

Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a “win-stay, lose-switch” strategy?

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Abstract Facultative shifts in nesting habitat selection in response to perceived predation risk may allow animals to increase the survival probability of sessile offspring. Previous studies on this behavioral strategy have primarily focused on single attributes, such as the distance moved or changes in nesting substrate. However, nest site choice often encompasses multiple habitat elements at both the nest site and nest patch scales. We studied the within-season re-nesting strategy of a multi-brooded songbird, the Brewer's sparrow (*Spizella breweri*), to determine whether pairs utilized a “win-stay, lose-switch” decision rule with respect to inter-nest distance, nest substrate and/or nest patch characteristics in response to previous nest fate. Pairs moved sequential nest sites slightly farther following nest predation versus success. When inter-nest distance was controlled, however, pairs changed nest patch attributes (shrub height, potential nest shrub density) associated with probability of nest predation to a greater extent following nest predation than success. The strategy appeared to be adaptive; daily nest survival probability for previously depredated pairs increased with greater Euclidian habitat distances between attempts, whereas previously successful pairs were more likely to fledge second attempts when nest sites were similar to those of previous attempts. Our results

suggest that nesting birds can use prior information and within-season plasticity in response to nest predation to increase re-nesting success, which may be a critical behavioral strategy within complex nest predator environments. Re-nesting site selection strategies also appeared to integrate multiple habitat components and inter-nest distances. The consideration of such proximate, facultative responses to predation risk may clarify often unexplained variation in habitat preferences and requirements.

Keywords Behavioral plasticity · Brewer's sparrow · Habitat selection · Prior information · Re-nesting

Introduction

The habitats selected by individual organisms can influence fitness and scale up to affect population and community dynamics (Martin 1992; Morris 2003; Schmidt 2004). Although ecologists have long realized that the process of habitat selection has both innate and learned components (Klopfer 1963; Hildén 1965), an understanding of the role of behavioral plasticity and decision rules in proximately shaping habitat selection patterns is currently limited (Greig-Smith 1982; Martin and Martin 2001; Schmidt 2004; Fontaine and Martin 2006) and may hamper our ability to understand overall habitat selection strategies (Forstmeier and Weiss 2004).

Breeding birds comprise a particularly interesting focal group for investigations of habitat selection. The habitat characteristics of nest sites chosen by parents can influence the probability that eggs or nestlings are discovered by predators or parasites (Martin 1993; Chalfoun and Martin 2009), and nest predation is the major cause of reproductive failure (Ricklefs 1969; Martin 1992). Nest predation should

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therefore exert strong selection on the choice of safer nesting habitats (Martin 1992, 1998; Clark and Shutler 1999; Arlt and Pärt 2007). Yet, nest site selection studies sometimes reveal a discordance between apparent nest site preferences and nest success (Holway 1991; Filliater et al. 1994; Howlett and Stutchbury 1997; Hoover and Brittingham 1998; Wilson and Cooper 1998; Luck 2002; Arlt and Pärt 2007). In some cases, birds may choose an inappropriate habitat (e.g., ecological traps—Robertson and Hutto 2006). In other cases, habitat choices may be adaptive, but simply difficult to recognize because of variability in predation relationships. Predation is impossible to completely escape in most systems, yet it varies in its predictability. Adaptive habitat selection strategies may therefore necessitate proximate shifts in habitat choices in response to prior experience with nest predation (Marzluff 1988; Jackson et al. 1989 and references therein; Martin and Martin 2001; Eggers et al. 2006; Fontaine and Martin 2006; Peluc et al. 2008), which is essentially a proximate form of the Red Queen hypothesis (i.e., Van Valen 1973). In particular, individuals may alter the location and/or characteristics of subsequent breeding sites following nest predation; this is especially the case for species with diverse predator assemblages that are difficult to assess (Pöysä et al. 2001; Forstmeier and Weiss 2004). In contrast, individuals should retain breeding site characteristics associated with previous success. Such a strategy (“win-stay, lose-switch”; Nowak and Sigmund 1993; Switzer 1993; Schmidt 2001) may be adaptive, but it is poorly studied with respect to nest site selection. Moreover, such shifting choices could make a clear delineation of habitat preferences difficult and obscure the adaptiveness of choices.

A “win-stay, lose-switch” strategy for mitigating predation risk could manifest in several different ways. First, parents could simply move some distance away following previous failure without necessarily changing habitat characteristics. In numerous studies, several bird species have been found to move their nest sites greater distances between years following nest predation or high perceived risk (Pinkowski 1977; Greenwood and Harvey 1982; Greig-Smith 1982; Dow and Fredga 1983; Sonerud 1985; Hakkarainen et al. 2001; Schroeder and Robb 2003; but see Morton 1997 and Pitman et al. 2006). Less well-known, however, is the extent to which individuals move nest sites within seasons (Howlett and Stutchbury 1997; Lima 2009), and distances may be more constrained within seasons, especially in territorial species. Alternatively, birds could change the habitat characteristics of subsequent nest sites without significant shifts in location. Plastic shifts in nest site attributes within the same territory have been documented in response to corvid nest predation pressure (Marzluff 1988; Eggers et al. 2006; Peluc et al. 2008). A final alternative is that parents could simultaneously shift

both the location and habitat attributes of subsequent nest sites. The latter alternative, however, requires that both variables are simultaneously tested within the same system in order to verify that habitat changes occur independently of location shifts (e.g., Howlett and Stutchbury 1997).

Examinations of nest site shifts have typically focused on one main habitat metric at the immediate nest site, such as nest substrate (Greig-Smith 1982), artificial nest substrates, such as nest boxes (Pinkowski 1977; Dow and Fredga 1983; Hakkarainen et al. 2001), nest cover (Marzluff 1988), nest height (Peluc et al. 2008), or habitat characteristics within 1 m of the nest (e.g., Howlett and Stutchbury 1997) (but see Eggers et al. 2006). Habitat characteristics influencing the probability of nest predation, however, may often operate at spatial scales beyond the nest substrate (Martin 1992, 1993, 1998; Tarvin and Garvin 2002; Chalfoun and Martin 2007). Such effects may require that individuals integrate habitat characteristics at both the nest site and nest patch scales within their habitat selection strategy. The ability of parents to incorporate multiple features in their habitat selection tactics at spatial scales larger than the immediate nest substrate in response to predation, however, remains largely unstudied.

We examined the nest site selection strategy of a songbird breeding within a spatially and temporally variable nest predation environment in order to assess behavioral plasticity in response to nest predation. Specifically, we asked whether pairs moved and/or changed habitat characteristics of the nest site and surrounding nest patch to a greater extent following nest predation compared to success (“win-stay, lose-switch” hypothesis). We tested this hypothesis against the alternative hypothesis (“stay-stay” hypothesis) that individuals tend to remain relatively fixed in their nest site selection strategies regardless of the previous fate of that nest. We focused on changes in habitat features previously identified as being influential in nest predation risk in this system (Chalfoun and Martin 2007, 2009). Finally, we evaluated the adaptive significance of the “win-stay, lose-switch” strategy for improving the probability of re-nest survival.

Materials and methods

Our focal species was the Brewer’s sparrow (*Spizella breweri*), a multi-brooded, open-cup shrub-nesting passerine inhabiting North American sagebrush steppe habitats. Sagebrush habitats are typically host to a diversity of potential nest predator species, including mammals, birds, and reptiles (Vander Haegen et al. 2002; Chalfoun and Martin 2007) that utilize diverse foraging strategies (visual, olfactory, heat-sensing). Simultaneously, nest predation rates within this system are extremely variable both across

locations and years (Rotenberry and Wiens 1989; Mahony et al. 2006; Chalfoun and Martin 2007). We hypothesized that such diversity and unpredictability in nest predation risk should favor the evolution of behavioral plasticity in nest site selection.

Our study took place during May–August, 2002–2005 at eight 25- to 30-ha sites separated by ≥ 1 km in Carbon County, south-central Montana, USA. Habitat structure (shrub cover, height, density) varied both within and among study sites (Chalfoun and Martin 2007). Sites were dominated by big sagebrush (*Artemisia tridentata*), with scattered greasewood (*Sarcobatus vermiculatus*) and rabbitbrush (*Chrysothamnus* spp.). Confirmed nest predators (via video evidence or fecal material in depredated nests) included the bullsnake (*Pituophis melanoleucus*), prairie rattlesnake (*Crotalis viridis*), least chipmunk (*Tamias minimus*), *Peromyscus* spp. mice, and loggerhead shrike (*Lanius ludovicianus*). Other potential nest predators observed included the black-billed magpie (*Pica hudsonia*), pinyon jay (*Gymnorhinus cyanocephalus*), common grackle (*Quiscalus quiscula*), brown-headed cowbird (*Molothrus ater*), voles (*Microtus* spp.), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), and raccoon (*Procyon lotor*).

Nests were located via behavioral observations of parents and systematic nest searches of known territories, which are relatively small (0.5–1.0 ha; Wiens et al. 1986; Chalfoun and Martin 2007). A sub-set of Brewer's sparrow pairs ($n = 5$ –10) at each site during each year were target-netted with mist-nets at their first nests of the season, fitted with unique combinations of colored leg bands, and monitored throughout all subsequent nest attempts. Females were flushed off nests during incubation or captured when attempting to return to the nest. Males were captured via song playbacks, flushing off during incubation, or when attempting to return. Brewer's sparrows are socially monogamous during individual nest attempts but occasionally divorce between nest attempts (A. Chalfoun, unpublished data). Moreover, some pairs abandoned their territories and our sites following early nest failure, so we only incorporated data for known females that we were able to monitor during at least two sequential nest attempts. Nests were monitored every 2–3 days and considered successful if they fledged at least one young, or depredated if contents disappeared earlier than 2 days prior to average fledge dates (Martin and Geupel 1993; Weidinger 2008). Observations at and near the nest (e.g., fecal material on nest rims, parents feeding fledglings nearby) were made following suspected fledging to rule out predation late in the nestling period (Manolis et al. 2000).

We focused on habitat attributes that we had previously identified as being significantly related (either positively or negatively) to the probability of nest predation. In particular, observational and experimental analyses demonstrated

that nest predation at our sites was negatively related to the density of potential nest shrubs in nest patches (Chalfoun and Martin 2007, 2009). Moreover, nest predation was positively related to nest patch height (Independent samples $t = 3.84$, $P < 0.001$, $n = 326$ nests). We therefore focused on these two habitat variables in our analyses of plasticity. Shrub height and potential nest shrub density were measured after nest completion within a 5-m radius (78.5 m²) around each nest during June 20–July 31 of each year (Chalfoun and Martin 2007, 2009). Nest concealment surrounding the immediate nest site was also initially included for comparison because it is a commonly measured attribute in the avian nest literature (see review in Martin 1992), although it showed no significant relationship with nest predation risk in our system ($t = 1.21$, $P = 0.23$, $n = 326$). Nest concealment was assessed by averaging ocular estimates from the four cardinal directions at nest height and overhead from a distance of 1 m from the nest shrub (Martin et al. 1997). Inter-nest dispersal distances were calculated using a measuring tape (if distances were ≤ 20 m) or via GPS UTM coordinates.

Re-nesting attempts were classified as either post-predation or post-success. We calculated the percentage change in each habitat attribute for each pair of nests (initial and re-nest of known females) using the following equation: $|(\text{re-nest} - \text{previous attempt})/\text{previous}| \times 100$. In addition, we calculated the composite change in nest patch habitat between attempts using Euclidian distances in ecological space (e.g., Landmann and Winding 1993), with nest patch height and potential nest shrub density as the two axes. Specifically, distances were calculated by the expression $E = [(X_2 - X_1)^2 + (Y_2 - Y_1)^2]^{1/2}$, where X_2 and Y_2 represent the value of shrub patch height and potential nest shrub density, respectively, for the sequential re-nest of a pair, and X_1 and Y_1 are values for first attempts. Inter-nest dispersal distances were compared between previously successful versus depredated attempts using a one-tailed t test. The percentage change in nest site attributes between nest attempts for pairs that failed versus fledged during their previous attempts was assessed using analyses of covariance (ANCOVAs) with nest type (previously failed versus fledged) as a fixed factor, year and site as random factors, and inter-nest distance and Julian date of nest initiation (date first egg laid) as covariates.

In order to assess whether nest site shifts were adaptive, we used the logistic exposure method (Shaffer 2004) to evaluate daily nest survival probability in relation to the extent that pairs changed nest site attributes following previous failure versus success, using Euclidian distances in ecological space as a continuous explanatory variable. We used Akaike's information criterion adjusted for small sample size (AIC_c ; Burnham and Anderson 2002) to rank four candidate logistic exposure models: (1) a constant survival model,

(2) an inter-nest distance model, (3) a Euclidian distance model, and (4) a model containing both changes in inter-nest distance and Euclidian distance as explanatory variables.

Finally, at the population level, proximately altering nest site selection strategies following nest predation should lead to the diversification of individual nest site choice. To test for this pattern, we used niche-width analysis (Roughgarden 1972; Bolnik et al. 2002) for continuous variables (within-individual component/total niche-width ratios, hereafter WIC/TNW). We specifically tested whether within-individual variation in nest site selection increased compared to overall habitat niche widths for females whose initial nests were depredated versus successful. The degree of within-individual diversity in use was calculated as $WIC = \text{Var}(x_{ji})$, with $TNW = \text{Var}(x_{ij})$, where X is a matrix of habitat attribute data with elements x_{ij} (shrub height and potential nest shrub density) representing the value of the j th nest for individual i (Bolnik et al. 2002).

Results

We located and monitored a total of 105 Brewer's sparrow re-nests ($n = 48$ post-predation re-nests and 57 post-success re-nests). Year was not significant in any of our models (all P values >0.10). Within-season inter-nest dispersal distances tended to be longer for post-predation than post-success attempts (one-tailed $t = 1.47$, $P = 0.08$; Fig. 1). Changes in nest concealment did not differ among attempt types (ANCOVA; $F_{1,104} = 0.03$, $P = 0.87$; Fig. 2) at any of our sites (site: $F_{1,7} = 1.08$, $P = 0.48$), and concealment was eliminated from further analysis. Shrub height consistently (site: $F_{1,7} = 1.14$, $P = 0.43$; Julian date: $F_{1,104} = 1.83$, $P = 0.18$) changed to a much greater extent following nest

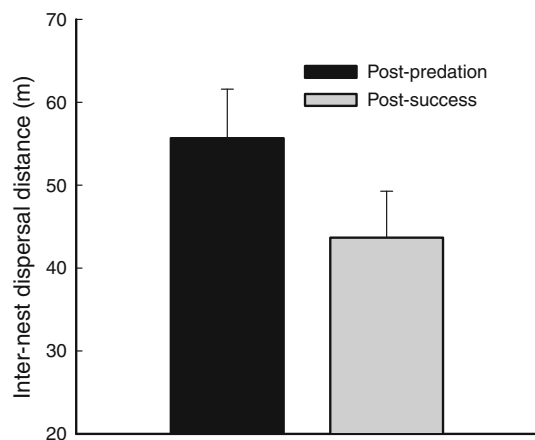


Fig. 1 Brewer's sparrow (*Spizella breweri*) within-season inter-nest dispersal distance [mean ± 1 standard error (SE)] was slightly greater following nest predation than nest success ($n = 105$ nests; sites and years pooled)

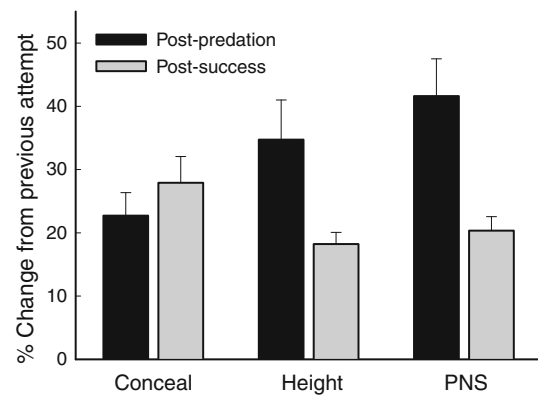


Fig. 2 Percentage change in Brewer's sparrow nest patch (5-m radius) attributes (percentage nest concealment, shrub height, and potential nest shrub density) for pairs whose nests were previously depredated versus those whose nests were successful. Bars mean ± 1 SE with sites and years pooled. PNS Potential nest shrubs

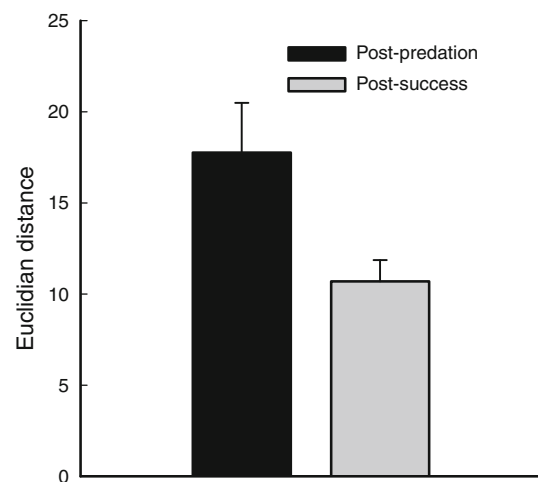


Fig. 3 Euclidian distances (mean ± 1 SE; see text for calculation) between nest patch structure (shrub height and potential nest shrub density) for sequential within-season Brewer's sparrow re-nests compared to previous attempts, following nest predation versus success

predation than following success ($F_{1,104} = 6.86$, $P = 0.01$; Fig. 2), even with inter-nest distance in the model (distance: $F_{1,104} = 0.19$, $P = 0.67$). Similarly, changes in the density of potential nest shrubs in nest patches were greater following predation than following success ($F_{1,104} = 8.56$, $P = 0.004$; Fig. 2) irrespective of the time of season (Julian date: $F_{1,104} = 1.29$, $P = 0.26$) or inter-nest distance ($F_{1,104} = 2.53$, $P = 0.12$), although responses varied to a small degree across sites ($F_{1,7} = 4.91$, $P = 0.02$). Euclidian distances of habitat change [change in nest patch height and potential nest shrubs (PNS)] were greater for post-predation than post-success nest attempts ($F_{1,104} = 6.09$, $P = 0.02$; Fig. 3) regardless of site ($F_{1,7} = 0.65$, $P = 0.71$), Julian date ($F_{1,104} = 0.15$, $P = 0.70$), or inter-nest distance ($F_{1,104} = 0.03$, $P = 0.87$).

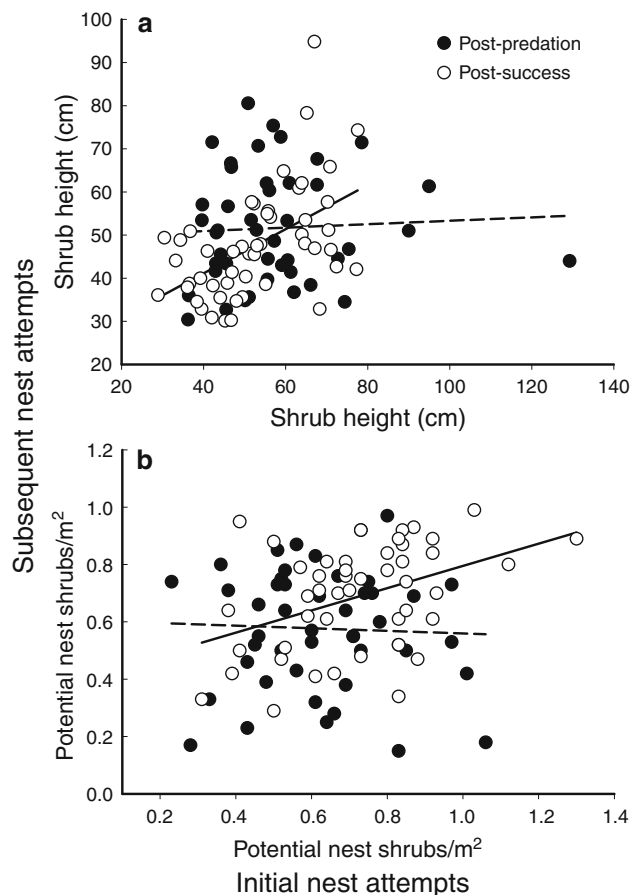


Fig. 4 Brewer's sparrow nest patch attributes (**a** shrub height, **b** potential nest shrub density) were correlated with previous attempts following nest success (*solid lines*), but not predation (*dashed lines*)

Shrub height surrounding re-nesting sites chosen by individual pairs was correlated with shrub height of previous attempts following nest success (Pearson $r = 0.52$, $P < 0.001$, $n = 57$) but not when the previous attempt was depredated ($r = -0.009$, $P = 0.95$, $n = 48$; Fig. 4). Similarly, the PNS density of re-nesting sites was correlated with previous attempts following success ($r = 0.29$, $P = 0.03$, $n = 57$), but not predation ($r = -0.04$, $P = 0.78$, $n = 48$; Fig. 4). The directionality of the habitat shifts was inconsistent; pairs with previously failed nests increased nest patch height on 20/48 occasions, compared to 19/57 attempts following nest success. PNS density was increased for 20/48 re-nests following predation versus 28/57 following success.

Daily nest survival probabilities of previously failed pairs were positively related [$\beta_0 = 0.044$, 95% confidence interval (CI) 0.019–0.086, $n = 264$ nest check intervals, total observation days: 570] to the Euclidian habitat distances between sequential attempts (Table 1, Fig. 5). Moreover, pairs with previously fledged nests had higher re-nest success ($\beta_0 = -0.046$, 95% CI -0.0080 to -0.013 , $n = 337$ nest check intervals, total observation days: 674) when

Table 1 Effects of within-season inter-nest distance (D) and changes in nest patch structure on daily nest survival probability for sequential re-nests of the Brewer's sparrow following nest predation (top) versus success (bottom)

Model	K	ΔAIC_c	w_i
Post-predation attempts			
S_D	2	5.578	0.031
S_{Constant}	1	3.622	0.071
S_{D+E}	3	1.709	0.271
S_E	2	0.000	0.627
Post-success attempts			
S_D	2	5.996	0.052
S_{Constant}	1	4.364	0.133
S_{D+E}	3	1.678	0.227
S_E	2	0.000	0.587

Nest patch changes were documented via Euclidian distances (E) in ecological space with shrub height and potential nest shrub density (within a 5-m radius of nests) as the two axes. Number of model parameters (K), information criterion (ΔAIC_c), and Akaike weights (w_i) are presented for four logistic-exposure models. The "Constant" is a constant-survival model

patches were more similar to their previous nest sites (Table 1, Fig. 5). Inter-nest distance did not significantly influence re-nest survival for previously failed ($\beta_0 = -0.002$, 95% CI -0.013 to 0.009) or successful ($\beta_0 = -0.002$, 95% CI -0.011 to 0.007) pairs (Table 1).

Within-individual component/total niche-width (WIC/TNW) ratios demonstrated that individuals increased their niche breadth relative to total niche width for both nest patch height and potential nest shrub density following nest predation compared to success (Fig. 6).

Discussion

The process of habitat selection in animals has both genetic and learned components that comprise an overall strategy tailored to predominant selection pressures, such as predation risk (Hildén 1965; Jaenike and Holt 1991; Martin 1993, 1998; Chalfoun and Martin 2007). Our results corroborate those of previous work demonstrating that behavioral plasticity and proximate facultative responses can add complexity and variability to baseline habitat selection patterns (Forstmeier and Weiss 2004; Lima 2009). Understanding how individuals respond plastically within a season to ambient selection pressures can therefore explain additional variation in habitat choices within a landscape (Martin and Martin 2001; Forstmeier and Weiss 2004; Fontaine and Martin 2006).

Greater inter-nest distances following predation is a commonly reported response for a wide variety of bird

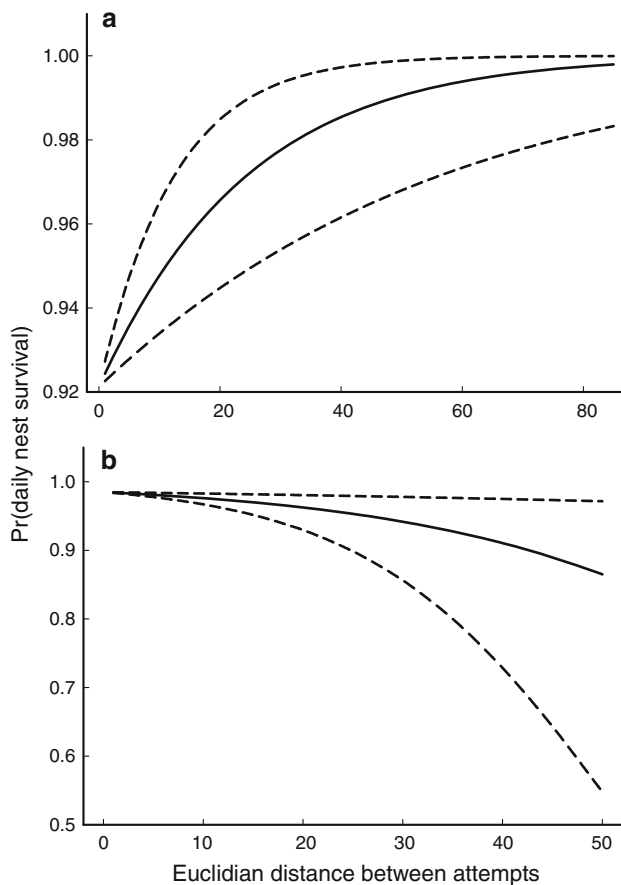


Fig. 5 Probability of Brewer's sparrow daily nest survival as a function of Euclidian distances incorporating changes in nest patch height and potential nest shrub density for pairs that were depredated (**a**) versus successful (**b**) in previous (sequential) attempts within a season. Dashed lines 95% confidence intervals around the predicted (back-transformed) values of daily nest survival based in the intercepts and slopes calculated via the logistic exposure method

species (e.g., Jackson et al. 1989; Martin 1992, and references therein). Brewer's sparrows, however, also significantly altered the physical characteristics of their nest patches independently of inter-nest dispersal distances. Our study is one of the first to present evidence for facultative shifts in habitat characteristics at the scale of the nest patch (also see Eggers et al. 2006). Still, our analyses suggest that pairs altered both nest patch attributes and inter-nest distance following nest predation much more than after a successful nest. We therefore reject the “stay-stay” hypothesis and suggest support for a “win-stay, lose-switch” nest-site selection strategy. The habitat characteristics that were altered following nest predation included metrics (shrub height and PNS density) that were related to the probability of nest predation within the system on average (Chalfoun and Martin 2007, 2009). Moreover, Euclidian distances of nest patch shifts that incorporated both average shrub height and PNS density suggested that individuals integrate

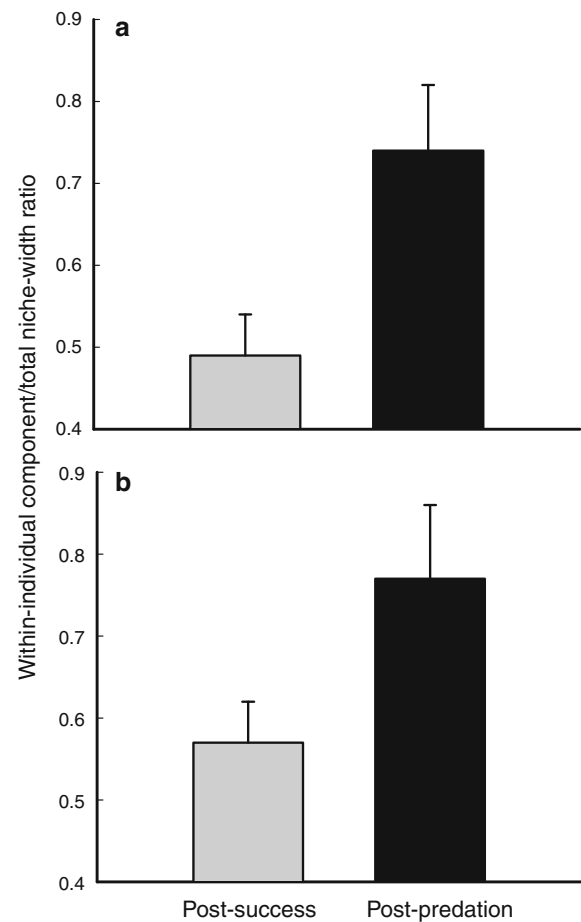


Fig. 6 Within-individual component/total-niche-width ratios (WIC/TNW; **a** nest patch height, **b** potential nest shrub density) for Brewer's sparrow re-nests following successful versus depredated previous nest attempts. Bars ratio means for eight sites $\pm$ 1 SE with years pooled

the two metrics when making nest site choices. Pairs varied in the extent to which they altered one habitat metric more than the other, but aggregate differences via Euclidian distances in ecological space simultaneously accounted for overall changes best.

Differences in the extent of habitat changes following nest predation versus success appeared to be adaptive. Larger changes following predation (“lose-switch” portion of the strategy) in the habitat niche reflected by Euclidian distance yielded higher probabilities of success, whereas minimal change was more successful following successful nests (“win-stay” portion of the strategy; Fig. 5). The directionality of the changes in nest patch habitat structure following predation was not consistent. The important aspect therefore appears to be changing habitat characteristics from what was attempted previously. A simple unidirectional nesting habitat switch may allow nest predators to learn and therefore compromise the effectiveness of the strategy, such that increased unpredictable changes following predation may be favored. We therefore hypothesize

that within-season switches in preferred habitats may act to limit the risk of predation to sessile prey via a couple of potential mechanisms. First, maintaining variation in prey sites would limit the ability of predators to develop specific search images, within the constraints imposed by overlap in nest sites with coexisting species (Sonerud 1985; Martin 1993, 1996). Second, for species within temporally and spatially variable predation environments (owing, for example, to a wide diversity of potential predators and/or fluctuations in predator abundance), optimal nest site characteristics may fluctuate rather than remain fixed. Indeed, nest predation risk can be much more unpredictable than other limiting factors, such as abiotic conditions and food availability (Marzluff 1988; Pöysä et al. 2001). Utilizing prior information (Schmidt et al. 2010) and a “win-stay, lose-switch” strategy within a season may therefore be an integral part of maximizing nest success. Further refinements on this theme may come from tests of Bayesian updating (Schmidt and Whelan 2010) if individuals can incorporate and respond to informational feedback accrued from all previous habitat (e.g., nest site) selection bouts.

On average, Brewer’s sparrows preferred—and were generally more successful when they selected—nest patches containing greater densities of potential nest shrubs (“potential-prey-site” hypothesis; Martin 1993) (Chalfoun and Martin 2009). Yet, a considerable amount of variation in the structure of nest patches remained (Chalfoun and Martin 2007). Nest patches chosen following nest predation could include either increased or decreased PNS density and, thereby, have caused increased niche breadth (Fig. 6). Such increased niche breadth caused by within-season nesting habitat switching, especially in high nest predation environments, may therefore account for some of the discordance that has been observed in many nest site selection studies between apparent nest site preferences and nest success.

In conclusion, our results suggest facultative, adaptive, within-season habitat switches in response to experience with offspring predation consistent with a “win-stay, lose-switch” strategy for a nesting bird. The extent to which individual parents may vary in their ability to utilize the strategy or to complement the strategy with other parental care behaviors, such as nest defense, remains unclear. We emphasize that improving our understanding of proximate behavioral strategies in habitat selection will lead to a more holistic view of overall habitat selection strategies. From a conservation and management perspective, our results suggest a focus on maintaining a range of possible nesting microhabitats in addition to providing critical features, such as high densities of potential nest sites. An accurate understanding of habitat relationships is critical for both advancing habitat selection theory and identifying important habitat features for conservation and management.

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