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EGG AND CHICK FATES DURING TIDAL FLOODING OF SALTMARSH SHARP-TAILED SPARROW NESTS

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Abstract. We determined nest attendance patterns of Saltmarsh Sharp-tailed Sparrows (*Ammodramus caudacutus*) in Connecticut using temperature data-loggers. In this species, only females incubate and feed the young. Females maintained a stable thermal environment in their nests during incubation by modifying their attendance behavior in relation to ambient temperature; during cooler conditions, females made shorter, but more frequent, trips away from their nests to feed. Once eggs hatched, average nest temperature increased significantly. The data-loggers also recorded information on rare and unpredictable events, such as nest flooding, depredation, and fledging. Eggs and nestlings apparently tolerated nest inundation for periods averaging more than 90 min. Nestlings fledged from their nests soon after sunset on the flooding tide. Detailed insight into nest attendance behavior and the circumstances surrounding rare events such as flooding are especially important for this species of high conservation concern in which tidal inundation is the major cause of breeding failure.

Key words: Ammodramus, *data-logger, incubation rhythm, microclimate, nesting behavior.*

Destino de los Huevos y Pichones de Nidos de *Ammodramus caudacutus* durante las Inundaciones Producidas por la Marea

Resumen. Determinamos los patrones de asistencia a los nidos de *Ammodramus caudacutus* en Connecticut usando aparatos automáticos de registro de temperatura. En esta especie, sólo las hembras incuban y alimentan a los pichones. Las hembras mantuvieron un ambiente térmico estable en sus nidos durante la incubación modificando su comportamiento de asistencia con relación a la temperatura del ambiente; durante condiciones más frescas, las hembras hacen viajes desde sus nidos para alimentarse más cortos pero más frecuentes. Una vez que los huevos eclosionan, la temperatura media del nido aumenta significativamente. Los aparatos de registro también obtuvieron información de eventos raros o imprevistos, como inundación del nido, depredación y emplumamiento de los polluelos. Los huevos y los pichones aparentemente toleraron la inundación del nido por períodos que promediaron más de 90 min. Los pichones dejaron sus nidos apenas pasada la puesta del sol en los periodos de inundación ocasionados por la subida de la marea. Las observaciones detalladas sobre el comportamiento de asistencia al nido y las circunstancias que rodean a los eventos raros como las inundaciones son especialmente importantes para esta especie de alta preocupación de conservación, en donde la inundación durante las mareas más altas es una causa principal de fracaso reproductivo.

In the breeding season, Saltmarsh Sharp-tailed Sparrows (*Ammodramus caudacutus*) are nonterritorial, do not form pair bonds, and mate with multiple partners (Post and Greenlaw 1982, Greenlaw and Rising 1994, C. E. Hill, CSE, and CG, unpubl. data). Males move around in search of receptive females, and females provide all parental care (Greenlaw and Rising 1994). Females build nests on the ground in saltmarsh habitat that is dominated by native saltmarsh plants such as saltmeadow cordgrass (*Spartina patens*), saltgrass (*Distichlis spicata*), and saltmeadow rush (*Juncus gerardii*; Woolfenden 1956, Benoit and Askins 1999, Shriver et al. 2004, Gjerdrum et al. 2005, 2008). This highly productive habitat is a likely cause of male emancipation from brood care and the female's success as the sole caregiver (Post and Greenlaw 1982).

Adaptation to tidal flooding, where breeding behavior is synchronized with the lunar cycle, may also help explain the evolution of the unusual mating system of Saltmarsh Sharp-tailed Sparrows (Shriver et al. 2007) and other aspects of the species' breeding biology (Humphreys et al. 2007). During high spring tides, which occur approximately every 28 days, nests frequently flood, sometimes causing eggs to float away (Humphreys et al. 2007). These predictable flooding events are the primary cause of nest failure in this species, accounting for more than 60% of failures (DeRagon 1988, Greenlaw and Rising 1994, Shriver 2002, Gjerdrum et al. 2005). By timing their breeding so that nesting fits between the extreme spring tides, Saltmarsh Sharp-tailed Sparrows achieve higher reproductive success and greater breeding synchrony (Gjerdrum et al. 2005, Shriver et al. 2007) than would otherwise be possible. A better understanding of how tidal flooding has shaped the biology of this species will require more information on the process by which flooding occurs and the effects flooding has on sparrow reproduction. Understanding this aspect of Saltmarsh Sharp-tailed Sparrow biology is especially pressing in light of projected sea level rise.

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Determining the precise details surrounding events such as nest flooding can be hampered by the difficulty of making sustained observations throughout the 24 hr cycle, especially during periods of darkness, for large samples of nests, and without any risk of observer effects. Even when observations are possible, detecting rare or unpredictable events, including fledging or predation, can be a logistical challenge, making the timing and circumstances of these events difficult to study. Here, we describe nest attendance in Saltmarsh Sharp-tailed Sparrows during incubation and chick rearing using remote data-loggers (Cooper et al. 2005, Cooper and Mills 2005). First, we asked whether females modify their incubation behavior in response to weather conditions (Davis et al. 1984, Norment 1995, Rauter and Reyer 1997, Wheelwright and Beagley 2005). We then obtained precise information on the duration and consequences of nest flooding, the ability of young sparrows to survive these events, and the circumstances surrounding depredation and fledging—events that are difficult to observe directly, but which have important consequences for nest productivity and hence, population dynamics.

METHODS

This study was conducted at nine sites along the Connecticut coast during the breeding seasons (May–August) of 2003 and 2004. We located nests throughout the summer by thoroughly searching 33 one-hectare study plots that had been set up for a larger study of saltmarsh sparrow breeding biology (Gjerdrum et al. 2005). We marked each nest with a flag positioned 5 m away so that the nest lay between the flag and the plot's center.

We used temperature data-loggers (Thermochron iButtons, Maxim, Sunnyvale, California; referred to hereafter as iButtons), 16 mm in diameter, to record nest temperatures at varying stages of the nesting cycle. Nest initiation dates were calculated following Gjerdrum et al. (2005). Every 3–5 days during nest monitoring activities, we deployed up to five iButtons, each placed in a randomly selected active nest. We placed iButtons into a total of 59 different Saltmarsh Sharp-tailed Sparrow nests, either underneath the eggs or among the chicks, with sampling distributed throughout the incubation and nestling phases. Nine nests were sampled during both incubation and chick rearing, but no statistical tests used both data points from the same nest. On no occasion did a bird remove the iButton from a nest, and we detected no other evidence to indicate that iButtons interfered with normal behavior. To compare nest and ambient temperatures, we simultaneously deployed a second iButton in an empty nest located within the same marsh as each active nest. Each data-logger recorded the temperature in the nest every minute for a maximum of 36 hr.

STATISTICAL ANALYSES

Nest temperature data were downloaded using iButton–TMEX Runtime Environment Version 3.21 Beta 3 software (Maxim Integrated Products, Sunnyvale, California) as a DOS text file, and imported into program Rhythm (Cooper and Mills 2005). Rhythm works in conjunction with the bioacoustical analysis program Raven (Charif et al. 2004) to automate the measurement of temperature time series. Based on visual examination of the temperature time series and observations from the field, we set the parameter values in Rhythm to define "off-bout" periods as times when there was at least a 2.5°C change in temperature lasting more than 2 min with a minimum of 0.4°C per min rate of cooling or rewarming. We assumed that these cooling periods were associated with the female leaving the nest. A rapid drop in temperature corresponding to the timing of a high tide was defined as a flooding event. We defined the start of each flooding event as the time that a nest's temperature first began to drop toward its minimum, and the end of the event as the time at which the temperature began to rise prior to stabilizing for more than 5 min. The output from Rhythm (number, length, and timing of off-bouts) was imported into SYSTAT 8.0 (SPSS 1998) for analyses. To standardize data collection across nests, we used temperatures measured over a 24 h period, between 12:01 and 12:00 (EDT) of the following day.

For the analyses summarizing incubation and chick-rearing behavior, we excluded nests with both eggs and chicks ($n = 4$), and one nest that was classified as depredated, as temperatures fluctuated widely during the depredation event. In nests where fledging occurred, we calculated the average nest temperature prior to the departure of nestlings. We compared nest temperatures between egg and chick stages using *t*-tests; only one, randomly selected sample, was used for nests that were sampled during both stages. We used a generalized linear model (GLM) to evaluate the effects of clutch size, nest age, and ambient temperature on female attendance behavior during incubation. Assumptions regarding normality of sampling distributions, linearity, and homoscedasticity of residuals (Tabachnick and Fidell 2001) were met. We accepted significance at $\alpha = 0.10$ because our sample sizes were small, and summary statistics are presented as mean ± SD.

Data on tidal height and timing were obtained from the National Oceanic and Atmospheric Administration (2007). We used values reported from Bridgeport, Connecticut and adjusted the timing of tidal fluctuations for each marsh site according to the Connecticut Department of Environmental Protection (2007) estimates for tidal differences. We considered daylight hours to be the period between sunrise and sunset in central Connecticut.

RESULTS

Eggs were laid between 28 May and 3 August in 2003, and between 27 May and 9 August in 2004. In 2003 and 2004, respectively, we deployed 11 and 26 iButtons in nests containing 2–5 eggs. At the time of deployment, hatching had begun in two of these nests, and flooding due to especially high tides was recorded in nine of the nests. In 2003 and 2004, respectively, we deployed 10 and 21 iButtons in nests with one to five nestlings between 0 and 10 days of age. Two of these nests had a mixture of eggs and nestlings at the time their iButtons were deployed; flooding was recorded in five nests; one brood was presumed depredated after flooding; and in another six nests, at least one chick fledged while temperatures were being logged.

During incubation, female Saltmarsh Sharp-tailed Sparrows alternated the time they spent incubating eggs with periods off the nest, during which they were presumably foraging. In general, they remained on their nests at night, maintaining temperatures that averaged 78% higher than ambient (nest: 33.6 ± 1.4°C, $n = 35$; ambient: 18.9 ± 2.1°C, $n = 20$; Fig. 1). The temperature of nests during daylight hours was 34% higher than the ambient daytime temperature (nest: 34.7 ± 1.0°C; ambient: 25.9 ± 2.8°C). Over a 24 hr period, females left their nest an average of 26 ± 10 times (range: 11–49), 98% of which were during daylight. On average, each off-bout lasted 11.8 ± 3.2 min (range: 8–19 min), and females were away from their nests for 33% (289 ± 80 min, range: 147–546 min) of the daylight hours.

The more often a female left her nest, the shorter the duration of each absence ($r = -0.64$, $P < 0.001$). Ambient temperature had a significant effect on the number of off-bouts taken by the

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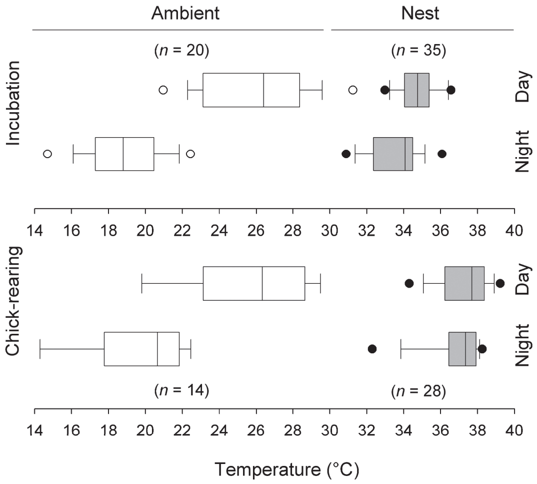

FIGURE 1. A comparison of ambient and Saltmarsh Sharp-tailed Sparrow nest temperatures during incubation and chick-rearing in Connecticut during 2003 and 2004. Each box represents the range of the central 50% of the data, with the interior line indicating the median, and the whiskers indicating the 5th and 95th percentiles.

female ($F_{1,16} = 6.7$, $P = 0.02$), and there was weak evidence for an effect on the average duration of off-bouts ($F_{1,16} = 3.4$, $P = 0.08$). These relationships were in opposite directions, such that during cooler conditions, females made shorter, but more frequent, trips away from their nests (Fig. 2A, B). We found no significant effect of clutch age on either the frequency of off-bouts ($F_{1,16} = 0.8$, $P = 0.82$) or their average duration ($F_{1,16} = 0.6$, $P = 0.43$), and only weak evidence for an effect of clutch size on their frequency ($F_{1,16} = 4.0$, $P = 0.06$) and duration ($F_{1,16} = 4.2$, $P = 0.06$), with females tending to leave the nest more often but for shorter periods of time when clutches were smaller. None of these variables had any detectable effect on the total time females spent away from their nests (all $P \geq 0.20$).

Once eggs hatched, the temperature of nests averaged 37.2 ± 1.4°C ($n = 28$) compared to an average ambient temperature of 25.0 ± 5.3°C ($n = 14$). Nest temperatures were similar day (37.3 ± 1.4°C) and night (36.8 ± 1.6°C), 46% and 88% higher than ambient temperatures, respectively (Fig. 1). Average nest temperatures during the chick stage were significantly higher than average nest temperatures during the egg stage ($t_{52} = 7.9$, $P < 0.001$), but their variances were similar ($t_{52} = -0.62$, $P = 0.54$).

Flooding during especially high tides was recorded in nine nests during incubation, and in six during the chick-rearing period (Fig. 3A). With one exception (Fig. 3B), all of these events occurred in the late evening or at night (range: 2 hr 19 min before sunset to 5 hr 33 min after sunset), which was when the highest tides occurred. For nests containing eggs, temperatures dropped an average of 12.6 ± 2.6°C, at a rate of 0.3 ± 0.2°C min^{-1}, to a mean of 21.8 ± 1.5°C. Nests warmed again at an average rate of 0.5 ± 0.2°C min^{-1}. Flooding depressed nest temperatures for 98 ± 41 min, on average.

For nests containing chicks, temperatures dropped 13.7 ± 1.4°C during flooding, cooled at a rate of 0.9 ± 0.4°C min^{-1}, and warmed again at a rate of 0.2 ± 0.1°C min^{-1}. Temperatures during flooding dropped to a low of 24.1 ± 1.7°C and were depressed for an average of 91 ± 42 min. Nests with chicks cooled faster ($t_{12} = 3.6$, $P = 0.003$), warmed more slowly ($t_{12} = -3.2$, $P = 0.008$), and had significantly higher minimum temperatures recorded ($t_{12} = 2.6$, $P = 0.02$) than those with eggs. The change in temperature during flooding and the amount of time temperature remained depressed did not differ between the two groups (both $P > 0.38$).

The flooding events recorded on the iButtons were the likely cause of failure for just 1 of the 14 flooded nests; from this nest, we documented one dead nestling just outside the nest cup when we retrieved the iButton. The remaining three nestlings may have been scavenged following flooding or floated away with the tide, as they were too young (5 days old) to have fledged. In this nest, temperature dropped to a low of 24.5°C but remained depressed for 174 min (67 min longer than the next-longest drop in temperature for a flooded nest with chicks). Two of the nests in which we recorded flooding failed on a subsequent high tide, and another three were later depredated. In one nest, the data-logger captured the immersion of three eggs and one recently hatched nestling during two consecutive high tide events (Fig. 3B). As no eggs or nestlings were found in the vicinity of the nest when we retrieved the iButton, and the nestlings were too young to have fledged, we originally classified this nest as depredated. The timing of the tidal events, however, raises the possibility that flooding may have been the ultimate

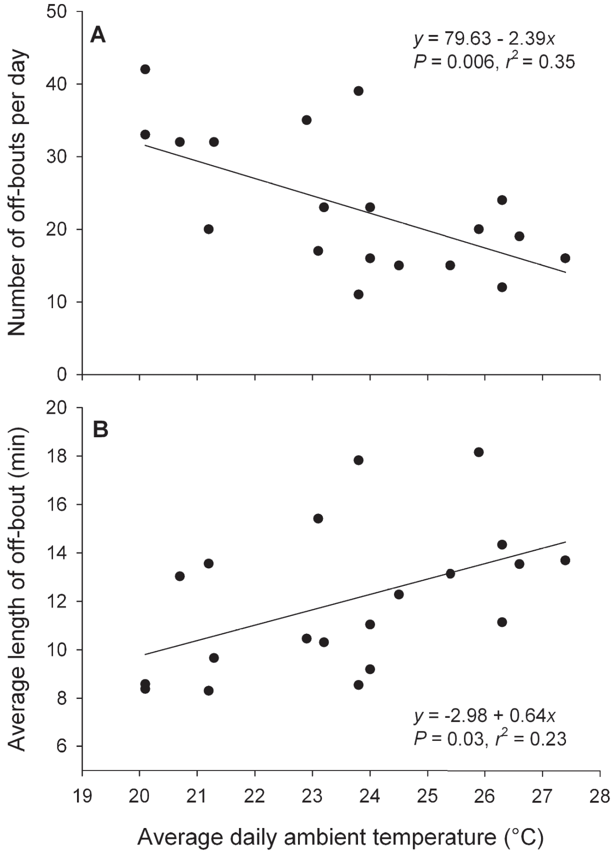

FIGURE 2. During 2003 and 2004, female Saltmarsh Sharp-tailed Sparrows in Connecticut (A) increased the number of off-bouts taken per day at lower ambient temperatures, but (B) decreased off-bout duration accordingly. Off-bout periods were defined as times when there was at least a 2.5°C change in temperature lasting more than 2 min with a minimum of 0.4°C per min rate of cooling or rewarming. Each data point represents one nest.

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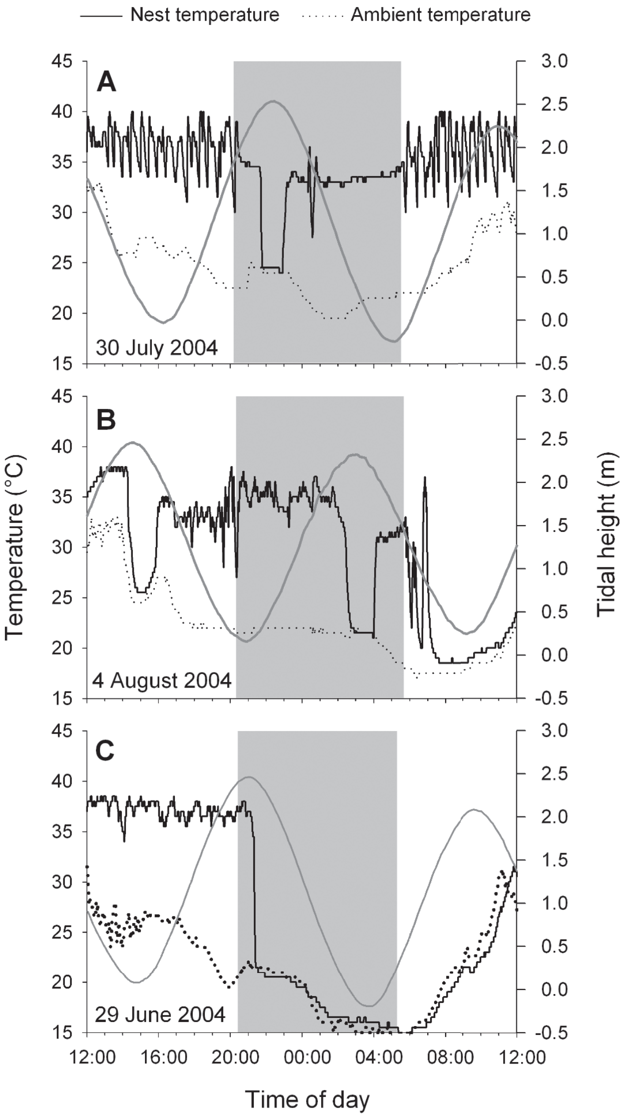

FIGURE 3. Nest and ambient temperatures over a 24 hr period for a nest in which (A) flooding occurred during high tide on the ninth day of incubation, but eggs survived, (B) there was apparent depredation of three eggs and one nestling the day after the nest contents had survived flooding twice, and (C) nestlings presumably fledged 52 min after sunset. Shaded areas indicate the period between sunset and sunrise, and tidal heights are indicated by the oscillating lines. Data were collected in Connecticut during 2003 and 2004.

cause of nest failure. Fledglings were produced from 8 of the 14 nests that flooded, demonstrating that offspring can survive nest inundation.

We retrieved iButtons from six empty nests from which the nestlings were presumed to have fledged because the nestlings were greater than eight days old, the minimum age for fledging (Greenlaw and Rising 1994). Temperature dropped precipitously in all cases (0.9–1.5°C min^{-1}), presumably representing the time when nestlings first departed the nest (Fig. 3C). In all six nests, this steep drop in temperature occurred early in the night, on average 70.0 ± 40.7 min after sunset (range: 37 to 141 min), and coincided with the high tide (Fig. 3C). In four of these six nests, temperatures rose back above the ambient temperature between 1 hr 30 min and 8 hr 35 min after the initial departure, suggesting that the chicks or the female returned to the nest.

DISCUSSION

Flooding during high spring tides is the primary cause of nest failure for Saltmarsh Sharp-tailed Sparrows (DeRagon 1988, Shriver 2002, Gjerdrum et al. 2005, Shriver et al. 2007), but eggs that remain in the nest following flooding often continue to develop and hatch (Humphreys et al. 2007). Since the highest tides often happen at night, the evidence for failure due to flooding generally consists of eggs found outside the nest cup or drowned chicks, rather than actual observation of the nest under water. Our data-loggers detected nest-flooding events when nest contents remained in nest cups, confirming that flooding actually occurred when other evidence was lacking, and gave precise information on the duration and consequences of flooding. In our study, flooded nests were inundated for 90–100 min on average. Eggs that did not float away survived flooding, as female activity continued at all monitored nests after the high tide retreated, and fledglings were produced from eggs that had been inundated. Most nestlings from nests that were confirmed as flooded also survived. It is unclear whether nest cups were completely underwater during flooding, but our data suggest that chicks must be able to tolerate the lower temperatures, and either keep their heads above the water level or climb high enough out of their nests to avoid drowning. One would expect older chicks to be more able to move around in the vegetation and thus be more likely to survive flooding than younger chicks. Fresh eggs, for which incubation has not yet begun, may also be less susceptible to the effects of cooling than older eggs, in which embryo development has started (O'Connor 1984, Tazawa and Whittow 1999).

Depredation also causes nest failure, although it is less prevalent than flooding in this system (Gjerdrum et al. 2005, Greenberg et al. 2006, Humphreys et al. 2007). Generally, failed nests at which there is no physical evidence of flooding are considered to have been depredated (Gjerdrum et al. 2005). Our iButton data, however, showed that one nest classified as depredated was first flooded during two consecutive high tides, and it is possible that flooding contributed to the final depredation event that occurred early the next morning. For instance, nestlings may be more conspicuous when forced out of the nest into the top of the vegetation. Clearly, inferences are limited from this one case, but it illustrates how direct information about nest flooding can provide a more complete picture of the circumstances preceding nest failure, which should improve inferences about nest fates. For example, knowing the precise time of depredation may enable one to distinguish between diurnal visual predators and nocturnal, scent-oriented ones (Weidinger 2006), and would be especially useful in systems where predation is common and for species of high conservation concern.

The data-loggers documented the cessation of nesting activity in eight nests. One nest failed by flooding during the nestling period, one was depredated, and the other six apparently fledged young successfully. The use of data-loggers for the classification of nest fates remains uncommon but is considered more accurate than frequent visits by an observer (Weidinger 2006). When we visited the nests to retrieve the iButtons, our classification of nest fates did not differ substantively from those indicated by the data-loggers. The loggers did, however, record the exact timing of nest

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fates, which is information that is rarely available through conventional nest monitoring. The six apparent fledging events all occurred at night, soon after sunset, on the flooding tide. We cannot rule out the possibility that these nests succumbed to predators, but in each case, the nestlings were old enough to leave the nest. Moreover, we did not see similar losses for younger chicks. In four of the six cases, temperatures rose again during the hours after the initial drop. Possible explanations for this result include the return of some chicks after their initial departures or the return of females.

Our data show that Saltmarsh Sharp-tailed Sparrows maintain a stable thermal environment in their nests during incubation by modifying their attendance behavior in relation to ambient temperature. During cool conditions, female Saltmarsh Sharp-tailed Sparrows left their nests unattended more frequently than during warmer conditions, but each absence tended to last for a shorter time period. In general, North American passerines compensate for shorter off-bouts by taking more of them (Conway and Martin 2000), and birds have been shown to modify incubation behavior in response to weather (Davis et al. 1984, Norment 1995, Rauter and Reyer 1997, Wheelwright and Beagley 2005). The iButtons used in this study also provided data on the thermal environment of nests during chick-rearing, which has received little attention in the literature (Chaplin et al. 2002), and recorded information on rare and unpredictable events. It would be important to learn whether food availability also influences attendance patterns (Conway and Martin 2000). If attendance behavior is linked to food availability, then monitoring nest temperatures across marshes could reveal information about marsh quality, which in turn might help explain why lower densities of sparrows are found in smaller marshes (Benoit and Askins 2002, Shriver et al. 2004).

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