

Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses

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Summary

1. Predation is an important and ubiquitous selective force that can shape habitat preferences of prey species, but tests of alternative mechanistic hypotheses of habitat influences on predation risk are lacking.
2. We studied predation risk at nest sites of a passerine bird and tested two hypotheses based on theories of predator foraging behaviour. The total-foliage hypothesis predicts that predation will decline in areas of greater overall vegetation density by impeding cues for detection by predators. The potential-prey-site hypothesis predicts that predation decreases where predators must search more unoccupied potential nest sites.
3. Both observational data and results from a habitat manipulation provided clear support for the potential-prey-site hypothesis and rejection of the total-foliage hypothesis. Birds chose nest patches containing both greater total foliage and potential nest site density (which were correlated in their abundance) than at random sites, yet only potential nest site density significantly influenced nest predation risk.
4. Our results therefore provided a clear and rare example of adaptive nest site selection that would have been missed had structural complexity or total vegetation density been considered alone.
5. Our results also demonstrated that interactions between predator foraging success and habitat structure can be more complex than simple impedance or occlusion by vegetation.

Key-words: Brewer's sparrow, habitat selection, nest site, potential-prey-site hypothesis, total-foliage hypothesis

Introduction

Predation can exert strong selection on prey in natural environments (Sih *et al.* 1985). Predation risk potentially can be affected by attributes of the habitat occupied by prey (Crowder & Cooper 1982; Clark & Shutler 1999; Warfe & Barmuta 2004), and thereby influence habitat choice of prey (e.g. Martin 1988, 1993, 1998; Thompson 1988; Lima & Dill 1990; Kolbe & Janzen 2002; Rieger, Binckley & Resetarits 2004). Habitat structure and composition become especially important for the survival of prey that are sessile during one or more life stages (Martin 1988, 1992; Thompson 1988; Thompson & Pellmyr 1991; Mayhew 1997; Clark & Shutler 1999; Poore & Steinberg 1999). The choice of oviposition or nest site, for example, can determine the probability that

enemies such as predators or parasites will discover young (Martin & Roper 1988; Thompson & Pellmyr 1991; Martin 1998; Clark & Shutler 1999; Kolbe & Janzen 2002). Such risks should impose strong selection for the evolution and maintenance of preferences for safer reproductive habitats. Understanding the factors influencing risk of reproductive site discovery by predators is therefore critical to understanding the evolution of habitat preferences and the resulting structure of ecological communities.

Clarifying which habitat features are likely to influence predation risk and habitat choices of prey requires consideration of how predators may interact with habitat structure (Crowder & Cooper 1982; Whelan 2001; Weatherhead & Blouin-Demers 2004). Yet, tests of alternative hypotheses of how habitat may influence predator foraging success are rare. A typical assumption is that structural habitat complexity acts as a physical impedance to predator search efforts (e.g. Crowder & Cooper 1982; Sugden & Beyersbergen 1986; DeLong, Crawford & DeLong 1995). In accordance with optimal foraging theory, such impedance is thought to lower foraging efficiency and

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cause shifts in resource utilization strategies. Thus, the total-foilage hypothesis suggests that increased vegetation density or structural heterogeneity in a habitat patch may hamper predator search efforts and/or inhibit the auditory, olfactory, or visual cues emitted by prey (Martin & Roper 1988; Martin 1993). Predation on bird nests (a sedentary prey) commonly is reduced at nests with greater concealment by foliage (reviewed in Martin 1992), which may indicate support for the total foliage hypothesis.

Yet, interactions of predators with their environment may be more complex than simple physical impedance. With similar underlying assumptions as the marginal value theorem (Charnov 1976), an alternative hypothesis suggests that the foraging efficiency of predators using search images to find sedentary prey may be hampered by the number of unoccupied prey sites in an area. The probability of discovery of sedentary prey is predicted to decrease with increasing numbers of unoccupied potential sites that must be searched (potential-prey-site hypothesis; Martin & Roper 1988; Martin 1993). These alternative hypotheses, however, remain largely untested despite their potential utility in developing a better understanding of habitat influences on predator search efficiency and therefore habitat preferences by sedentary prey. The few correlative tests have yielded mixed results (see Martin & Roper 1988; Martin 1998; Liebezeit & George 2002; Mezquida & Marone 2002), and experimental tests are lacking entirely.

In this study, we collected observational data on reproductive site choice and reproductive success across multiple study sites and years, and conducted the first experimental test designed to differentiate between the total-foilage and potential-prey-site hypotheses. Specifically, we focused on predation risk in relation to microhabitat structure for nests of a passerine bird.

Materials and methods

Our focal species was the Brewer's sparrow (*Spizella breweri*), a common inhabitant of North American sagebrush steppe. Brewer's sparrows are locally abundant during the breeding season, select nest sites across a gradient of microhabitat structure, and nest in shrubs, which constitute discrete and quantifiable nest sites. Moreover, nest predation is the primary cause of reproductive failure in this system (Rotenberry & Wiens 1989, Chalfoun & Martin 2007).

Data were collected during May–August 2003–05 on public and private lands within southern Carbon County, Montana, USA. Eight 25–30-ha study sites, each separated by 1–15 km, were chosen that represented the full range of structural habitat variation typical of sagebrush systems. Sites were dominated by big sagebrush (*Artemisia tridentata*), with scattered greasewood (*Sarcobatus vermiculatus*) and rabbitbrush (*Chrysothamnus* spp.). Confirmed nest predators (via video evidence, observed predation events, or faecal material in depredated nests) in the study area 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*), coyote (*Canis latrans*) and raccoon (*Procyon lotor*).

OBSERVATIONAL DATA

Nests were primarily located via intensive systematic searches within known Brewer's sparrow territories. Brewer's sparrow males possess a unique song type (i.e. the 'long song') which is indicative of being paired with a female and possessing an active nest (A.D.C., personal observation). Identifying areas with long-singing male territories therefore provided a mechanism by which to focus nest-searching efforts regardless of habitat type and restrict potential bias in the types of nests found (e.g. more or less concealed). Nests were monitored every 2–3 days (Martin & Geupel 1993) and considered successful if they fledged at least one young, or depredated if nestlings disappeared earlier than 2 days before average fledge dates. Careful behavioural observations (e.g. faecal material on nest rims, parents feeding fledgling nearby, unhatched eggs still in nest) were made following suspected fledging to rule out depredation late in the nestling period (Manolis, Andersen & Cuthbert 2000). Rare instances of nest failures ($n = 24$) due to weather or abandonment were not included in analyses.

During June 20–July 31 of each year, we measured within a 5-m radius patch surrounding each nest: (i) the total number of shrubs greater than 20 cm in height as an indicator of the total amount of foliage (shrubs smaller than this do not contribute significantly to patch structure), and (ii) the total number of shrubs in the patch with the proper attributes to potentially accommodate a Brewer's sparrow nest (i.e. potential prey sites) (Chalfoun & Martin 2007). The designation of a potential nest shrub was based on 2 years of prior study in which 334 shrubs used as nest sites were observed and their attributes (e.g. height, crown dimensions, percent live crown) measured. Specific quantitative and qualitative criteria used for designating potential nest shrubs, as summarized in Table 1, included approximately 99% of prior nests. Note that because of the qualitative stipulations, potential nest shrubs were not, on average, necessarily larger than other shrubs within a patch. Illustrative photographs demonstrating examples of the qualitative criteria used to delineate potential nest shrubs can be viewed in Fig. S1, Supporting information.

We estimated the density of total foliage and potential nest shrubs within 5-m radius sampling plots located systematically throughout all eight study sites (approximately one sampling plot per hectare per site). Systematic sample plots were chosen a priori using site maps before sparrow arrivals each year, and used to determine the distribution of total foliage and potential nest shrub densities available to nesting birds.

Table 1. Criteria (quantitative measurement ranges and additional qualitative metrics) used in the determination of potential nest shrubs during the study. Means (± 1 SE) are also given for quantitative metrics taken from 334 nest shrubs versus a systematic sample of nests ($n = 210$) during 2 years of prior study

| Quantitative | Qualitative |
|--|---|
| Shrub height: 20–175 cm (69.90 \pm 3.0 vs. 49.41 \pm 2.11) | |
| Maximum width of shrub crown: 30–250 cm (87.48 \pm 1.9 vs. 68.48 \pm 2.15) | Presence of ≥ 1 semi-concealed 'niche' within branch structure to accommodate a nest |
| Minimum percentage of live crown: 50 (82.12 \pm 0.86 vs. 66.26 \pm 1.31) | Crown not so dense as to preclude entry by a parent bird and/or nest structure |

Total foliage and potential nest shrub density were compared between nest versus systematic patches to document nest patch preferences using logistic regression, with year and study site included as random factors (Chalfoun & Martin 2007). We used the logistic exposure method (Shaffer 2004) to evaluate nest survival in relation to microhabitat choice, with total foliage and potential nest shrub density as continuous explanatory variables and year and study site as categorical variables. We used Akaike's information criterion adjusted for sample size (AIC_c ; Burnham & Anderson 2002) to subsequently rank four candidate models: (i) constant survival, (ii) year and site, (iii) year, site and total foliage, and (iv) year, site and potential nest shrub density. Year and site were retained in the total foliage and potential nest shrub density models because they substantially improved model fit over the constant model. Interaction terms were tested but dropped from presented models when they were not significant. Total foliage and potential nest shrub density were not included in the same model because they were correlated in our study system; more potential nest shrubs in an area were associated with increased total density of vegetation (Pearson $r = 0.51$, $P < 0.0001$, $n = 958$), although they only explained about 25% of the variance in each other.

MICROHABITAT MANIPULATION EXPERIMENT

To more conclusively differentiate between the total-foliage and potential-prey-site hypotheses, we also conducted a microhabitat manipulation experiment. Four additional study sites were chosen for experimental tests in 2004 and 2005. We grouped nests into triads and randomly designated one as a control, one for experimental manipulation of total foliage, and one for manipulation of potential prey sites. Nests within each triad were initiated (date first egg laid) within 5 days of one another and separated by no more than 500 m to control potential temporal or spatial effects. Nest patches within a triad contained a similar initial density of shrubs ($\pm 10\%$), and all patches initially contained a minimum of 50 potential nest shrubs (approximate mean for previously measured Brewer's sparrow nest patches). Manipulation of each nest patch occurred early in the incubation period (day 1 to day 6) to ensure adequate exposure to treatments. The order of manipulation of nest patches within a triad was randomized. During each year, nest triads were replicated 7–10 times within each of the four sites.

For the total foliage experimental nest within each triad, we removed 50% of shrubs > 20 cm in height within the 5-m radius patch relative to the total counted within paired control nests using pruning shears, but only those shrubs deemed unlikely to be used as nest shrubs. Cut shrubs were deposited ≥ 50 m from the nest patch. At the potential-prey-site experimental nest patch, we also removed 50% of shrubs relative to controls, but only shrubs classified as potential nest shrubs. In the latter treatment, if a patch did not contain enough potential nest shrubs to reduce the overall density to 50% of the control shrub density, the treatment was completed by cutting shrubs unlikely to be used as potential nest shrubs ($n = 20$ out of 71 triads). The potential-prey-site manipulation was therefore conservative, but the experiment successfully eliminated the correlation between the amount of total foliage and potential nest sites within patches (Fig. 1, Table 2). Within control nest patches, we counted the total number of shrubs > 20 cm in height and the total number of potential nest shrubs, and made small clippings of shrub tips to mimic the disturbance and potential scent of shrub cuttings that occurred at experimental nests. All experimental treatments were conducted on the same day for each nest within a triad. Manipulations took 15–20 min to complete, and we spent the same amount of time

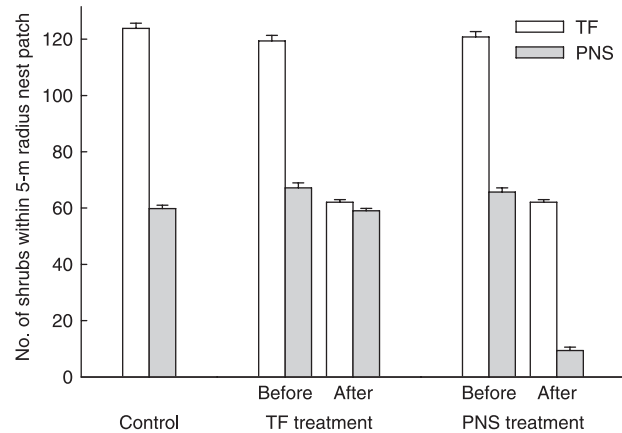


Fig. 1. Means (± 1 SE) of total foliage (TF; all shrubs > 20 cm) and potential nest shrubs (PNS) within Brewer's sparrow nest patches before and after experimental manipulation. See text for full explanation of the experimental protocol.

Table 2. Pearson correlations (two-tailed) between the amount of total foliage (all shrubs > 20 cm) and potential nest shrubs within Brewer's sparrow nest patches before and after the habitat manipulation experiment 2004–05 ($n = 71$ nest triads)

| Treatment Type | | Pearson r | P |
|------------------------------|--------|-------------|-----------|
| Control | | 0.56 | < 0.001 |
| Total foliage removal | Before | 0.56 | < 0.001 |
| | After | 0.82 | < 0.001 |
| Potential nest shrub removal | Before | 0.42 | < 0.001 |
| | After | -0.04 | 0.78 |

within control nest patches to account for possible disturbance effects. Each nest was monitored every 2 days to document nest fate.

We used the logistic exposure method (Shaffer 2004) to evaluate daily nest survival of control and experimental nests, with the first exposure period beginning on the day of experimental treatments. Treatment type (control versus total-foliage and potential-prey-site), year and study site were included as categorical variables. Akaike's information criterion adjusted for sample size (AIC_c ; Burnham & Anderson 2002) was used to rank eight candidate models (constant survival, and all combinations of treatment, year and site). Daily nest survival rates of both types of removals relative to controls were further evaluated by examining resulting 95% confidence intervals around estimates. Under the total-foliage hypothesis, we predicted that both types of experimental removals would significantly decrease nest survival relative to control nests, given that both effectively decreased the total amount of vegetation in the patch. Under the potential-prey-site hypothesis, we predicted that only the removal of potential nest shrubs would significantly decrease nest survival relative to controls.

Results

TOTAL-FOLIAGE HYPOTHESIS

Birds consistently (year: Wald = 2.93, d.f. = 2, $P = 0.23$) chose nest patches with more total foliage than available on

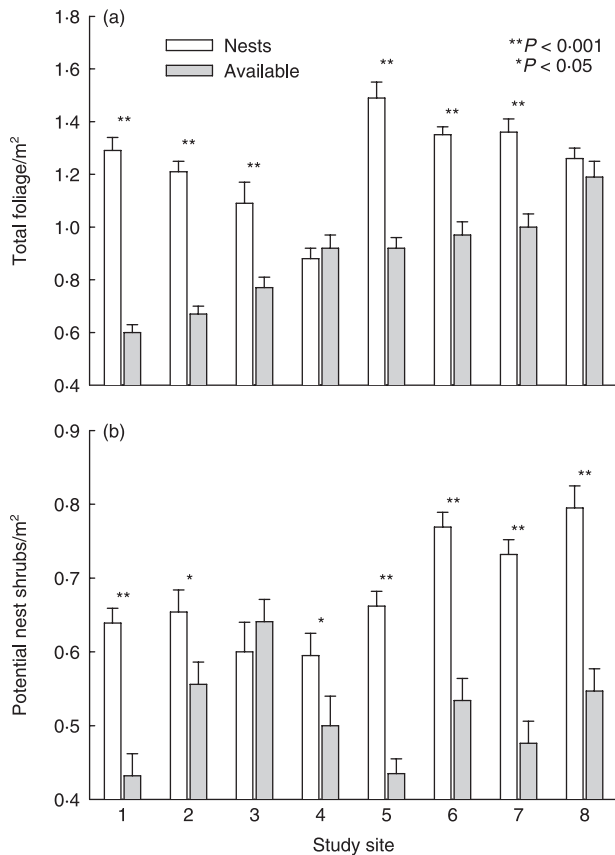


Fig. 2. Brewer's sparrow nest patch (5-m radius) choice in relation to the total amount of foliage (density of shrubs > 20 cm in height) (a), and potential nest shrub density (b) within patches during 2003–2005 in Montana, USA. Data are means \pm 1 SE. White bars represent nest patches and gray bars are systematic vegetation plots, within each of eight study sites. Asterisks indicate the significance of the patch type comparison within individual plots, from independent samples *t*-tests with critical *P* values adjusted for multiple comparisons.

average in the landscape (Wald = 101.10, d.f. = 1, $P < 0.001$; $n = 547$ nest and 624 systematic patches). Identical patterns were found when only those nests found before the start of incubation (i.e. building or laying) were included in the analysis (Wald = 59.15, d.f. = 1, $P < 0.001$; $n = 248$ nests). The amount of total foliage in nest and systematic patches differed among study sites (study site: Wald = 42.41, d.f. = 7, $P < 0.001$). Nest patches contained a significantly greater amount of total foliage than systematic patches within six of the eight individual study sites (Fig. 2a).

The amount of total foliage in nest patches did not influence daily nest survival; adding total foliage to the model including year and site effects did not improve model performance ($\Delta\text{AIC}_c = 1.22$; Table 3). Moreover, the model slope coefficient for total foliage density was low ($\beta_0 = 0.14$) with a 95% confidence interval that overlapped zero (–0.18–0.47).

Observational results were confirmed in microhabitat manipulation experiments (Table 4). Treatment and study year (due to higher overall nest survival during 2005) comprised

Table 3. Effects of total foliage and potential nest shrub density on daily nest survival probability of the Brewer's sparrow at eight sites in Montana, 2003–05. Number of model parameters (*K*), the difference between models and the best-fitting model (ΔAIC_c), and Akaike weights (ω_i) are presented for four logistic-exposure models. C is a constant-survival model, TF and PNS represent linear effects of total foliage and potential nest shrub density, respectively, and Y and S are year and site effects

| Model | <i>K</i> | ΔAIC_c | ω_i |
|---------------|----------|----------------------|------------|
| $S_{Y+S+PNS}$ | 11 | 0.00 | 0.9996 |
| S_{Y+S} | 10 | 16.37 | 0.0003 |
| S_{Y+S+TF} | 11 | 17.59 | 0.0002 |
| S_C | 1 | 35.44 | 0.0000 |

Table 4. Effects of experimental removal of total foliage versus potential nest shrubs on daily nest survival probability of the Brewer's sparrow at four sites in Montana during 2004 and 2005. Number of model parameters (*K*), the difference between models and the best-fitting model (ΔAIC_c), and Akaike weights (ω_i) are presented for eight logistic-exposure models. C is a constant-survival model, T is treatment type which differentiates controls versus total-foliage and potential nest shrub removals, and Y and S represent year and site effects

| Model | <i>K</i> | ΔAIC_c | ω_i |
|-------------|----------|----------------------|------------|
| S_{Y+T} | 4 | 0.00 | 0.9053 |
| S_{Y+S+T} | 7 | 4.79 | 0.0827 |
| S_T | 3 | 8.78 | 0.0113 |
| S_{S+T} | 6 | 14.49 | 0.0006 |
| S_{Y+S} | 5 | 17.27 | 0.0001 |
| S_C | 1 | 21.38 | 0.0000 |
| S_Y | 2 | 26.84 | 0.0000 |
| S_S | 4 | 26.84 | 0.0000 |

the strongest model examined (Akaike weight > 0.90). Treatment effects were due to potential prey sites (see next) rather than total foliage. Experimentally reducing the amount of total foliage (95% nest survival CI: 0.965–0.985) in nest patches did not affect rates of nest predation compared with controls (95% CI: 0.963–0.983) during either year (Fig. 4).

POTENTIAL-PREY-SITE HYPOTHESIS

Patches chosen for nesting contained a greater density of potential nest shrubs than available on average within the landscape (Wald = 4.14, d.f. = 1, $P = 0.04$; $n = 547$ nest and 624 systematic patches), although densities varied across study sites (Fig. 2b). Similar results were obtained when only nests found before the start of incubation were included in analyses (Wald = 4.14, d.f. = 1, $P = 0.04$; $n = 248$). Nest patches contained a significantly greater density of potential nest shrubs within seven of eight study sites (Fig. 2b).

The density of potential nest shrubs in nest patches successfully predicted daily nest survival probability with survival rates increasing with increasing density of nest shrubs

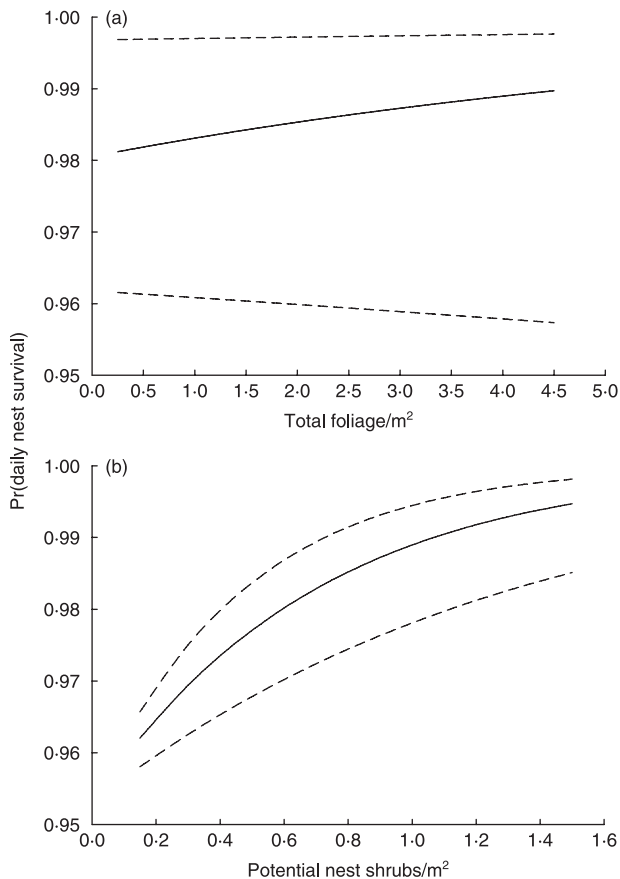


Fig. 3. Probability of daily nest survival for Brewer's sparrows as a function of the density of total foliage (a), and potential nest shrubs (b) within 5-m radius nest patches. Dashed lines indicate 95% confidence intervals around the predicted (back-transformed) values of nest survival based on the intercepts and slopes calculated via the logistic exposure method.

(Fig. 3b). Adding potential nest shrub density to the model including year and site effects significantly improved model performance (Table 3) and was clearly the strongest model evaluated (Akaike weight > 0.99), with the next best model having no support (Akaike weight = 0.00). The model slope coefficient for potential nest shrub density was much larger than for total foliage density ($\beta_0 = 1.49$) with a 95% confidence interval that did not overlap zero (0.79–2.18).

Finally, experiments again confirmed observational results (Table 4). Experimental removal of potential nest shrubs (95% CI: 0.922–0.956) from patches significantly decreased rates of nest survival compared to controls (95% CI: 0.963–0.983) even after accounting for annual variation in nest survival rates (Table 4, Fig. 4).

Discussion

Advances in understanding habitat selection and resulting community structure in natural environments require consideration of possible selective forces and alternative hypotheses of how

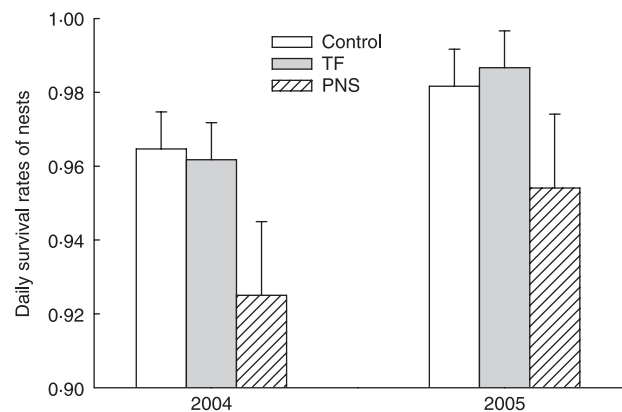


Fig. 4. Results of a microhabitat manipulation experiment in which the amount of total foliage (gray bars) and density of potential nest shrubs (hatched bars) within 5-m radius Brewer's sparrow nest patches were reduced relative to controls (white bars; see text for complete experimental protocol). Data are daily nest survival probabilities \pm 1 SE calculated using logistic exposure analyses.

habitat features may influence them. Predation of young is often the primary source of reproductive failure across many taxa (e.g. Price *et al.* 1980; Martin 1992; Clark & Shuter 1999; Kolbe & Janzen 2002), suggesting that alternative hypotheses of habitat influences on predation risk can be particularly pertinent. Such hypotheses need to consider both search behaviour of the predators and possible habitat features that may impede that search. Our study highlights the utility of such approaches, and provides new insight into why habitat features may influence predation risk of sedentary young and therefore selection on reproductive site choice.

Many studies of reproductive site selection and success in diverse taxa have focused on factors related to the density of vegetation surrounding nest or oviposition sites (e.g. Klatt & Getz 1987; Holway 1991; Wilson 1998; Braden 1999; Jones & Robertson 2001; Kolbe & Janzen 2002). Brewer's sparrows in our study used nest patches containing a greater amount of total foliage than available on average. These results could yield the conclusion that total foliage forms an important basis of habitat preference, when it simply may be correlated with a more relevant habitat feature, such as potential nest sites. Similarly, if total foliage was the only habitat attribute identified in advance as potentially important and measured with respect to nesting success, we would have concluded that habitat preference was unrelated to reproductive success and not adaptive because total foliage did not influence nest success or exhibit directional selection. Both conclusions would have been incorrect, and highlight the need for careful a priori consideration of ecologically important habitat features and explicit alternative hypotheses in assessments of adaptive habitat preference.

Detailed analyses in our system suggested that the density of potential nest shrubs was positively correlated with nest survival and demonstrated strong directional selection. Moreover, experimental manipulation of microhabitats confirmed the importance of potential nest sites within nest

patches as a critical feature influencing predation risk, while eliminating the role of total foliage. Our observational and experimental results therefore suggest rejection of the total-foliage hypothesis and clear support for the potential-prey-site hypothesis. The potential-prey-site hypothesis has rarely been investigated (but see Martin & Roper 1988; Liebezeit & George 2002; Mezquida & Marone 2002). Several researchers identified potential-nest-site density as a possible post-hoc explanation for habitat-nest success relationships (Holway 1991; Martin 1998; Ricketts & Ritchison 2000; Jones & Robertson 2001; Moorman, Guynn & Kilgo 2002), but explicit experimental tests have been lacking. Experimental tests are especially useful because of the demonstrated covariation that can occur between potential nest sites and total foliage (and possibly other habitat attributes).

The results of our study therefore provide a clear example of adaptive reproductive patch selection, which has been rarely demonstrated in taxa from insects to birds (Thompson 1988; Clark & Shutler 1999; Misenhelter & Rotenberry 2000; but see Jaenike & Holt 1991; Martin 1998). Birds preferentially nested in habitat patches containing greater densities of potential nest sites than available on average throughout the landscape. These preferences conferred a fitness advantage via reduced nest predation probability. The results suggest that the interaction between predator search behaviours and habitat structure can be more complex than simple physical barriers serving as impediments to predator foraging efficiency or the overall concealment of a prey site within a patch.

Undoubtedly, the extent to which the total-foliage hypothesis, potential-prey-site hypothesis or other hypotheses will be supported within any given system will depend on habitat type, the composition of the predator assemblage, and the dominant search strategies employed by specific predator types (Schmidt 1999; Martin & Joron 2003). For example, within a desert scrubland dominated by avian nest predators, Mezquida & Marone (2002) found no support for the potential-prey-site hypothesis. In contrast, in a more vegetated forest system dominated by small mammalian predators, Martin (1988, 1998) found that patches containing a greater number of plant stems of the type used for nesting significantly decreased rates of nest predation. Further examination of the interactions between predator foraging strategies and reproductive site attributes are clearly needed.

In conclusion, our observational and experimental analyses showed strong support for the potential-prey-site hypothesis for a common bird species in shrubsteppe habitats, across multiple spatial replicates and several years of study. Interactions between predator foraging success and habitat structure therefore can be more complex than simple impedance or occlusion by vegetation. Future tests of the potential-prey-site hypothesis in other ecological systems will aid in the determination of its ubiquity.

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