Demographic and behavioral responses of breeding birds to variation in food nest predation and habitat structure across multiple spatial scales

Anna D. Chalfoun
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DEMOGRAPHIC AND BEHAVIORAL RESPONSES OF BREEDING BIRDS TO VARIATION IN FOOD, NEST PREDATION, AND HABITAT STRUCTURE ACROSS MULTIPLE SPATIAL SCALES

by

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Presented in partial fulfillment of the requirements for the degree of
Doctor of Philosophy
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May, 2006

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Demographic and behavioral responses of breeding birds to variation in food, nest predation, and habitat structure across multiple spatial scales.

Chairperson: Thomas E. Martin

Birds show huge spatial variation in breeding behaviors and demography, from the global scale to the local. Yet the causes of this variation remain poorly understood. We reviewed the literature and document a worldwide pattern that southern-latitude passerine birds show consistently lower nest attentiveness during incubation than related northern species. We experimentally tested the hypothesis that greater food limitation may be responsible for low nest attentiveness in southern birds, by providing supplemental food during incubation to the karoo prinia (*Prinia maculosa*), a southern-hemisphere species with low attentiveness. Attentiveness was significantly higher in food-supplemented females than controls, but was still substantially below that of other related northern species. We therefore reject the hypothesis that food limitation is the main cause of latitudinal variation in incubation behavior.

Habitat selection is another critical behavior with substantial fitness consequences. A main assumption of habitat selection theory has been that habitat preferences are adaptive. Yet, mismatches between habitat preferences and reproductive performance have been prevalent across a wide variety of taxa. We take an integrative and comprehensive approach to the evaluation of habitat selection in a breeding songbird, the Brewer’s sparrow (*Spizella breweri*), by examining habitat preferences and a suite of fitness components across multiple spatial scales. We show that habitat preferences and resulting fitness consequences vary across spatial scales, and different environmental factors (e.g., food versus nest predation) may be more important at different scales. At the largest scale, birds preferred landscapes with higher shrub cover, which was associated with greater offspring size and the ability of parents to attempt more nests within a season. At the smallest scale, parents chose nest patches containing higher densities of shrubs, which was associated with higher nest success. We experimentally tested two hypotheses (total-foliage and potential-prey-site) for why microhabitat structure influences nest predation rates, and found strong support for the potential-prey-site hypothesis that predators may abandon search efforts sooner in areas where more potential nest sites must be searched prior to finding actual sites. Together, our results demonstrate the utility of conceptually thorough approaches and experimental analyses towards a better understanding of habitat selection and other important behaviors.
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CHAPTER 1

LATITUDINAL VARIATION IN AVIAN INCUBATION ATTENTIVENESS AND A
TEST OF THE FOOD LIMITATION HYPOTHESIS
ABSTRACT

Avian incubation attentiveness has important fitness consequences through its influence on the number and quality of hatched young and energetic costs imposed on parents. Nest attentiveness is highly variable across species and geographic regions. We reviewed the literature and show a worldwide pattern that nest attentiveness is generally lower in southern compared with northern-latitude passerine species. We then experimentally tested the hypothesis that greater food limitation may be responsible for low nest attentiveness in southern birds. We used the karoo prinia (*Prinia maculosa*) in South Africa, which has very low nest attentiveness (~ 50%) compared with average (~ 73%) north-temperate species. We provided supplemental food during early incubation to experimental females and measured nest attentiveness and on-and off-bout lengths compared to paired control females. Nest attentiveness was significantly increased at food-provisioned nests (57% versus 49%). Food-supplemented females spent significantly less time off the nest than control females, whereas mean on-bout lengths did not differ. However, mean nest attentiveness of food-provisioned females was still substantially below attentiveness of other similar bird species worldwide. We suggest that food can be an important proximate influence on parental care behavior within species, but the low attentiveness of many southern bird species appears to represent an evolved trait that is not simply constrained by food.
INTRODUCTION

The extent of parental care can greatly influence reproductive success and the quantity and quality of reared young (Clutton-Brock 1991). Yet, parents inevitably face tradeoffs in terms of how much energy to allocate to their developing young versus their own condition and longevity (Martin 1987, Clutton-Brock 1991, Martin 2002, Royle et al. 2004). Species differ in their parental care strategies for resolving these trade-offs (Clutton-Brock 1991, Martin et al. 2000), but the causes underlying this variation remain poorly understood.

Parental care strategies include a number of behavioral components, and one that has important fitness consequences for birds is nest attentiveness (the percentage of time parents spend on the nest during incubation). Nest attentiveness affects egg temperatures (White and Kinney 1974, Haftom 1988), which influence the length of the incubation period (Price 1998, Martin 2002, Martin et al. in review), and thereby the extent to which young and attending parents are exposed to time-dependent mortality from nest predators (Magrath 1988, Martin 2002). Such risks suggest that individuals should be under selection to increase attentiveness in order to minimize the incubation period (Bosque and Bosque 1995). Yet, even within environments with high nest predation risk, birds display extensive interspecific variation in nest attentiveness (Martin 2002, Martin et al. in review). Potential causes underlying variation in nest attentiveness, therefore, remain a critical question in need of study.

Avian nest attentiveness appears to vary geographically even within a single order such as Passeriformes (Martin 2002). Phylogenetically matched pairs of species in several passerine families show lower nest attentiveness at a southern-hemisphere
(Argentina) study site compared to a north-temperate (Arizona) site (Martin 2002). Here, we review existing literature to assess the ubiquity of this pattern and find worldwide evidence for geographic variation in nest attentiveness (Figure 1). Southern latitude species consistently show lower attentiveness even when controlling for phylogeny. The factors responsible for this pattern, however, remain unclear.

One potential cause of this latitudinal pattern might be food limitation. Nest attentiveness reflects on-bouts to keep eggs warm and temporary off-bouts to forage because parents must balance their own energetic requirements with the needs of their developing embryos (reviewed in Deeming 2002; Martin 2002). Energetic expenditures during incubation are considerable, and can influence future prospects of parents (Thomson et al. 1998, Visser and Lessells 2001, Tinbergen and Williams 2002). If food availability is more limited in southern areas, then energetic constraints from greater food limitation may require more and/or longer off-bouts, potentially explaining lower nest attentiveness of southern birds.

Some evidence suggests that food may be an important proximate influence on nest attentiveness (Nilsson and Smith 1988, Smith et al. 1989, Sanz 1996, Eikenaar et al. 2003, Pearse et al. 2004), but the ability of food to explain latitudinal patterns in attentiveness is unstudied. First, experimental tests of food limits on attentiveness have not considered latitudinal differences. Indeed, four of six species tested in previous studies were from north-temperate regions (Table 1). Second, four of six species were cavity nesters. Cavity nesting species engage in nest guarding in order to protect the cavity from usurpers, so presence in the nest in response to food does not separate attentiveness from guarding components. Finally, all but one of the studies were on
species with relatively high nest attentiveness (Table 1), which does not address the question of why southern species have low attentiveness. Thus, experimental studies are needed on non-cavity-nesting, southern species with low nest attentiveness.

The karoo prinia (*Prinia maculosa*; Cisticolidae) is a southern species that provides a good example for experimentally testing the relationship between food availability and incubation behavior. The karoo prinia is a southern hemisphere warbler that builds its own nest and has low mean incubation attentiveness (52%, Martin et al. in review) compared to other passerine species worldwide (Deeming 2002, Martin 2002). Karoo prinias experience high rates of nest predation (daily nest mortality of 9.3%, Martin et al. in review) and should be under selection to reduce the length of the incubation period. We therefore explored the hypothesis that the low attentiveness of prinias reflected greater food limitation compared with similar northern species. Specifically, we tested the prediction that if food limitation is responsible for variation in attentiveness across latitudes, then increasing food availability to this southern species should increase attentiveness levels to at least the lower limits of related northern species.

**METHODS**

**Summary of Nest Attentiveness Across Latitudes**

To assess the generality of latitudinal variation in nest attentiveness, we reviewed the literature for published estimates of nest attentiveness of passerine birds around the world. We limited our review to species with female-only incubation so as not to confound the issue with number of incubating parents. We categorized species as northern if they breed within north-temperate latitudes, and southern if they breed ≤ 23.5°
N latitude, which is the northern demarcation point for the tropics (Tropic of Cancer). We grouped south-temperate and tropical species together based on evidence that they share more similar life histories with each other than either do with north-temperate species (Martin 1996 and references therein). All attentiveness estimates were obtained from visual observations (either direct or by video recordings). If more than one source provided an estimate of nest attentiveness for the same species, we averaged estimates. Species means were averaged within each family for northern versus southern locations and compared as pairs within families to control for potential phylogenetic effects (Møller and Birkhead 1992). For families endemic to either northern or southern latitudes, and those for which we only had estimates from one latitude class, we conducted a phylogenetic analysis using independent contrasts (Felsenstein 1985) through the BRUNCH option of program CAIC (Purvis and Rambaut 1995) for dichotomous contrasts. The phylogeny for these contrasts was taken from Sibley and Ahlquist (1990) and is illustrated in Fig. 2. The resulting contrasts were then compared to 0 in a one-sample, one-tailed t-test to determine whether attentiveness was significantly higher in northern compared with southern families.

**Food Supplementation Experiment**

We conducted our food manipulation experiment during September to early November, 2004 at the Koeberg Nature Reserve (33°41'S, 18°27'E) in the Western Cape Province of South Africa. The region has a Mediterranean climate, consisting of warm, dry summers (10 - 38 °C) and cool, wet winters (2 - 25 °C). The reserve consists of a mosaic of strandveld succulent karoo, dune thicket and sand plain fynbos vegetation.
types (Nalwanga et al. 2004a). The karoo prinia is a small (9 g), territorial warbler and a common resident at this site. Nests are enclosed and dome-shaped, built off the ground in restio plants (Restionaceae) and various shrub species (Nalwanga et al. 2004b). Only females incubate the eggs, and mate feeding in this species is minimal. Females must leave the nest intermittently to forage and meet nutritional requirements.

Prinia nests were located by observing parental behavior during the nest-building stage (e.g., the male or female carrying nest material). We controlled for any potential confounding effects of clutch size (Thomson et al. 1998, Reid et al. 2002, Tinbergen and Williams 2002) by pairing nests of the same clutch size when possible and only using nests containing the modal number of eggs (3 or 4). Moreover, because ambient temperature may influence incubation rhythms (White and Kinney 1974, Conway and Martin 2000a, Deeming 2002), we paired nests by initiation date and collected data on experimental and control nests simultaneously on the same days. For each pair of nests, we randomly assigned one to the experimental treatment and one as the control. We performed the experiment during early incubation (2 or 3 days after clutch completion) for all birds to control for possible stage effects (e.g. Deeming 2002).

Experimental nests received a small, clear plastic cup with mealworms (larvae of *Tenebrio molitor*) just below the nest entrance and within 10 cm of the nest. Initial feeding trials were conducted to determine how many mealworms birds were willing to consume during the experimental observational period. As a result, approximately 60 mealworms (5-6 g) were placed in each cup. The average daily energy requirement for birds of similar body size to the karoo prinia is 45 kJ/day (Williams 1993). Mealworms have an energy content of 11.6 kJ/g and a minimum assimilation efficiency of 0.71 in
birds (Bell 1990), so we provided females with 92-110% of their daily energetic requirements— a major energetic augmentation. Control nests received an empty cup in the same location. We placed the plastic cup with an equal number of mealworms near the nest for 6 to 8 hours on the day prior to the actual experimental trial to ensure that experimental females: (1) were accustomed to the presence of the cup, (2) learned to take the novel food, and (3) had augmented energy intake prior to measuring incubation responses. In most cases, females rapidly learned to utilize the additional food. Control nests were similarly primed, but with an empty cup.

On the day we measured responses, food containers were placed at nests within one-half hour of sunrise. Data on nest attentiveness for experimental and control nests were collected by videotaping nests for 6-8 hours beginning when the cups were placed. We calculated three parameters from the videos: mean incubation on-bout length, mean off-bout length, and overall percent attentiveness. Mean bout lengths were calculated by averaging all of the complete on-bouts and off-bouts observed during an entire filming. Attentiveness was calculated as the total percentage of time the female spent on the nest incubating during the 6-8 hours, following Martin (2002). Mean bout lengths and percent attentiveness for experimental versus control nests were compared using paired T-tests. We arcsine transformed attentiveness data for statistical analysis, but present raw data in figures for ease of interpretation. Bout length data were not transformed prior to analyses as they were approximately normally distributed, and Levene tests (Dytham 2003) were insignificant indicating homogeneity of variances.

In order to examine whether food availability could be responsible for latitudinal differences in attentiveness, we tested two predictions. First, we examined whether nest
attentiveness of food-supplemented karoo prinias increased to at least the lower limits of attentiveness reported for related species at northern latitudes. Second, we predicted that southern birds should show a larger increase in nest attentiveness with supplemental food than similar northern species if food is more limiting in southern latitudes. In order to test this prediction, we compared the increase in attentiveness obtained in passerine food-supplementation experiments (Table 1) for northern versus southern locations.

RESULTS

Summary of Nest Attentiveness Across Latitudes

We found a consistent and statistically significant difference (Paired t test: \( t_{11} = 5.27, P < 0.001 \)) in nest attentiveness across families of passerine birds represented in both northern and southern latitudes (Figure 1). Almost all families for which we found nest attentiveness estimates for both northern and southern species showed lower attentiveness in the south (Figure 1). This pattern was further reflected in families found primarily or exclusively in either the north or the south (Figure 2). Three contrasts were obtained between families with purely north or south data (see Figure 2) and these contrasts also demonstrated that southern families had lower overall attentiveness than northern \( (t_2 = 6.21, P = 0.01) \).

Food Supplementation Experiment

We observed a total of 20 karoo prinia nests (10 food-supplemented and 10 control). Incubation attentiveness was significantly higher in experimental than control nests \( (t_9 = 2.31, P < 0.05; \text{Figure 3}) \). The difference in nest attentiveness between
treatments was caused by a disparity in the amount of time females spent off the nest. Mean off-bout length was significantly shorter at experimental nests ($t_9 = -3.34, P < 0.01$), whereas mean on-bout length was virtually identical between treatments ($t_9 = 0.18, P = 0.86$) (Figure 4).

Mean attentiveness even for experimental females fed ad libitum (57 % ± 3.5), however, remained far below unmanipulated estimates of incubation attentiveness for most other songbird species with female-only incubation (e.g., 73 %, n = 231 species; Deeming 2002), especially those in the north (Figures 1 and 2). We were unable to locate published estimates of nest attentiveness for other northern members of the family Cisticolidae for direct comparison. However, estimates were available for many northern species of the superfamily Sylvioidea, to which karoo prinias belong (Sibley & Alquist 1990). Mean nest attentiveness for 22 species of northern members of Sylvioidea averaged 74.8% ± 9.1, well out of the range of attentiveness for food-supplemented prinias in this study (One-Sample $t$ test: $t_1 = 7.40, P = 0.04$). Moreover, contrary to the prediction that southern species should respond more strongly to increased food, northern species actually showed a greater increase in attentiveness with supplemental food than southern species (One-way ANOVA: $F_1 = 7.01, P < 0.05$; Table 1).

**DISCUSSION**

Our review demonstrated a worldwide, latitudinal pattern in an important avian breeding behavior. Passerine incubation attentiveness was consistently lower in southern latitude species than for their northern counterparts (Figures 1 and 2). Our experimental test of the hypothesis that food limitation was the basis of this latitudinal pattern yielded
an increase in nest attentiveness in a southern species with low attentiveness. This result corroborates the long-standing view that food can have important proximate effects on parental behaviors (Lack 1954, Lack 1968, Martin 1987).

Previous food supplementation experiments for incubation behavior in other species have yielded mixed results. Two studies (Nilsson and Smith 1988, Sanz 1996) documented a decrease in the incubation period length of blue tits and pied flycatchers, respectively, suggesting that nest attentiveness was increased, but actual nest attentiveness was not measured. In studies directly measuring attentiveness, supplemental food increased attentiveness in five species, and had no effect in two (Table 1). Few studies had a large increase in attentiveness (Table 1) compared with the variation among species (Figures 1 and 2).

Although prinias in our study altered their incubation behaviors in response to supplemental food, incubation attentiveness even for females given access to unlimited food remained very low relative to attentiveness of other female-only incubators, especially in the north (Deeming 2002, Martin 2002, Martin et al. in review). The lack of a larger response is unlikely to be due to a lack of behavioral flexibility of attentiveness in prinias, as attentiveness was variable among individuals and as high as 74% in one experimental female. We also observed females loafing and preening at the food cup, indicating they had free time that could have been allocated to nest attentiveness but was not. The Australian reed warbler, another southern-hemisphere songbird with similarly low nest attentiveness (51%, Eikenaar et al. 2003) showed the identical pattern; attentiveness was significantly increased with supplemental food, but still remained low (57%). Interestingly, Eikenaar et al. (2003) focused on the significant increase and argued
food was an important limit on attentiveness, while overlooking the fact that attentiveness was extremely low in the broader geographic context that we document.

Several other lines of evidence also suggest that food is not the cause of broad species differences in attentiveness. First, our comparison of attentiveness responses to supplemental food in the north versus the south yielded a result opposite to that predicted; northern species actually showed a greater increase in attentiveness with increased food than southern species. Food availability is therefore unlikely to be more limited in the south. Similarly, in a comparative analysis across passerine species, Conway and Martin (2000b) found no effect of two potential correlates of food limitation (diet and foraging strategy) on nest attentiveness. Finally, after nearly a century of being introduced to a novel, food-rich environment (Vancouver, British Columbia) the subtropical crested mynah (*Sturnus cristatellus*) still exhibits very low (47%) nest attentiveness, typical of southern species (Johnson and Cowan 1974). The results of our study and others, therefore, do not support the hypothesis that food limitation is the sole cause of evolved differences in nest attentiveness between latitudes (Figure 5). Low attentiveness in the karoo prinia and other species instead appears to be an evolved parental strategy, independent of food effects.

In conclusion, food may be an important proximate factor affecting the extent of parental care in birds but only within limits. Food limitation alone cannot explain large-scale, across-species geographic variation in parental care strategies, and alternative explanations for this pattern require further examination. Latitudinal variation in attentiveness is unlikely to be driven by variation in nest predation risk selecting for shorter developmental periods, as nest predation is variable both within and across
latitudes and with no clear north-south gradient (Martin 1996, Martin et al. 2000).
Moreover, many southern species experience very high rates of nest predation, yet
maintain relatively low nest attentiveness. Climatic variation across latitudes may play a
role in the amount of time parents spend on the nest, although temperatures at many
south-temperate sites often approximate those at north-temperate sites during the
breeding season (Martin 2002). One promising alternative explanation for geographic
patterns in nest attentiveness is variation in adult mortality across latitudes (Martin 2002).
According to classic life history theory (e.g. Roff 1992), if southern birds experience
lower adult mortality, they should be less willing to invest as much in nest attentiveness
and other components of current reproduction. Testing for the existence of a trade-off
between adult mortality and nest attentiveness across latitudes is therefore a critical next
step in addressing geographic variation in parental care strategies.

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this manuscript. This work was supported by U. S. National Science Foundation grants to
LITERATURE CITED


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* Latitude: N = North temperate; S = Tropics or south temperate
FIGURE LEGENDS

**Figure 1.** Paired family means (± SE) of nest attentiveness (% time spent on the nest) for passerine species with female-only incubation in north temperate (black bars) versus tropical/south temperate (≤ 23.5° N; gray bars) latitudes. Species sample sizes are indicated after the family names. Data were obtained from the literature (Appendix A).

**Figure 2.** Nest attentiveness of passerine families (± SE) found primarily or exclusively in either northern (black bars) or southern (≤ 23.5° N; gray bars) latitudes. Species sample sizes are indicated after the family names. Data were obtained from the literature (Appendix A), and phylogenetic relationships from Sibley and Ahlquist (1990).

**Figure 3.** Mean nest attentiveness (± SE) during early incubation for food-supplemented versus control nests of the Karoo Prinia, *Prinia maculosa*, (*n* = 10 matched pairs) in South Africa during September – November 2004.

**Figure 4.** Mean on-bout and off-bout lengths (± SE) during early incubation for food-supplemented versus control nests of the Karoo Prinia, *Prinia maculosa*, (*n* = 10 matched pairs) in South Africa during September – November 2004.

**Figure 5.** Hypothesized relationship of food availability and avian nest attentiveness across species and latitudes. Both northern (black line) and southern (dashed line) species are expected to show proximate increases in attentiveness in response to increased food availability, and preliminary data (Table 1) further suggest that northern species show slightly stronger responses. Food availability alone, however, cannot ultimately explain why southern species generally show lower nest attentiveness than similar northern species (gray arrows).
Figure 1.

<table>
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Nest Attentiveness (%)

North
South

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Figure 2.
Figure 3.
Figure 4.
Figure 5.
Appendix A. References for summary (shown in Figures 1 and 2) of passerine nest attentiveness by family in northern versus southern latitudes. Avian families are listed in taxonomic order; references alphabetically.

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References


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CHAPTER II

MISMATCHES BETWEEN HABITAT PREFERENCES AND REPRODUCTIVE PERFORMANCE: TRADE-OFFS AMONG FITNESS COMPONENTS AND SPATIAL SCALES
ABSTRACT

Ecological theory predicts that habitat choices should be adaptive, such that fitness is higher in preferred habitats. However, studies often report mismatches between habitat preferences and reproductive outcomes across a wide variety of taxa. We examined whether the matching of habitat preferences with multiple fitness components changed with spatial scale (landscape, territory, nest patch) in a breeding songbird, the Brewer's sparrow (*Spizella breweri*). Birds settled earlier and in higher densities in landscapes with greater shrub cover and height. Yet, nesting success was similar across landscapes. However, nestling mass and the number of nesting attempts per pair increased with shrub cover and height, raising the possibility that landscapes were chosen on the basis of food availability rather than safe nest sites. At the opposite spatial extreme, nest patches contained greater densities of shrubs and potential nest shrubs than random patches, and nest success was higher in patches with higher potential nest shrub densities. Pairs that established territories with higher potential nest shrub densities also showed greater seasonal reproductive success. Territories were placed in areas with greater shrub cover, height, density, and density of potential nest shrubs, indicating a potential strategy to maximize the inclusion of all attributes with potential fitness consequences at larger and smaller scales. Habitat preferences may therefore reflect the integration of multiple environmental factors across multiple spatial scales, and individuals may have more than one option in terms of optimizing fitness via habitat selection strategies.
INTRODUCTION

Under natural conditions, habitat preferences are assumed to be shaped by the fitness outcomes of using particular habitats (Hildén 1965, Orians and Wittenberger 1991, Jaenike and Holt 1991, Martin 1998). However, unambiguous examples of adaptive habitat preferences are uncommon (Martin 1998, Clark and Shutler 1999, Misenhelter and Rotenberry 2000, Robertson and Hutto 2006). Actual habitat preferences and the resulting fitness consequences are often not quantified (Martin 1998, Clark and Shutler 1999, Garshelis 2000, Jones 2001), and when they are, many results suggest neutral or even inverse relationships between preferred habitats and indices of fitness across a wide variety of taxa (e.g., Thompson 1988, Valladares and Lawton 1991, Misenhelter and Rotenberry 2000, Kolbe and Janzen 2002, but see Martin 1998). Such results pose a potential paradox: why should animals ever choose habitats that yield lower fitness?

Habitat choices determine the acquisition of critical resources such as food (MacArthur et al. 1966, Cody 1974, Willson 1974, Rotenberry and Wiens 1998) and refugia from predators (Leber 1985, Martin 1988, Söderström 2001, Heithaus and Dill 2002, Eggers et al. 2006), which in turn influence fitness consequences. Different resource types, however, may influence different fitness components to varying degrees. In breeding birds, for example, food availability often manifests in terms of the ability of parents to invest in offspring (e.g., clutch size, clutch mass, offspring size, numbers of nesting attempts (Martin 1987, Arcese and Smith 1988, Holmes et al. 1992, Bolton et al. 1993, Martin 1995, Nagy and Holmes 2004) whereas nest predation risk influences the probability of nesting success for each attempt. Because food and nest predation can
both affect the overall reproductive output within a season, individuals may adopt alternative habitat selection strategies to achieve the same net fitness. For example, individuals that select food-rich habitats may be able to compensate for higher predation risk via the ability to renest more quickly and more often, and/or by rearing higher quality young that are more likely to survive to breeding age. Identifying such tradeoffs among fitness components, however, necessitates the simultaneous examination of multiple fitness components; an approach that has been extremely rare in studies of habitat selection.

Selection pressures imposed by food versus predation may also act more strongly at particular spatial scales (Pribil and Picman 1997). Food availability often varies across fairly large spatial scales coincident with climatic and edaphic variation (Orians and Wittenberger 1991, Rotenberry and Wiens 1991), though food may also vary on finer scales. Predation risk is often the result of complex interactions between predator abundance and behavior, availability of alternative prey, and habitat structure, and can therefore vary significantly both temporally and spatially (Crowder and Cooper 1982, Salamolard et al. 2000, Weatherhead and Blouin-Demers 2004). Yet, predicting predator-prey encounter rates may be more feasible at smaller spatial scales where habitat attributes often proximately influence predator success rates. Accordingly, multiple spatial scales need to be incorporated into studies of habitat selection (Allan and Starr 1982, Hutto 1985, Wiens 1989, Menge and Olson 1990, Orians and Wittenberger 1991, Levin 1992, Saab 1999, Clark et al. 1999). Spatial scales should be chosen based on the biology of focal species, and indices of habitat preference and subsequent fitness outcomes should be specifically tailored to each spatial scale.
Detailed empirical studies that measure habitat preferences and a suite of fitness components across multiple spatial scales are therefore needed to more effectively delineate the potential evolutionary bases of habitat preferences. Such an approach may also help resolve the apparent paradox between habitat preferences and reproductive performance. Here, we examine breeding habitat preferences and several demographic components (fledging success, seasonal reproductive success, clutch size, clutch mass, nestling mass, and numbers of nesting attempts) of a passerine bird across multiple, ecologically-relevant spatial scales: the landscape, territory, and nest patch. Specifically, we test whether tradeoffs among multiple fitness components across spatial scales can help explain habitat preference-performance mismatches that are often observed when fitness components and spatial scales are examined in isolation.

METHODS

Study System

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, thereby permitting intensive and replicated data collection. Shrubsteppe consists of both local and landscape-scale gradients in habitat structure, thus permitting habitat selection comparisons across spatial scales. Nest predation is the main cause of reproductive failure in the Brewer’s sparrow, and varies with variation in habitat structure (Chapter 3). Nest predation therefore imposes strong fitness consequences in this system, and likely influences habitat choice. Food resources are also known to vary spatially and temporally in shrubsteppe (Rotenberry and Wiens 1998). Therefore, our
study system permitted simultaneous evaluation of multiple fitness components likely to be influenced by variation in habitat structure.

Data collection took place during May to August of 2003-2005 within public and private lands in Carbon County, Montana. The predominant overstory plant species in the study area was big sagebrush (*Artemisia tridentata*), mixed with greasewood (*Sarcobates vermiculatum*) and rabbitbrush (*Chrysothamnus spp.*). The understory was sparse due to the dry climate (approximately 20 cm of annual precipitation) and consisted of various small forbs, native grasses, and cactus. We established eight 25- to 30-ha study sites separated by at least 1 km within which to conduct analyses. Sites represented the landscape scale for the purposes of our study, as each encompassed multiple individual Brewer's sparrow territories/home ranges. Sites were selected so as to capture the full range of regional structural variation in sagebrush steppe, and differed in terms of their overall shrub cover, height and density. Each plot also contained microhabitat gradients according to localized variation in soil moisture content.

Confirmed nest predators in the study area were the bullsnake (*Pituophis melanoleucus*), prairie rattlesnake (*Crotalis viridis*), various rodent species, and loggerhead shrike (*Lanius ludovicianus*). Other potential nest predators observed included the black-billed Magpie (*Pica hudsonia*), pinyon jay (*Gymnorhinus cyanoccephalus*), common grackle (*Quiscalus quiscula*), brown-headed cowbird (*Molothrus ater*), coyote (*Canis latrans*) and raccoon (*Procyon lotor*).
Habitat Preferences

We used Brewer's sparrow density as an indicator of habitat preference at the landscape scale. Density may sometimes be a misleading indicator of actual habitat preference and/or quality (Van Horne 1983), so we also examined densities with respect to initiation dates (day the first egg was laid) of first nests within each breeding season. First nest initiation dates should reflect the chronology of settlement and/or the quality of settling individuals, and therefore provide an additional metric of habitat preference (Robertson and Hutto 2006). At the territory scale, within each study site we compared the habitat structure within Brewer's sparrow territories to that in surrounding unused but available habitat. Nest patch preferences were similarly measured by comparing attributes of 5-m nest patches to unused but available patches.

Fitness Consequences

Nesting success was used as a fitness proxy at all spatial scales. We estimated nest survival at the landscape scale by pooling all nests within each landscape (study site) during each year and calculating daily nest survival probabilities (Mayfield 1975). We calculated the seasonal reproductive success (total offspring fledged per year) of pairs of birds within a subset of territories within each landscape to estimate the relative success of different territories and landscapes. Finally, we compared the habitat structure of successful versus depredated nest patches within each landscape.

Within each study site we also collected information on demographic parameters indicative of parental investment and/or offspring quality including clutch size, clutch mass, nestling mass, and numbers of nesting attempts.
Territory Density

We mapped male territories during each breeding season in order to compare Brewer’s Sparrow densities across landscapes. Plots were flagged into 50 x 50 m grids, and each received 8-10 survey visits every 2 to 5 days from early May to mid-June. During survey visits, a surveyor slowly walked and mapped observations of male singing locations, as well as visual observations of birds. Individual survey data from each study site within each year were transposed onto a single composite map showing the location and number of individual territories. The total number of territories was divided by the total study site area to calculate territory density/ha. Territories whose locations were only partially covered by the study site were counted as one-half of a territory.

Nest Searching and Monitoring

Nests were located within each study site using behavioral observations and systematic searches. Nests were monitored every other day until completion following protocols outlined in Martin and Geupel (1993). For each nest, we calculated nest initiation date, and fate (successful, depredated or mortality due to other causes). Nests that fledged at least one young were considered successful. Observations of nestlings within 1-2 days of fledging age, fledglings near the nest or parents with food in the vicinity of the nest were taken as evidence of a successful nest (Martin 1998). Nests were considered to have been depredated when nest contents (eggs or nestlings too young to have fledged) disappeared.
Focal-Pair Monitoring

Each year we randomly selected 5-10 Brewer’s sparrow pairs within each study site to monitor intensively throughout the entire breeding period. Brewer’s sparrows are socially monogamous, multi-brooded, and will renest following nest failure. We therefore attempted to document the fates of every nesting attempt of focal pairs in order to calculate season-long reproductive success. Focal pairs were dispersed throughout study plots to obtain variation in territory habitat structure. The male and female of each focal pair were captured via target-netting at their first nest of the season and given a unique combination of color bands with which to identify and subsequently monitor individual birds. We calculated seasonal reproductive success for each pair by tallying the total number of young successfully fledged from all nesting attempts within a season.

Egg and Nestling Measurements

Clutch size, clutch mass, and nestling size were recorded at all sites. Clutch size was recorded for nests that we were able to observe at least twice following the laying of the last egg. Sufficient sample sizes of clutch and nestling mass across all 8 sites were obtained during 2005 only. Mass measurements were recorded using a portable 0.001-g sensitivity balance. Egg mass was only recorded for nests with known nest initiation dates and within 3 days of clutch completion, to limit variation due to egg water loss later in the incubation period (Martin et al. 2006). Values for all eggs within a clutch were averaged to record mean clutch masses. Nestling mass was obtained only from nests with known hatch dates and modal brood sizes (3 or 4) so as to standardize measurements across nests and locations. Nestlings were always weighed on day 6 of the nestling
period (out of approximately 9 days) to reduce force-fledging after handling and control for stage day.

**Habitat Measurement**

Brewer's Sparrows concentrate their activities within the shrub layer, i.e., nesting, foraging, perching, and singing all take place within or from the tops of shrubs (Wiens et al. 1987, Rotenberry and Wiens 1989). We therefore identified four main shrub-layer habitat attributes relevant to the ecology and behavior of Brewer's sparrows on which to focus our habitat analyses: percent shrub cover, shrub height, shrub density, and density of potential nest shrubs. Shrub height, however, was redundant with shrub cover (Pearson correlation: 0.48, $P < 0.001$) and showed identical preference/performance patterns across scales, so we only present data on shrub cover. Designation of potential nest shrubs was based on two years of prior study in which attributes (height, maximum crown width, and % live crown) were measured and used to establish criteria for nest shrubs. Specifically, potentially suitable nest shrubs needed to be between 20 – 175 cm in height, 30 – 250 cm in width, and with a minimum of 25 % live crown. In addition, shrubs needed to contain at least one semi-concealed “niche” within its branch structure that could potentially accommodate a Brewer’s sparrow nest.

Habitat structure was measured within 5 m-radius vegetation plots (Martin et al. 1997). Plots were centered at nests, and at systematically located points throughout each site (approximately one per ha). Systematic vegetation plots were established *a priori* using site maps prior to bird arrivals, and so, by chance, some fell within territories and some outside. Therefore, mean habitat attributes could be compared within versus
outside of areas chosen for territories during each year. In 2004 and 2005, two additional vegetation plots were randomly established within each focal-pair territory, for more precise quantification of potential differences in vegetation structure among territories and in relation to reproductive performance.

Each vegetation plot was marked into 4 quadrants using a tent stake and 4 attached 5-m lengths of rope spread in the 4 cardinal directions from plot center. Within each quadrant, we visually estimated the percent shrub cover, and counted the number of shrubs in four different size classes (0-20, 20-50, 50-100 and > 100 cm) and the number of potential Brewer’s sparrow nest shrubs. We also recorded the shrub species and height of each shrub touching the rope lines. Habitat measurements from the four quadrants at each plot were averaged. Only shrubs larger than 20 cm in height were included in total shrub density estimates.

Data Analysis

Three unique sets of preference and fitness metrics were used to assess habitat relationships of Brewer’s sparrows across the three spatial scales (Table 1). We initially explored the relationship between Brewer’s sparrow nesting chronology and densities using ANCOVA with year as an additional factor, in order to determine whether density was a suitable index of habitat preference at the landscape scale. We specifically predicted that Brewer’s sparrows should initiate first nests earlier within landscapes with higher densities. We also tested for density-dependent effects by examining the relationship between sparrow density and seasonal fecundity (number of offspring produced per pair) (Fretwell and Lucas 1970).
Landscape-level analyses of habitat preference and reproductive performance were conducted using ANCOVA, with year as a factor in both models. Territory density was the dependent variable in habitat preference models, with percent shrub cover, shrub density, and potential nest shrub density, respectively, as covariates. Daily nest survival probability was the dependent variable in models evaluating landscape-level fitness consequences. We also compared nest survival probabilities with actual seasonal fecundity estimates from each site and year to assess the efficacy of using Mayfield nest survival probabilities as an accurate fitness metric.

Territory-level habitat preferences were assessed by comparing means of the three shrub attributes between territory and non-territory areas using ANCOVA. Year and study site were included as additional factors. Fitness consequences at the territory scale were compared to each habitat attribute using ANCOVA with seasonal fecundity as the dependent variable, and year and study site as additional factors.

Habitat attributes were compared between nest and systematic patches to document nest patch preferences, and between successful and depredated nests to examine reproductive success in relation to nest patch choice, using ANOVA. Year and study site were included as additional factors in all models.

Comparisons of additional demographic components (clutch size, clutch mass, nestling mass, and numbers of nesting attempts) were conducted only at the landscape scale. Brewer’s sparrows can forage and obtain resources outside of territory boundaries, and therefore, landscape-scale analyses of fitness components were most appropriate. Clutch size and estimates of numbers of nesting attempts were examined with respect to
site-level habitat means using ANCOVA, with year as a fixed factor. Clutch and nestling mass data from 2005 were compared across study sites using linear regression.

RESULTS

Brewer’s sparrow pairs initiated first nests earlier at study sites with higher breeding densities during all 3 years of the study (date: $F_{1,252} = 53.18, P < 0.001$; year: $F_{2,252} = 1.39, P = 0.25$), though the relationship was slightly relaxed in 2005 (year x density: $F_{2,252} = 4.63, P = 0.01$) (Figure 1). Moreover, seasonal reproductive success, while annually variable (year: $F_{2,23} = 5.73, P = 0.01$), did not decline with increased Brewer’s sparrow density (success: $F_{1,23} = 1.57, P = 0.23$; year x density: $F_{2,23} = 1.57, P = 0.24$) (Figure 2). We therefore focused on density as an index of habitat preference in subsequent landscape-scale analyses.

Mayfield nest survival probabilities were positively correlated with season-long reproductive success across sites during all years of the study (success: $F_{1,23} = 7.54, P = 0.01$; year: $F_{2,23} = 0.40, P = 0.68$; success x year: $F_{2,23} = 0.82, P = 0.46$) (Figure 3). The use of nest survival probabilities as an index of fitness in subsequent landscape-level analyses therefore seemed justified.

Brewer’s sparrows preferentially settled in landscapes with higher shrub cover ($F_{1,23} = 71.77, P < 0.001$) and slightly lower shrub density ($F_{1,23} = 8.84, P = 0.008$) during all 3 years of the study (year: $F_{2,23} = 0.38, P = 0.69$) (Figure 4). Landscape-scale settlement was unrelated to potential nest shrub densities ($F_{1,23} = 0.006, P = 0.94$; Figure 4). Landscape-scale nest survival showed no relationship with shrub cover ($F_{1,23} = 0.71, P = 0.41$), density ($F_{1,23} = 0.10, P = 0.75$), or potential nest shrub density ($F_{1,23} = 0.12, P = 0.41$).
= 0.73) during any year of the study (year: $F_{1,23} = 3.37, P = 0.06$) (Figure 4). Seasonal reproductive success was similarly unrelated to shrub cover ($F_{1,23} = 0.25, P = 0.62$), density ($F_{1,23} = 0.10, P = 0.75$), or potential nest shrub density ($F_{1,23} = 0.10, P = 0.75$), though reproductive output was higher in 2005 (year: $F_{2,23} = 5.62, P = 0.01$) (Figure 4).

Clutch size varied annually ($F_{2,23} = 42.85, P < 0.001$) but not in relation to any of the habitat attributes (all $P$ values $> 0.05$). Clutch mass in 2005 was similarly unrelated to any of the landscape-scale habitat variables (overall model: $F_7 = 0.45, P = 0.77$). The number of nesting attempts per pair increased with shrub cover ($F_{1,23} = 8.58, P = 0.009$) but not shrub density ($F_{1,23} = 1.62, P = 0.22$) or potential nest shrub density ($F_{1,23} = 0.53, P = 0.48$) with no year effect ($F_{2,23} = 0.54, P = 0.59$) (Figure 4). Nestling mass also increased with shrub cover ($t = 2.69, P = 0.04$) but decreased with potential nest shrub density ($t = -2.75, P = 0.04$) (Figure 4).

Brewer's sparrows selected territories containing greater shrub cover ($F_{1,623} = 31.98, P < 0.001$) and potential nest shrub density ($F_{1,623} = 13.44, P < 0.001$) but not shrub density ($F_{1,623} = 2.35, P = 0.13$) after accounting for variation across study sites ($F_{7,623} = 4.53, P < 0.001$) (Figure 5). Patterns were similar across years (year: $F_{2,623} = 0.10, P = 0.91$; year x site: $F_{14,623} = 0.56, P = 0.90$). Seasonal reproductive success was higher within territories with higher potential nest shrub density ($F_{1,96} = 4.17, P = 0.04$) but not shrub cover ($F_{1,96} = 0.30, P = 0.59$) or density ($F_{1,96} = 0.16, P = 0.69$) (Figure 5). Overall territory-level reproductive success was higher in 2005 than 2004 (year: $F_{1,96} = 8.46, P = 0.005$).

Shrub cover did not differ between nest and systematic patches ($F_{1,1366} = 1.45, P = 0.23$; Figure 6), even after accounting for variation due to year ($F_{2,1366} = 17.42, P <
0.001) and study site ($F_{7,1366} = 15.34, P < 0.001$). Shrub cover was also similar between successful versus depredated nest patches ($F_{1,508} = 0.008, P = 0.93$) (Figure 6). Both shrub density and potential nest shrub density were higher in nest patches compared to systematic patches, yet nest success was only higher in patches containing greater potential nest shrub density (Figure 6; Chapter 3).

**DISCUSSION**

Brewer's sparrows showed clear habitat preferences within each spatial scale that we examined, but preferences varied across scale. At the largest scale, Brewer's sparrows preferentially settled in landscapes with higher shrub cover and greater shrub height throughout the duration of the study. At the smallest scale, birds selected nest patches with higher shrub density and potential nest shrub density. Choices at the intermediate scale of the territory seemed to reflect a "best of all worlds" scenario in which all attributes examined (shrub cover, shrub density and potential nest shrub density) were greater than available, on average, throughout the landscape.

Concordance between habitat preferences and nesting success was especially evident at the nest patch scale. Successful nest patches clearly contained higher densities of shrubs that were suitable for nesting. In Chapter 3, we experimentally examine the potential processes underlying the relationship between potential nest shrub density and nest predation rates, within the context of the interaction between predator foraging strategies and microhabitat structure. Potential nest site density also corresponded with higher seasonal fecundity of Brewer's sparrow pairs at the territory scale, further
emphasizing the importance of this previously largely unrecognized and unappreciated habitat attribute.

Birds settled earlier and in higher densities in landscapes containing greater overall shrub cover and taller shrubs. Yet, nesting success and seasonal reproductive success were not higher in such landscapes. The apparent mismatch between landscape-scale habitat preferences and reproductive performance in our study is therefore an intriguing result. The pattern that nesting success was relatively similar across sites regardless of habitat structure and density is consistent with the predictions of the Ideal Free Distribution (Fretwell and Lucas 1970). According to the IFD model, individuals should settle in the highest quality habitats first, but fitness declines as densities increase in preferred habitats. The end result can therefore be similar reproductive outputs across sites of varying territory density.

Yet, the Ideal Free Distribution model does not explain why Brewer's sparrows in our study preferred landscapes with higher shrub cover. One explanation is because of benefits accrued through fitness components other than nesting success. Indeed, both numbers of nesting attempts and offspring size increased with shrub cover. Maximizing renesting ability may be especially critical when nest predation rates are high, but may also permit exceptional breeding performance during lower predation periods (Holmes et al. 1992, Nagy and Holmes 2004, Grzybowski and Pease 2005). Settling in landscapes that maximize renesting potential should also be beneficial in systems where nest predation rates are highly temporally and spatially variable, as they are at our sites. Nestling mass was also significantly greater in landscapes containing higher shrub cover. Such landscapes may therefore act in a cumulative way to enhance offspring quality via
greater overall productivity of the shrub layer and associated insect prey (Rotenberry and Wiens 1998, Morrison and Bolger 2002). If offspring quality subsequently influences the lifetime fitness and/or performance of individuals as in other systems (Roff 1992, Sinervo 1990), landscape preferences may reflect selection on offspring quality in addition to quantity.

Large-scale habitat preferences may also reflect more long-term optima than we were able to characterize during our study. Conversely, if critical attributes of shrubsteppe habitats in our study area or surrounding areas have been changed from historical conditions, populations may not have had enough time to respond and readjust habitat preferences accordingly. The vast majority of high cover, tall sagebrush areas in Carbon County have been converted for agriculture and/or altered due to livestock grazing. Habitat loss may therefore now be concentrating many different organisms (many of which will depredate nests upon incidental contact) into the remaining high-cover, tall sage patches. Nest predation rates in these remaining patches may thus be higher relative to historic levels and represent an ecological trap (Robertson and Hutto 2006).

The mismatches that we document between landscape-scale habitat preferences and nesting success are unlikely to due to methodological artifact. First, while many researchers correctly caution that density is not always a suitable indicator of habitat preference and/or quality (Van Horne 1983, Wheatley et al. 2002), Brewer's sparrow densities at our study sites were positively correlated with habitat preferences and several aspects of breeding habitat quality. Birds settled earlier and reared larger offspring in landscapes with greater shrub cover and height, and territory density was significantly
related to the overall number of offspring fledged per unit area. Interestingly, occupancy patterns also remained consistent among sites across years, a pattern that further suggests habitat preference and is contrary to previous results in this system (Rotenberry and Wiens 1980). Controversy has also arisen over whether aggregate estimates of nest survival such as Mayfield (1975) represent actual seasonal fecundity (Jones et al. 2005). However, we ensured upfront that our fitness indices accurately reflected fitness components. Daily Mayfield nest survival probabilities were significantly positively correlated with seasonal fecundity estimates during all three years of the study.

In conclusion, animal habitat preferences are scale-dependent. Apparent mismatches between habitat preferences and resulting fitness consequences could therefore occur when preferences and performance are only examined within a single spatial scale. Our results are also consistent with the hypothesis that the resources forming the basis for habitat choice (such as refugia from predators and food availability) may vary in importance across spatial scales, and may manifest in different (but potentially equally important) ways in terms of fitness consequences. Our study therefore emphasizes the utility of integrating multiple spatial scales and resulting fitness components into studies of habitat selection. Understanding which habitat characteristics are important across different, ecologically-relevant scales will help elucidate factors truly underlying habitat choices, and will lead to improved assessment of habitat quality for the successful maintenance of animal populations.

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ACKNOWLEDGEMENTS

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LITERATURE CITED


Table 1. Indices used for quantification of habitat preferences and fitness/demographic consequences of Brewer’s Sparrows at each spatial scale.

<table>
<thead>
<tr>
<th>Habitat Preference Indices</th>
<th>Fitness Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Landscape</strong></td>
<td></td>
</tr>
<tr>
<td>Territory density and initiation dates of first nests in relation to site-level habitat characteristics</td>
<td>Daily nest survival probabilities, seasonal reproductive success, clutch size, clutch mass, nestling mass, numbers of nesting attempts/pair</td>
</tr>
<tr>
<td><strong>Territory</strong></td>
<td></td>
</tr>
<tr>
<td>Habitat attributes of territories versus non-territory areas</td>
<td>Seasonal reproductive success</td>
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<tr>
<td><strong>Nest Patch</strong></td>
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<tr>
<td>Habitat attributes of nest patches versus systematic points</td>
<td>Individual nest fates</td>
</tr>
</tbody>
</table>
FIGURE LEGENDS

**Figure 1.** Chronology of Brewer’s sparrow first nest initiations (Julian date) in relation to breeding densities during 2003-2005 in Carbon County, MT.

**Figure 2.** Brewer’s sparrow seasonal reproductive success (total number of offspring fledged per pair) in relation to breeding densities in Carbon County, MT.

**Figure 3.** Landscape-scale daily nest survival probabilities in relation to seasonal reproductive success estimates (number of young fledged/pair) from a sub-set of color-marked Brewer’s sparrow pairs on each site during 2003-2005 in Carbon County, MT.

**Figure 4.** Landscape-scale habitat preferences and associated fitness consequences of the Brewer’s sparrow in Carbon County, MT during 2003-2005 in relation to % shrub cover (left column), shrub density (center column), and potential nest shrub density (right column). Rows display density (territories/ha), daily nest survival, seasonal reproductive success (total offspring fledged/pair), numbers of nesting attempts per pair, and mass of six-day-old nestlings (2005 only) respectively, from top to bottom. Asterisks in upper left indicate significance at the $P < 0.05$ level; double asterisks indicate $P < 0.01$.

**Figure 5.** Territory-scale habitat preferences (left column) and seasonal reproductive success (right column) of Brewer’s sparrows during 2003-2005. Rows display data for % shrub cover, shrub density, and potential nest shrub density, respectively, from top to bottom.

**Figure 6.** Brewer’s sparrow patch-scale habitat preferences (left column) and nest success (right column) in relation to % shrub cover (top row), shrub density (center row), and potential nest shrub density (bottom row) during 2003-2005.
Figure 1.

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Figure 3.
Figure 4.
Figure 5.
Figure 6.
ABSTRACT

Breeding habitat preferences are assumed to result from natural selection favoring choice of sites with the greatest potential for reproductive success. Yet, many studies of reproductive site selection across diverse taxa have reported mismatches between habitat preferences and reproductive performance. Such mismatches may be explained by intercorrelated habitat variables that obscure patterns, and/or a lack of understanding of how important agents of selection interact with habitat attributes. We used observational data and a habitat manipulation experiment to test two hypotheses for why microhabitat structure may influence nest site preferences and rates of nest predation (an important agent of selection) in the Brewer’s sparrow (Spizella breweri). The total-foliage hypothesis predicts that nest predation will decline in areas of greater overall vegetative density, whereas the potential-prey-site hypothesis predicts that nest predation should be lower in areas where predators must search among a greater number of potential nest sites. Our results show clear support for the potential-prey-site hypothesis, and reject the total-foliage hypothesis. We show, moreover, that when these two correlated ecological variables (total foliage and potential prey site density) are included in measures of site-specific reproductive performance, actual variation in nest site quality matches very closely with nest site preferences. Developing a better understanding of habitat selection may therefore require a more explicit understanding of how important processes such as nest predation are mediated by habitat features.
INTRODUCTION

Understanding why animals select particular habitats over others is of critical importance for explaining distributional patterns of organisms and differentiating between habitats of different value. Under natural conditions, habitat preferences are assumed to be shaped by fitness outcomes (Jaenike and Holt 1991, Orians and Wittenberger 1991, Martin 1998). Choice of habitat in which young are reared are particularly critical, especially for temporarily sessile offspring (Price 1998, Lindström 1999, Brown and Shine 2004). The choice of oviposition or nest site, for example, can determine the probability that enemies such as predators or parasites will discover young (Thompson and Pellmyr 1991, Martin 1992, 1993, 1998; Clark and Shutler 1999, Kolbe and Janzen 2002). Such risks should impose strong selection for the evolution and maintenance of preferences for safer habitats.


Apparent mismatches between reproductive site preferences and resulting reproductive performance may result in some cases due to intercorrelations between important and unimportant habitat variables. If two habitat variables are correlated, and
only one is measured and related to preferences and reproductive performance, researchers may not correctly identify which habitat attribute actually influences the fitness consequences of habitat use and habitat choices.

Clarifying which habitat features are likely to be important in terms of fitness consequences and habitat choices also requires consideration of how important selective agents such as predators interact with habitat structure. Past research has emphasized the relationship between habitat structural complexity and predator foraging success, especially in aquatic systems (e.g., Crowder and Cooper 1982, Warfe and Barmuta 2004). However, the specific mechanisms for why microhabitat structure influences predator foraging strategies or success are unclear.

For avian systems, the total amount of vegetation surrounding reproductive sites is often examined relative to reproductive success (e.g., Holway 1991, Howlett and Stutchbury 1996, Hoover and Brittingham 1998, Braden 1999), and may be an important influence on predation risk. However, we need to carefully consider how such habitat factors may influence processes such as predation. Two specific scenarios could lead to a relationship between vegetation structure and nest predation risk (Martin and Roper 1988, Martin 1992, 1993). First, individuals might benefit by selecting habitat patches containing denser foliage because this better conceals reproductive sites from predators and/or physically impedes predator search efforts (total-foliage hypothesis). Second, individuals may benefit by selecting patches containing a greater number of potential reproductive sites because predators should abandon search efforts sooner where more unoccupied potential prey sites must be searched before finding occupied sites (potential-prey-site hypothesis). Yet, these alternative hypotheses of specific habitat factors and
their influence on predation risk have rarely been explicitly tested (but see Martin and Roper 1988, Martin 1998, Liebezeit and George 2002, and Mezquida and Marone 2002).

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-foliage and potential-prey-site hypotheses. Specifically, we focused on nest predation rates in relation to microhabitat structure for a passerine bird.

METHODS

We identified a songbird species that breeds within North American shrubsteppe habitats, the Brewer's sparrow (Spizella breweri), as a promising study species with which to test the two hypotheses. 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. Brewer's sparrow nests are depredated by a diverse suite of predators, including two species of snakes, rodents, medium-sized mammals, and corvids (ADC personal observation). Moreover, nest predation is the primary cause of reproductive failure in this system (Rotenberry and Wiens 1989).

Data were collected during May-August 2003-2005 on public and private lands within southern Carbon County, Montana, USA. Eight 30-ha study sites, each separated by > 1 km, were chosen that represent the full range of structural habitat variation typical of shrubsteppe systems. Sites were dominated by big sagebrush (Artemisia tridentata),
with scattered greasewood (*Sarcobatus vermiculatus*) and rabbitbrush (*Chrysothamnus spp.*).

**Observational Data**

Nests were located by observing parental behaviors and/or by systematically searching shrubs within an active territory, and monitored every 2-3 days (Martin and Geupel 1993). Nests were considered successful if they fledged at least one young, and depredated if nest contents disappeared earlier than possible fledge dates. Following nest completion, we measured (1) the total number of shrubs greater than 20 cm in height as a proxy for the total amount of foliage, and (2) the total number of shrubs in the patch that could potentially accommodate a Brewer’s sparrow nest (potential prey sites), within a 5 m-radius patch surrounding each nest. The designation of a potential nest shrub was based on two years of prior study in which attributes (height, crown dimensions, percent live crown) of 334 shrubs used as nest sites were measured to determine the range of these attributes for identifying potential nest shrubs. We also estimated the density of total foliage and potential nest shrubs within 5 m-radius vegetation sampling plots located systematically throughout all 8 study sites (approximately one sampling plot per ha per site). Systematic samples were used to determine the distribution of total foliage and potential nest shrub densities available to the birds on average.

Total foliage and potential nest shrub density were compared between nest versus systematic patches to document nest patch preferences, and between successful and depredated nests to examine reproductive success in relation to microhabitat choice, using ANOVA. Year and study site were included as additional factors in all models.
Year was not significant in any model, and data were pooled across years for subsequent analysis. Study sites differed in nest site choice analyses, so comparisons of nest site choice were also made within each plot using t-tests for independent samples, with critical p-values adjusted for 8 comparisons using a Bonferroni correction.

Measuring the resulting fitness components of phenotypic traits such as reproductive site choice also affords the opportunity to examine the actual form and significance of natural selection operating on traits (Lande and Arnold 1983, Schluter 1988, Brodie et al. 1995, Martin 1998). We estimated the fitness surfaces for nest survival relative to total foliage and potential nest shrub density in patches using non-parametric cubic spline regression (Schluter 1988). Cubic spline regression was applied to binomial (successful versus depredated) data as in Martin (1998). These analyses determined the relative intensity of selection via the coefficient of variation in relative fitness, measured as predicted fitness (Schluter 1988, Brodie et al. 1995). Confidence limits for splines were estimated by bootstrapping in which the original data were resampled 200 times (Schluter 1988, Martin 1998). Analyses were conducted using software provided by D. Schluter. Selection differentials, or the phenotypic response to selection within a generation, were calculated following Lande and Arnold (1983) and Schluter (1988). Specifically, we estimated the selection differential, $s$, as the slope of the univariate regression of relative fitness on total foliage and potential nest shrub density, respectively.
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 and two as experimental nests. 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 for potential temporal or spatial effects. Nest patches initially contained a minimum of 50 potential nest shrubs (approximate mean for previously measured Brewer’s sparrow nest patches). Manipulation of each nest occurred early in the incubation period (day 1 to day 6) to ensure adequate exposure to treatments. During each year, nest triads were replicated 7-10 times within each site.

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 paired control nests using pruning shears, but only those shrubs deemed unlikely to be used as nest shrubs. 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. 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 10-20 minutes to complete, and we spent the same amount of time within control nest patches to account for possible disturbance effects. Each nest was monitored every 2 days to document nest fate.
For each nest, we calculated the proportion of potential post-treatment survival days using 11 days for the incubation period and 8 for the nestling period. For example, if a nest was manipulated on day 2 of the incubation period and it failed on day 4, survival was 2/17 days, or 0.12. Nests that survived to fledge received a 1.00. Data were arcsine transformed and survival of experimental nests was compared to control nests within each year using paired t-tests. Responses were similar across study plots (independent samples t-tests, all P values > 0.05) so plots were pooled for further analysis.

Under the total-foliage hypothesis, we predicted that both types of experimental removals would significantly decrease nest survival relative to control nests. 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 chose nest patches with more total foliage than available on average in the landscape (patch type: $F_{1,1132} = 205.99, P < 0.0001$; Figure 1a). The amount of total foliage in nest and systematic patches differed among study sites (study site: $F_{7,1132} = 10.97, P < 0.0001$) to differing extents (study site x patch type: $F_{7,1132} = 11.86, P < 0.0001$). Nest patches contained a significantly greater amount of total foliage than systematic patches within 6 of the 8 individual study sites (Figure 1a).

The amount of total foliage in nest patches did not differ between failed versus successful nests (nest fate: $F_{1,457} = 0.12, P = 0.73$). Total foliage again differed among study sites (study site: $F_{7,457} = 8.20, P < 0.0001$), but the lack of difference in total
foliage between successful and failed nests remained consistent across sites (study site x nest fate: $F_{7,457} = 0.52, P = 0.82$). Brewer’s sparrows showed no selection for the amount of total foliage in nest patches ($P = 0.68$, Figure 2a) as also indicated by a selection differential, $s$, of $0.02 \pm 0.048$ that does not differ from zero.

Observational results were confirmed in microhabitat manipulation experiments. Experimentally reducing the total amount of foliage in nest patches did not affect rates of nest predation in 2004 ($t = 0.34, P = 0.73$) or 2005 ($t = 0.12, P = 0.91$) (Figure 3).

**Potential-Prey-Site Hypothesis**

Patches chosen for nesting contained a greater density of potential nest shrubs than available on average within the landscape (patch type: $F_{1,1125} = 130.81, P < 0.0001$), though densities varied across study sites (study site: $F_{7,1125} = 6.61, P < 0.0001$) to differing extents for nest and systematic patches (study site x patch type: $F_{7,1125} = 5.34, P < 0.0001$) (Figure 1b). Nest patches contained a significantly greater density of potential nest shrubs within 7 of 8 individual study sites (Figure 1b).

The density of potential nest shrubs in nest patches was greater at successful than failed nests (nest fate: $F_{1,457} = 5.25, P = 0.02$; study site x nest fate: $F_{7,457} = 0.73, P = 0.65$). Brewer’s sparrows showed strong directional selection for the density of potential nest shrubs in nest patches ($P = 0.001$, Figure 2b.) as further indicated by a large selection differential, $s$, of $0.365 \pm 0.105$.

Finally, experiments again confirmed observational results. Experimental removal of potential nest shrubs from patches significantly decreased rates of nest survival in 2004 ($t = 2.18, P = 0.04$) and 2005 ($t = 2.95, P = 0.006$) (Figure 3).
DISCUSSION

While Brewer's sparrows in our study preferred nest patches containing both a significantly greater amount of total foliage and density of potential nest sites than available on average, only the density of potential nest sites was positively correlated with nest survival. Notably, cubic spline analysis showed strong directional selection for nest patches containing greater densities of potential nest shrubs, and no selection operating on total foliage density. Experimental manipulation of microhabitats further confirmed the importance of potential nest sites within nest patches to nesting success. Therefore, our observational and experimental results suggest: (1) that birds in our study system are exhibiting adaptive nest site selection behaviors at a local scale, (2) support for the potential-prey-site hypothesis, and (3) rejection of the total-foliage hypothesis.

Many previous studies of nest site selection and reproductive success have focused on factors related to the total amount of foliage within nest patches (e.g., Holway 1991, Wilson and Cooper 1998, Hoover and Brittingham, Braden 1999, Jones and Robertson 2001) whereas the concept of potential-prey-site density has rarely been explicitly investigated (but see Martin and Roper 1988, Martin 1988, 1992, 1993, 1998; Liebezeit and George 2002, Mezquida and Marone 2002). Several researchers, however, identified potential-nest-site density in nest patches as a possible post hoc explanation for habitat-nest success relationships (Holway 1991, Ricketts and Ritchison 2000, Jones and Robertson 2001, Moorman et al. 2002).

Our study raises an important caveat to future studies designed to assess habitat preferences and the fitness consequences of habitat use. Total foliage and potential nest site density were correlated in our study system; more potential nest shrubs in an area
were associated with increased total density of vegetation (Pearson $r = 0.51$, $P < 0.0001$, $n = 958$). Nest patches chosen by birds contained more total foliage than available on average, and thus, a study that merely looked at habitat choice relative to random would have concluded that total foliage forms an important basis of habitat preference. Moreover, if the total amount of foliage within nest patches were the only habitat attribute identified in advance as potentially important and measured with respect to nesting success, we would have failed to find the reason for why birds likely choose patches containing a greater amount of total foliage. Indeed, we would have concluded, as many previous habitat selection studies have, that preferred habitats were unrelated to reproductive success. If habitat attributes actually driving habitat choice are not identified, researchers may incorrectly conclude that habitat preferences are not adaptive, and/or subsequent habitat priorities may be developed and management actions implemented that impart neutral or even negative consequences to the target population.

Undoubtedly, the extent to which the total-foliage hypothesis, potential-prey-site hypothesis or other habitat hypotheses will be supported within any given system will depend on the nature of the habitat, as well as the composition of the predator assemblage and the dominant search strategies employed by specific predator types (Martin and Joron 2003). For example, within a desert scrubland dominated by avian nest predators, Mezquida and Marone (2002) found no support for the potential-prey-site hypothesis, whereas 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 would be a fruitful line of research.

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 is therefore more complex than simple impedance by vegetation. Future tests of the potential-prey-site hypothesis in other ecological systems will aid in the determination of its ubiquity. Our results further highlight the utility of experimental manipulations for clearly differentiating between correlated habitat characteristics and identifying those that are truly important in terms of fitness consequences.

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LITERATURE CITED


FIGURE LEGENDS

Figure 1. Brewer's sparrow nest patch (0.5-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 ± 1 SE. White bars represent nest patches and gray bars are systematic vegetation plots, within each of 8 study plots. 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.

Figure 2. Fitness surfaces (probability of nest survival) of Brewer's sparrows as a function of the density of total foliage (a) and potential nest shrubs (b) in nest patches. Dashed lines indicate ± 1 SE around the predicted probability of nest survival based on 200 bootstrap replicates of the fitness function.

Figure 3. Results of a microhabitat manipulation experiment in which the amount of total foliage (light gray bars) and density of potential nest shrubs (hatched bars) within 0.5 m-radius Brewer's sparrow nest patches were reduced relative to controls (white bars; see text for complete experimental protocol). Data are means of the proportion of post-treatment survival days relative to possible survival days ± 1 SE.
Figure 1.
Figure 2.
Figure 3.