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Threat predictability influences seaside sparrow nest site selection when facing trade-offs from predation and flooding

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Habitat selection trade-offs between avoiding predation and gaining energy are well studied, but similar trade-offs resulting from multiple threats to survival remain poorly understood. We studied how seaside sparrows, *Ammodramus maritimus*, approach nest site selection decisions to avoid threats to nesting success from predation and tidal flooding. Along a nest height gradient, nest site selection to avoid tidal flooding (i.e. placing nests higher) may make seaside sparrow nests more vulnerable to predation, and selection to avoid predation may make nests susceptible to flooding. We monitored nesting success rates and nest site selection decisions of breeding seaside sparrow pairs at five sites near Brunswick, Georgia in April–July of 2013–2015. We found that seaside sparrows encountered a nest site selection trade-off along a gradient of nest height. Nest height had an effect on survival probability during each of our study years, with positive effects of nest height on predation probability and negative effects of nest height on flooding probability observed in some years. Sparrows dealt with this trade-off by altering their nest site selection in relation to a threat's predictability; low within-season variability in predation risk and high information about predator presence in open marshes make predation risk more predictable than the magnitude of tidal flooding, which is governed by unpredictable and variable winds. Sparrows responded to predictable predation threats by nesting at lower nest heights in years with higher predation risk, but sparrows responded to unpredictable flooding threats by placing nests higher off the ground but only following nest failure from flooding. Understanding decision making through a lens of threat predictability could provide a useful approach for studies of other animals' habitat selection trade-offs.

The threat of predation drives many habitat selection trade-offs (Houston, McNamara, & Hutchinson, 1993), particularly during an animal's nesting stage when movement to avoid predators is not possible (Clark & Shutler, 1999; Martin, 1995). Avian responses to predation have evolved to produce life history trade-offs among clutch sizes, number of renesting attempts and nest site selection (Martin, 1995), and these traits are also affected by predation on an ecological timescale (e.g. within a breeding season; Lima, 2009). Many bird species change the location of their nests following predation (Chalfoun & Martin, 2010; Clark & Shutler, 1999; Lima, 2009), which may improve their chances of finding an area with lower predator densities. Birds also shift their nest site placement after predation along habitat gradients to improve nest concealment or avoid predators (Chalfoun & Martin, 2010; Forstmeier & Weiss, 2004; Marzluff, 1988). In addition to making renesting decisions after a nest failure, birds can assess predation risk at the beginning of a breeding season and alter their nest site selection and other behaviours accordingly (Fontaine & Martin, 2006; Kearns & Rodewald, 2012).

Habitat selection to avoid predation often comes at a cost of reduced foraging opportunities (Forstmeier & Weiss, 2004; Werner & Hall, 1988), but less well understood is whether nest site selection to avoid predators might make nests more vulnerable to other threats (as opposed to simply increasing foraging effort for parents). For example, ectothermic animals (such as reptiles, fish and insects) that are unable to incubate their eggs must select nest or oviposition sites that protect nests from both the threat of overheating or underheating and the threat of predation, which can cause a trade-off in habitat selection (Stahlschmidt & Adamo, 2013; Warner & Shine, 2008). However, it is not necessarily the case that the proper thermal habitat overlaps with high predator abundances or low concealment opportunities, and so solutions that

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simultaneously minimize both threats may exist (Kolbe & Janzen, 2002). A similar possible trade-off is faced by marsh-nesting birds that encounter threats from nest predation and from nest flooding (Greenberg et al., 2006). It is unknown whether these threats trade off to prohibit parents from avoiding both predation and flooding, or whether parents can obtain sufficient information about temporally varying threats to optimize this trade-off in ecological time. Can adults assess the relative strength and predictability of multiple, opposing threats and respond by selecting favourable nesting sites?

We addressed this question in seaside sparrows, *Ammodramus maritimus*, a bird species that breeds in coastal areas where many nesting species face dual threats of predation and tidal flooding. Salt marsh breeding birds, such as seaside sparrows, have adapted to tidal flooding by rapid renesting to ensure that nesting cycles fit between high lunar tides that occur approximately every 28 days during the breeding season (Reinert, 2006; Shriver, Vickery, Hodgman, & Gibbs, 2007). The frequency of lunar tide events is predictable, but the magnitude varies widely with wind speed and direction, which makes the minimum nest height for flood avoidance unpredictable. Salt marsh breeding birds avoid tidal flood waters by building nests higher above the ground compared to nests of inland breeding relatives (Greenberg et al., 2006), but this response may put nests at a higher risk of predation because nests closer to the ground often have a lower predation risk, likely due to greater concealment from predators (Martin, 1993; Pietz & Granfors, 2000). Thus, nest site selection solutions to avoid tidal flooding may make seaside sparrow nests more vulnerable to predation, and vice versa.

We studied how seaside sparrows approach this trade-off in coastal Georgia, U.S.A., where tidal amplitudes are the highest along the southeastern Atlantic coast of the United States. Seaside sparrows at our study area near Brunswick, Georgia, are also exposed to a variety of nest predators including raccoons, *Procyon lotor*, mink, *Neovison vison*, rice rats, *Oryzomys palustris*, fish crows, *Corvus ossifragus*, boat-tailed grackles, *Quiscalus major*, red-winged blackbirds, *Agelaius phoeniceus*, and marsh wrens, *Cistothorus palustris* (E. A. Hunter, personal observation). Seaside sparrows renest multiple times, often four or more times, throughout the breeding season following unsuccessful nesting attempts, which is predicted for species exposed to a variety of predators (Filliater, Breitwisch, & Nealen, 1994; Kearns & Rodewald, 2012). We predicted that seaside sparrows would (1) be able to affect their nest success rate through nest site selection and (2) respond to threats of predation and tidal flooding by shifting their nest site selection for renesting attempts along habitat gradients that affect nesting success.

METHODS

Location Description

This study took place in April–July 2013–2015 in five 10–15 ha salt marsh sites near the city of Brunswick, Georgia. Sites were chosen based on observed moderate to high densities of breeding seaside sparrows (~2 pairs/ha), which are typical of occupied seaside sparrow breeding sites elsewhere in the species' range (Lehmicke, 2014; Post & Greenlaw, 2009). Two sites were monitored for 3 years, one site was monitored for 2 years, and two sites were monitored for 1 year. Because no site differences were detected in daily survival or failure rates (indicating a lack of difference in predation or flooding risks among sites), sites were grouped for analysis (see Analysis). All sites were relatively mature high-elevation salt marshes, dominated by smooth cordgrass (*Spartina alterniflora*), with salt marsh pickleweed (*Salicornia virginica*) present at the highest marsh elevations (Fig. 1). Small, well-defined channels (1–3 m wide) with tall *S. alterniflora* grasses (1–2 m tall) intersect higher-elevation marsh with shorter *S. alterniflora* (~0.5 m). Seaside sparrows tended to nest in higher grasses near channels, but a few nests were found in shorter grasses as well (Fig. 1). All nests at our sites were woven out of and placed in *S. alterniflora* grasses.

Nest Searching and Monitoring

We searched for and monitored nests from mid-May to late July in 2013 and for the entire breeding season in 2014–2015 (early April – late July). Searches took approximately 4–5 person-hours per site to search for nests at all known seaside sparrow territories, identified by the activities of singing males. In 2013, we conducted nest searches and nest checks every 2–4 days, but in subsequent years this interval was extended to once per week to reduce trampling and disturbance of sites and nests. Searches were conducted using a combination of systematic searching in known nesting territories and locating nests from behavioural cues of breeding pairs (Martin & Geupel, 1993).

Upon finding a nest, we collected information on nest height above ground (measured from the top of the nest cup, Fig. 1), the number of eggs or nestlings, and parental identity, if banded (see Pair Identification). We also placed an iButton temperature data logger (Thermochron iButton DS1921G, Maxim Integrated Products, San Diego, CA, U.S.A.) in each nest to aid in the determination of the timing and cause of nest fates (Bayard & Elphick, 2011). To determine nest fates (depredated, flooded or fledged), we used a combination of field information and iButton temperature data. Field information for depredated nests included eggshells or eggshell fragments in the nest, mammal tracks near the nest, tilted or pulled apart nests and adult bird faecal matter (single, discrete dropping from a presumed predator) in the nest. Field information for flooded nests included mud inside the nest, and wet and cold eggs. Field information for fledged nests included adult nest-guarding behaviour when no chicks were in the nest, sightings of fledglings, and young bird faecal matter (messy accumulation of droppings throughout the nest deposited by fledglings immediately before nest departure) in the nest. Nest abandonment was documented only four times as determined by the presence of eggs with no initiation of incubation or incubation termination. Nests' fates were corroborated with iButton temperature data, as well as nest fate time and date, by comparing nest temperatures to ambient temperatures collected from iButtons placed in inactive nests (Bayard & Elphick, 2011).

In addition to nest height, we measured other nest habitat variables that could affect nest fate, including stem density around the nest (a measure of nest concealment from predators), total height (nest height plus elevation, which likely affects flooding probability; Fig. 1) and distance to forested areas (which can be predator sources, Picman, Milks, & Leptich, 1993). These data were collected after nests fledged or failed. Stem density was measured by centering a 1 m^2 quadrat on a nest, placing a dowel marked in 20 cm increments in each corner and counting stems touching the dowel within each increment (Lehmicke, 2014). In 2014–2015, we collected elevation data with a real-time kinematic global position system (RTK GPS) with a Trimble R6 RTK Glonass-enabled antenna (Trimble Navigation Limited, Sunnyvale, CA) with corrections through eGPS Virtual Reference System and elevations derived using Geoid12a. We did not collect RTK GPS elevations in 2013, but instead used elevation data from a Digital Elevation Model (DEM, 1.2 m cell size) derived from Light Detection and Ranging (LiDAR) data collected in 2008–2010 for Glynn and Camden counties. We corrected nest elevations from LiDAR data using vegetation species and height at each nest as outlined in Hladik and Alber (2012), thus