al. 2004, Olson et al. 2006, Ardia et al. 2010, Nord and Nilsson 2011). However, it appears that though temperature often shapes parental behaviors once daily activities begin, it does not affect the time of first nest departure in this population.

Our study supports the idea that birds outside the arctic and subarctic may leave the nest when it becomes light enough to see (Fig. 1; Lack 1947, Sanz 1999, Sanz et al. 2000; but see Kluijver 1950). However, we could not evaluate whether birds woke up substantially earlier than they left the nest, and we can only speculate regarding the factors that led to a pattern of greater variability in nest departure times during incubation compared with the nestling stage (Fig. 2). Nevertheless, previous studies have also suggested that females depart the nest earlier during the nestling period (Kluijver 1950, Nolan 1978) and that first nest departure times can be more variable during incubation (Nolan 1978). Although some variation among nests could be explained by differences in light levels at nest sites, this is unlikely to explain differences in the amount of variability in nest departure times between the 2 nesting stages. Instead, it is plausible that birds brooding young generally leave the nest as soon as light levels allow in order to collect food for their nestlings, whereas incubating females may either leave as early as possible or may remain on the nest somewhat longer, perhaps reflecting the adult's energetic needs.

Our finding that first nest departure time was not affected by temperature aligns with observations from 2 previous studies of breeding passerines (Kluijver 1950, Nolan 1978), but stands in contrast to the results of most studies of roosting birds, which have found that cold temperatures delay roost departure times (Brodsky and Weatherhead 1984, Reebs 1986, Warkentin 1986, Everding and Jones 2006, Xu et al. 2008). This difference could reflect differences between the breeding and nonbreeding periods or greater thermoregulatory challenges posed by colder temperatures during the nonbreeding season. Alternatively, the difference could reflect the fact that most studies evaluating the effects of temperature on roosting behavior have focused on relatively large-bodied species such as waterfowl, corvids, and small raptors. The higher capacity for fat storage in these species may afford them more flexibility to remain at relatively protected roosting sites on cold mornings, whereas small passerines may more often be obligated to forage at daybreak, either because of their own energetic needs or those of their nestlings. Therefore, future studies might evaluate whether body size affects the relationship between temperature and the time of first activity relative to sunrise.

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