

Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness

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Summary

1. Identifying the habitat features that influence habitat selection and enhance fitness is critical for effective management. Ecological theory predicts that habitat choices should be adaptive, such that fitness is enhanced in preferred habitats. However, studies often report mismatches between habitat preferences and fitness consequences across a wide variety of taxa based on a single spatial scale and/or a single fitness component.

2. We examined whether habitat preferences of a declining shrub steppe songbird, the Brewer's sparrow *Spizella breweri*, were adaptive when multiple reproductive fitness components and spatial scales (landscape, territory and nest patch) were considered.

3. We found that birds settled earlier and in higher densities, together suggesting preference, in landscapes with greater shrub cover and height. Yet nest success was not higher in these landscapes; nest success was primarily determined by nest predation rates. Thus landscape preferences did not match nest predation risk. Instead, nestling mass and the number of nesting attempts per pair increased in preferred landscapes, raising the possibility that landscapes were chosen on the basis of food availability rather than safe nest sites.

4. At smaller spatial scales (territory and nest patch), birds preferred different habitat features (i.e. density of potential nest shrubs) that reduced nest predation risk and allowed greater season-long reproductive success.

5. *Synthesis and applications.* Habitat preferences reflect the integration of multiple environmental factors across multiple spatial scales, and individuals may have more than one option for optimizing fitness via habitat selection strategies. Assessments of habitat quality for management prescriptions should ideally include analysis of diverse fitness consequences across multiple ecologically relevant spatial scales.

Key-words: Brewer's sparrow, food, habitat selection, landscape, nest patch, nest predation, shrub steppe, *Spizella breweri*, territory

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Introduction

Understanding the basis for habitat choices of animal species has important implications for explaining the distribution of organisms in the wild and differentiating between habitats of different quality for effective management. Under natural conditions, habitat preferences are assumed to be shaped by the fitness consequences

of using particular habitats (Hildén 1965; Jaenike & Holt 1991; Orians & Wittenberger 1991; Martin 1998). However, unambiguous examples of adaptive habitat preferences are uncommon (Mayhew 1997; Martin 1998; Clark & Shutler 1999; Misenhelter & Rotenberry 2000; Robertson & Hutto 2006). Actual habitat preferences and the resulting fitness consequences are seldom quantified (Martin 1998; Clark & 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 (Thompson 1988; Valladares & Lawton 1991; Misenhelter & Rotenberry 2000; Kolbe & Janzen 2002; but see Martin 1998). Such results pose

a potential paradox: why should animals ever choose habitats that yield lower fitness?

Habitat choices in some cases may indeed be maladaptive, particularly in human-altered environments where habitat cues have become decoupled from historic outcomes (Kokko & Sutherland 2001; Battin 2004; Bock & Jones 2004; Robertson & Hutto 2006). However, in other cases, researchers may fail to identify adaptive habitat selection strategies because of complex relationships among differing ecological resources, fitness components and spatial scales.

Habitat choices determine the acquisition of critical resources such as food (MacArthur, Recher & Cody 1966; Cody 1974; Willson 1974; Rotenberry & Wiens 1998) and refugia from predators (Leber 1985; Martin 1988; Söderström 2001; Heithaus & Dill 2002; Eggers *et al.* 2005), which in turn influence fitness and demography. Different resource types, however, may influence different fitness components to varying degrees. In breeding birds, for example, food availability often affects the ability of parents to invest in offspring (e.g. clutch size, offspring size and numbers of nesting attempts; Martin 1987, 1995; Arcese & Smith 1988; Holmes *et al.* 1992; Bolton, Monaghan & Houston 1993; Nagy & Holmes 2004; Zanette, Clinchy & Smith 2006) whereas nest predation risk primarily influences the probability of nesting success. Individuals must integrate these differing environmental influences on reproductive success in their habitat selection strategies, which may allow alternative 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 renege more quickly and more often, and/or by rearing higher quality young that are more likely to survive to breeding age. Identifying such trade-offs among fitness components, however, necessitates the simultaneous examination of multiple fitness consequences (Houston & McNamara 1999; Clark & Mangel 2000), a rare approach in studies of habitat selection.

Selection pressures imposed by food vs. predation may also act more strongly at differing spatial scales (Pribil & Picman 1997). Food availability often varies across fairly large spatial scales coincident with climatic and edaphic variation (Orians & Wittenberger 1991; Rotenberry & Wiens 1991), although food may also vary at finer scales. Predation risk is often the result of complex interactions between predator abundance and behaviour, availability of alternative prey, landscape context and habitat structure, and can therefore vary significantly both temporally and spatially (Crowder & Cooper 1982; Salamolard *et al.* 2000; Chalfoun, Thompson & Ratnaswamy 2002; Weatherhead & Blouin-Demers 2004; Lloyd *et al.* 2005; Tewksbury *et al.* 2006). Habitat attributes at small spatial scales, however, may be particularly important in terms of the success of predators in locating prey (Martin 1993, 1998; A. Chalfoun & T. Martin, unpublished). Accordingly, multiple spatial scales need to be incorporated into

studies of habitat selection (Allen & Starr 1982; Hutto 1985; Wiens 1989; Menge & Olson 1990; Orians & Wittenberger 1991; Levin 1992; Clark, Schmitz & Bogenschutz 1999; Saab 1999; Jones 2001). Spatial scales should be chosen based on the ecology of focal species, and indices of habitat preference and fitness consequences should be specifically tailored to each spatial scale.

Detailed empirical studies that measure habitat preferences and a suite of fitness consequences across multiple spatial scales are therefore required to assess more effectively the adaptive nature of habitat preferences. We examined breeding habitat preferences and several fitness components (nest success, seasonal reproductive success, clutch size, clutch mass, nestling mass and numbers of nesting attempts) of a migratory passerine bird across multiple ecologically relevant spatial scales: the landscape, territory and nest patch. Specifically, we examined whether the importance of different habitat features changes with respect to critical fitness consequences across scales, and can help to explain mismatches between habitat preferences and fitness consequences, aiding future approaches to determining habitat quality for management prescriptions.

Materials and methods

STUDY SYSTEM

Our focal species was the Brewer's sparrow *Spizella breweri* Cassin, 1856, a declining migratory passerine bird (Saab & Rich 1997; Rotenberry, Patten & Preston 1999; Knick *et al.* 2003) and common inhabitant of North American sagebrush steppe. Brewer's sparrows (sparrows hereafter) are locally abundant during the breeding season, enabling intensive and replicated data collection. Shrub steppe consists of both local and landscape-scale gradients in habitat structure (Wiens & Rotenberry 1981), facilitating habitat selection comparisons across spatial scales. Nest predation, the main cause of reproductive failure in the sparrow, varies with habitat structure (A. Chalfoun & T. Martin, unpublished). Food resources also vary spatially and temporally in shrub steppe (Rotenberry & Wiens 1998). Therefore the shrub steppe included potentially large ambient variation in habitat structure and two environmental factors (nest predation risk and food abundance) that are thought to exert strong influences on fitness and possibly operate at differing spatial scales.

Data collection took place during May–August 2003–05 within public and private lands in Carbon County, Montana, USA. The predominant overstorey plant species in the study area is big sagebrush *Artemisia tridentata* mixed with greasewood *Sarcobates vermiculatum* and rabbitbrush *Chrysothamnus* spp. The understorey is sparse because of the dry climate (approximately 20 cm of annual precipitation) and consists of various small forbs, native grasses and cacti. Sites were devoid of the exotic annual cheatgrass *Bromus tectorum*, which

has contributed to structural alteration of sagebrush habitats in other locations (Knick *et al.* 2003).

We established eight 25–30-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 sparrow territories (≤ 90 per site). Sites were selected to capture the full range of regional structural variation in sagebrush steppe, and differed in terms of their overall shrub cover, height and density. Areas containing extreme topography (e.g. cliffs) or attributes obviously inappropriate to be considered Brewer's sparrow habitat (e.g. large rocky patches or extremely sparse shrub cover) were avoided to meet the assumption that all portions of the study plots could be considered 'available' habitat for habitat selection analyses (Rotenberry, Patten & Preston 1999; Garshelis 2000). Each plot also contained microhabitat gradients according to local 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 cyanocephalus*, common grackle *Quiscalus quiscula*, brown-headed cowbird *Molothrus ater*, coyote *Canis latrans* and raccoon *Procyon lotor*.

HABITAT PREFERENCES

We used 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; Wheatley, Larsen & Boutin 2002) 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 & Hutto 2006). We assessed territory preferences within each study site by comparing the habitat structure within sparrow territories to that in surrounding unused but available habitat. Nest patch preferences were similarly assessed by comparing attributes of 5-m nest patches to unused but available patches.

FITNESS CONSEQUENCES

Nesting success was used as one fitness metric 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 also calculated the seasonal reproductive success (total offspring fledged per year) of pairs of birds within a subset of territories at each site during each year. These data were used as an additional metric of nesting success at

the landscape scale and, more specifically, to compare the reproductive success of different territories. Finally, we compared the habitat structure of successful vs. depredated nest patches within each site to assess habitat features associated with reduced predation risk.

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

TERRITORY DENSITY

Sparrow densities at the landscape scale were determined via territory mapping. Sites were flagged into 50 × 50-m grids, and each received 8–10 survey visits every 2–5 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 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 study site area to calculate territory density per hectare. 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 behavioural observations and systematic searches. Nests were monitored every other day until completion, following protocols in Martin & Geupel (1993). For each nest, we calculated nest initiation date and fate (successful, depredated or mortality as a result of 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 assumed depredated when nest contents (eggs or nestlings too young to have fledged) disappeared.

FOCAL PAIR MONITORING

Each year we randomly selected 5–10 focal pairs within each study site to monitor intensively throughout the entire breeding period. Brewer's sparrows are socially monogamous, multibrooded and will reneest following nest failure or success. We therefore tried to document the fates of every nesting attempt of these focal pairs in order to calculate season-long reproductive success. Focal pairs were dispersed throughout study plots to incorporate variation in 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 colour 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 found prior to the start of incubation and those we observed at least twice following the laying of the final egg. Sufficient sample sizes of clutch and nestling mass across all eight 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 as a result of egg water loss later in the incubation period (Martin *et al.* 2006). Clutch mass was recorded as the total mass of all eggs within a clutch. Nestling mass was only obtained from nests with known hatch dates and modal brood sizes (three or four) in order 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, Van Horne & Rotenberry 1987; Rotenberry & Wiens 1989). We therefore restricted our habitat analyses to four main shrub-layer attributes that are relevant to the ecology and behaviour of sparrows, and that characterize the majority of structural variation within shrub steppe systems: percentage shrub cover, shrub height, shrub density and density of potential nest shrubs. Shrub height, however, was related to shrub cover (Pearson correlation 0.48, $P < 0.001$, $n = 1321$) and showed identical preference/performance patterns across scales, so we only present data on shrub cover. Designation of potential nest shrubs was based on 2 years of prior study in which attributes (height, maximum crown width and percentage live crown) were measured and used to establish criteria for nest shrubs (A. Chalfoun & T. Martin, unpublished). Specifically, potentially suitable nest shrubs were between 20 and 175 cm in height and 30–250 cm in width, had

a minimum of 50% live crown, contained at least one semi-concealed 'niche' (with the potential to accommodate a sparrow nest) within the branch structure, and had crowns of a density that would not preclude entry by a parent bird.

Habitat structure was measured within 5-m radius vegetation plots (Martin *et al.* 1997). Plots were centred at nests, and at systematically located points throughout each site (approximately 1 ha⁻¹). Systematic plots were established a priori using site maps prior to bird arrivals, and so some fell within territories and some outside. Therefore mean habitat attributes could be compared (i) across sites, (ii) within vs. outside of territories and (iii) at nest sites vs. non-nest sites. Non-nest site plots were not always located within known territories; however, all fell within suitable (i.e. available) sparrow habitat. Nest site plots were not used in territory-level comparisons. 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 four quadrants using a tent stake and four attached 5-m lengths of rope arranged in the four cardinal directions from the plot's centre. Within each quadrant, we estimated visually the percentage shrub cover and counted the number of shrubs in four different size classes (0–20, 20–50, 50–100 and > 100 cm in height) and the number of potential 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 ≥ 20 cm in height were included in total shrub density estimates.

DATA ANALYSIS

Three sets of preference and fitness metrics were used to assess the habitat relationships of sparrows across the three spatial scales (Table 1). In order to determine whether density was a suitable index of habitat preference at the landscape scale, we initially explored the relationship between sparrow nesting chronology and density using general linear models (GLM). Site (landscape) means of Julian dates of first nest initiation served as the response variable, with density as a covariate and year as a fixed factor. We specifically predicted that sparrows should initiate first nests earlier within landscapes with higher densities.

Table 1. Indices used for quantification of habitat preferences and fitness consequences of Brewer's sparrows at each spatial scale

Scale	Habitat preference indices	Fitness indices
Landscape	Territory density and initiation dates of first nests in relation to site-level habitat characteristics	Daily nest survival probabilities, seasonal reproductive success, clutch size, clutch mass, nestling mass, numbers of nesting attempts per pair
Territory	Habitat attributes of territories vs. non-territory areas	Seasonal reproductive success
Nest patch	Habitat attributes of nest patches vs. systematic points	Individual nest fates

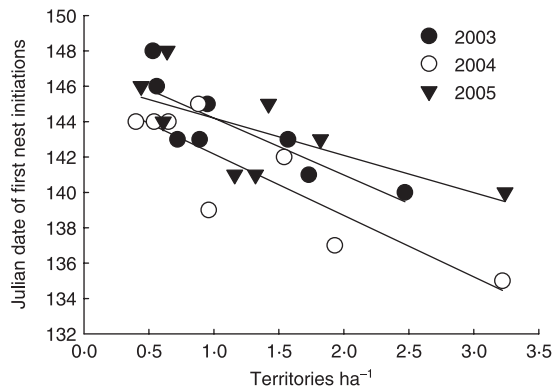


Fig. 1. Brewer's sparrow first nest initiations (mean Julian date) were consistently earlier within landscapes (sites) containing higher breeding densities (ANCOVA $F_{1,23} = 32.49$, $P < 0.001$) during 2003–05 (year $F_{2,23} = 0.45$, $P = 0.64$; year \times density $F_{2,23} = 0.80$, $P = 0.46$) in Carbon County, Montana, USA.

Landscape-level analyses of habitat preference and reproductive performance were conducted using GLM, with year as a factor in both models. Density (territories per hectare) was the dependent variable in habitat

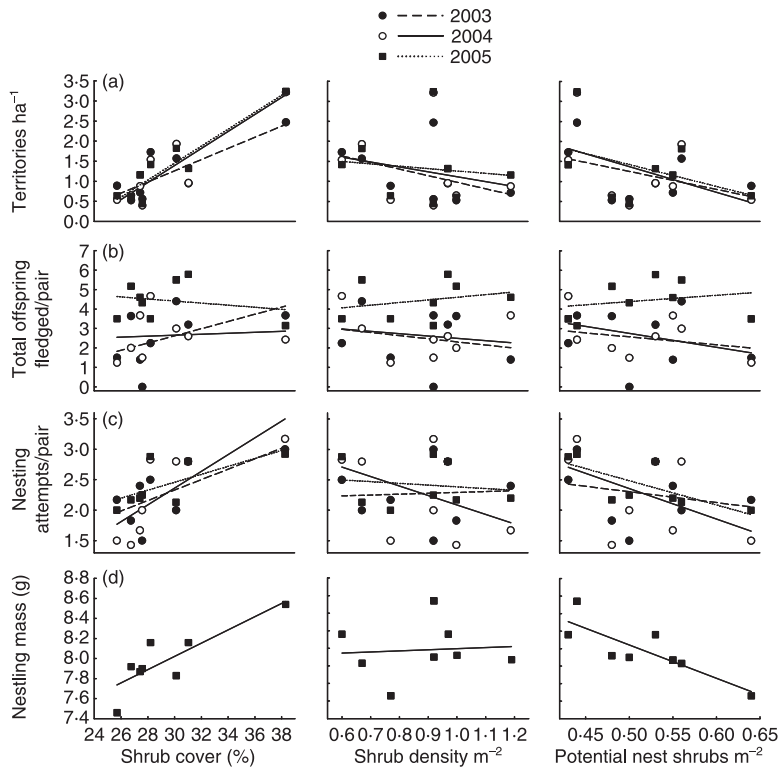


Fig. 2. Landscape-scale habitat preferences and associated fitness consequences of the Brewer's sparrow in relation to percentage shrub cover (left column), shrub density (centre) and potential nest shrub density (right). Sparrow densities increased with shrub cover ($F_{1,23} = 71.77$, $P < 0.001$) and lower shrub density ($F_{1,23} = 8.84$, $P = 0.008$) but not potential nest shrub density ($F_{1,23} = 0.006$, $P = 0.94$) (a), regardless of year ($F_{2,23} = 0.38$, $P = 0.69$). Seasonal reproductive success (b) was unrelated to any habitat variable (shrubs cover $F_{1,23} = 0.004$, $P = 0.95$; shrub density $F_{1,23} = 0.02$, $P = 0.88$; potential nest shrub density $F_{1,23} = 0.10$, $P = 0.76$), with a year effect ($F_{2,23} = 5.06$, $P = 0.02$). The number of nesting attempts per pair (c) increased with shrub cover ($F_{1,23} = 8.58$, $P = 0.009$) but was unrelated to shrub density ($F_{1,23} = 1.62$, $P = 0.22$) or potential nest shrub density ($F_{1,23} = 0.53$, $P = 0.48$), independent of year ($F_{2,23} = 0.54$, $P = 0.59$). Nestling mass in 2005 (d) increased with shrub cover ($F_7 = 7.24$, $P = 0.04$) but was negatively associated with potential nest shrub density ($F_7 = 7.55$, $P = 0.04$).

preference models, with percentage shrub cover, shrub density and potential nest shrub density 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 using binary logistic regression, where territory vs. non-territory areas was the dependent variable, the three shrub attributes were continuous factors, and year and site were included as categorical factors. Fitness consequences at the territory scale were examined using a GLM, with seasonal fecundity (total offspring fledged per season) as the dependent variable, habitat attributes as covariates and year and study site as factors.

At the nest patch scale, we used logistic regression to examine nest patch preference, with nest vs. systematic (non-use) patches as the dependent variable and the three habitat metrics as factors. Fitness consequences were also evaluated using logistic regression, with successful vs. depredated nests as the dependent variable. Year and study site were categorical factors in both models.

Comparisons of additional demographic components (clutch size, clutch mass, nestling mass and numbers of nesting attempts) were conducted only at the landscape scale. Sparrows can forage and obtain resources outside 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 GLM, with year as a fixed factor. Clutch and nestling mass data from 2005 were compared across study sites using GLM.

Results

LANDSCAPE SCALE

Initiation dates of first nests were consistently earlier at sites (i.e. landscapes) with higher breeding densities (Fig. 1). Thus initiation dates supported density as an index of preference at the landscape scale.

Sparrows settled at higher densities in landscapes with higher shrub cover and lower shrub density during all 3 years of the study (Fig. 2a). Sparrow densities were unrelated to potential nest shrub densities at the landscape scale. Thus sparrows preferred landscapes with more shrub cover but lower shrub density.

Daily nest survival probabilities were one reasonable index of reproductive fitness at the landscape scale because site-level nest survival probability and season-long reproductive success were consistently positively related (Fig. 3). Variation in daily nest survival across landscapes was not related to sparrow density ($F_{1,23} = 1.19$, $P = 0.29$), habitat features reflecting landscape preference (shrubs cover $F_{1,23} = 0.35$, $P = 0.56$; shrub

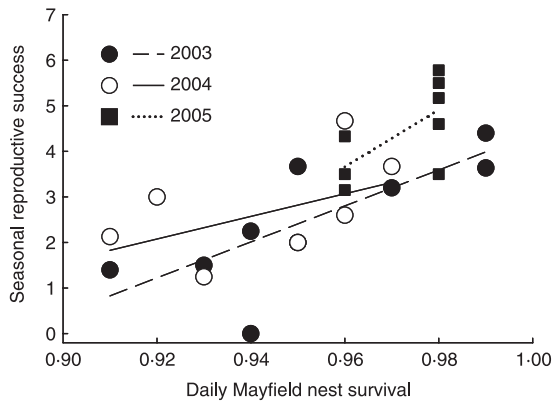


Fig. 3. Landscape-scale daily nest survival probabilities were positively related to seasonal reproductive success estimates (number of young fledged/pair) derived from a subset of colour-marked Brewer's sparrow pairs on each of eight sites in Carbon County, Montana, USA (daily nest survival $F_{1,23} = 7.54$, $P = 0.01$; year $F_{2,23} = 0.40$, $P = 0.68$).

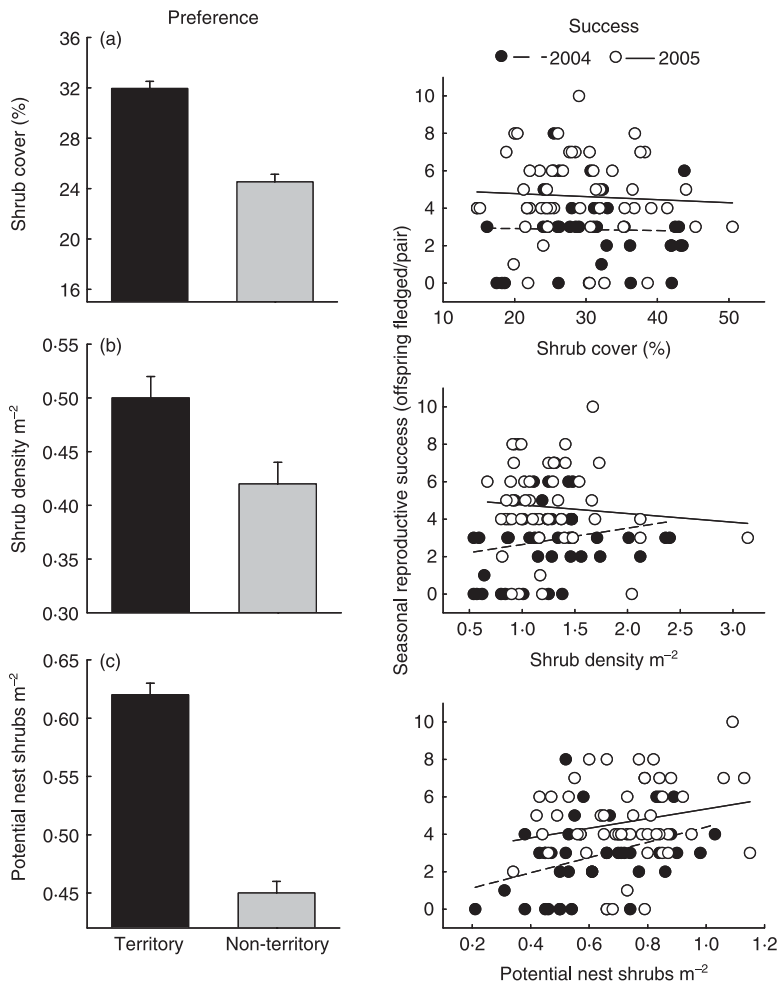


Fig. 4. Brewer's sparrows consistently (year; Wald = 0.21, d.f. = 2, $P = 0.90$) selected territories (left column) with greater shrub cover (a; Wald = 24.46, d.f. = 1, $P < 0.001$) and potential nest shrub density (c; Wald = 9.32, d.f. = 1, $P = 0.002$) but not shrub density (b; Wald = 2.84, d.f. = 1, $P = 0.09$) even after accounting for variation because of site (Wald = 27.23, d.f. = 7, $P < 0.001$). Seasonal reproductive success (total number of offspring produced per season; right column) was unrelated to shrub cover (a; $F_{1,96} = 0.30$, $P = 0.59$) or shrub density (b; $F_{1,96} = 0.16$, $P = 0.69$) but increased with potential nest shrub density (c; $F_{1,96} = 4.17$, $P = 0.04$) despite variation because of year ($F_{1,96} = 8.46$, $P = 0.005$).

density $F_{1,23} = 0.13$, $P = 0.72$) or habitat features unrelated to preference (potential nest shrub density $F_{1,23} = 0.14$, $P = 0.72$), although nest survival varied among years ($F_{1,23} = 3.72$, $P = 0.05$). Seasonal reproductive success was similarly unrelated to sparrow density ($F_{1,23} = 0.03$, $P = 0.87$) or any habitat features, although reproductive output was higher in 2005 (Fig. 2b). Thus both individual and season-long measures of nesting success at the landscape scale were not associated with habitat features that reflected sparrow preferences at this scale.

Average clutch size on each landscape varied among years ($F_{2,23} = 42.85$, $P < 0.001$) but not in relation to any of the habitat attributes measured (all P -values > 0.20). Clutch mass in 2005, the only year with sufficient data, was similarly unrelated to any of the landscape-scale habitat variables (overall model $F_7 = 0.45$, $P = 0.77$). Thus clutch size and mass were also not associated with habitat preference at the landscape scale.

The number of nesting attempts per pair (Fig. 2c) increased with shrub cover, one of the key habitat predictors of landscape preference, but not with other habitat features, during all study years. Nestling mass also increased with shrub cover, but decreased with potential nest shrub density (Fig. 2d). Thus landscape-scale habitat preferences were positively associated with fitness consequences based on numbers of nesting attempts per season and nestling size, but not daily nest survival, seasonal reproductive success, clutch size and clutch mass.

TERRITORY SCALE

Compared with habitat outside territories, sparrows consistently selected territories containing greater shrub cover and potential nest shrub density, but not total shrub density, even after accounting for variation across study sites (Fig. 4). Fitness consequences (seasonal reproductive success) matched the preference for territories with higher potential nest shrub density, but were not related to shrub cover or total shrub density, even when accounting for variation among years (Fig. 4).

NEST PATCH SCALE

Similar to the territory scale, both shrub density and potential nest shrub density were consistently greater in nest patches compared with systematic patches (Fig. 5). Shrubs cover did not differ between nest vs. systematic patches, even after accounting for variation as a result of study site (Fig. 5). Fitness consequences (nest success) again matched nest patch preferences based on potential nest shrub density, but not total shrub density or shrub cover, although nest success varied across study sites (Fig. 5).

Discussion

Brewer's sparrows showed clear breeding habitat preferences within each spatial scale that we examined,

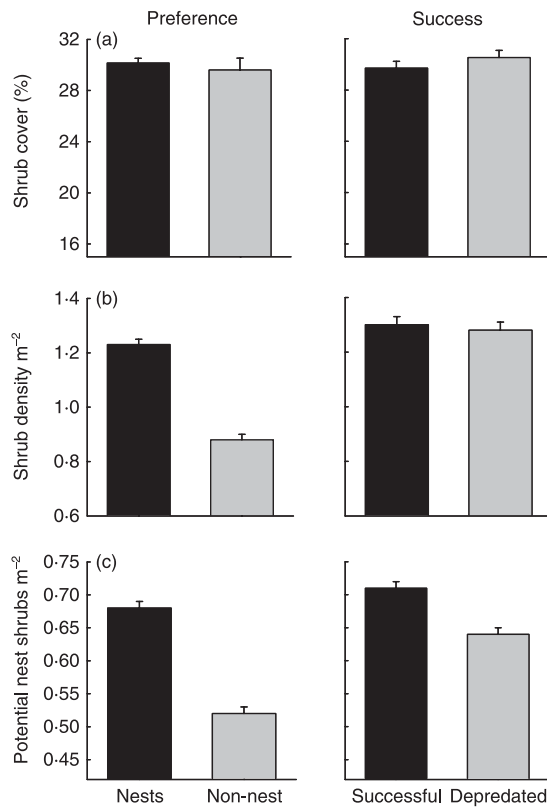


Fig. 5. Brewer's sparrow patch-scale habitat preferences (left column) and nest success (right column) in relation to three habitat variables during 2003–05 in Carbon County, Montana, USA. Sparrows consistently preferred patches with greater shrub density (b; Wald = 101.10, d.f. = 1, $P < 0.001$) and potential nest shrub density (c; Wald = 18.83, d.f. = 1, $P < 0.001$) but not shrub cover (a; Wald = 1.25, d.f. = 1, $P = 0.26$) (year; Wald = 0.57, d.f. = 2, $P = 0.75$) despite variation across sites (Wald = 31.87, d.f. = 7, $P < 0.001$). Nest success was not influenced by shrub cover (a; Wald = 0.30, d.f. = 1, $P = 0.58$) or density (b; Wald = 0.11, d.f. = 1, $P = 0.74$) but increased with potential nest shrub density (c; Wald = 6.29, d.f. = 1, $P = 0.01$) regardless of year (Wald = 5.18, d.f. = 2, $P = 0.08$) and variation because of site (Wald = 15.80, d.f. = 7, $P = 0.03$).

but the habitat features reflecting preferences differed across scales. At the largest scale, birds preferentially and consistently settled in landscapes with higher shrub cover. At the smallest scale, birds selected nest patches with greater total shrub density and potential nest shrub density. Choices at the intermediate (territory) scale included habitat attributes (shrubs cover and potential nest shrub density) that reflected preferences and fitness benefits at both larger (landscape) and smaller (nest patch) scales.

Fitness consequences did not match habitat preferences across scales when based on a single fitness component. At the landscape scale, seasonal reproductive success and its correlate, nest survival, were unrelated to preference: neither habitat features associated with density or chronology of settlement, nor density directly, were related to reproductive success. The apparent mismatch between landscape-scale habitat preferences and resulting fitness based on reproductive success

therefore raises the question of whether reproductive success accurately assays habitat quality at this scale (Petit & Petit 1996). The ideal free model of habitat selection (Fretwell & Lucas 1970) predicts that individuals should settle in the highest quality habitats first, but fitness declines as densities increase in preferred habitats, such that reproductive output can be similar across habitats of differing quality and population density. We found similar reproductive output across sites that differed in density and indices of preference, which may suggest the possible operation of such effects.

The possibility that sites with higher population density are of higher quality was supported by the finding that numbers of nesting attempts and nestling mass were greater on such sites. Both of these fitness metrics are sensitive to food abundance (Martin 1987; Nagy & Holmes 2004) and may suggest that birds are choosing landscapes with greater food availability. Yet advantages of food (to reproductive success) may be offset by nest predation or other factors such as intraspecific competition. As part of an overall habitat selection strategy, however, individuals that focus on habitat factors related to food resources at the landscape scale may derive considerable advantages in particular contexts. Maximizing re-nesting ability, for example, may be particularly critical when nest predation rates are high, but may also permit exceptional breeding performance during periods of relaxed nest predation (Holmes *et al.* 1992; Nagy & Holmes 2004; Grzybowski & Pease 2005). Settling in landscapes that maximize re-nesting potential should also be beneficial in systems where nest predation rates are highly temporally and spatially variable, as they are at our sites. Moreover, the ability of parents to produce larger offspring may increase aspects of offspring performance and hence future survival prospects and lifetime fitness (Roff 1992; Sinervo 1990; Lindström 1999). In shrub steppe habitats in particular, landscapes with high shrub cover and tall shrubs probably enhance offspring quality via greater overall productivity of the shrub layer and associated insect prey (Rotenberry & Wiens 1998; Morrison & Bolger 2002). Such results further suggest that landscape-scale habitat preferences may reflect selection on offspring quality in addition to quantity. Although not assessed during our study, such preferences may also reflect selection on adult survival and lifetime fitness, via effects of food availability on energy budgets and body condition (Davis, Nager & Furness 2005).

The mismatches that we have documented between landscape-scale habitat preferences and nesting success are unlikely to be methodological artefacts. Controversy has arisen about whether aggregate estimates of nest survival (Mayfield 1975) represent actual seasonal fecundity (Jones *et al.* 2005). However, in our study, Mayfield daily nest survival probabilities were significantly positively correlated with seasonal fecundity estimates during all 3 years of the study. Yet neither

of these was correlated with landscape preferences. Landscape preferences indicated by sparrow densities were further corroborated by earlier nest initiation. Moreover, occupancy patterns remained consistent among sites across years, a pattern that further suggests habitat preferences. Ultimately, while these preferences were not related to seasonal nesting success, they were associated with other enhanced fitness components, such as rearing larger offspring, and reneating more quickly and more often.

Concordance between habitat preferences and nesting success was particularly evident at the nest patch scale. Successful nest patches clearly contained higher densities of shrubs that were suitable for nesting. We have examined experimentally (A. Chalfoun & T. Martin, unpublished) the relationship between potential nest shrub density and other habitat structure components on nest predation rates. Potential nest site density also corresponded with higher seasonal fecundity of sparrow pairs at the territory scale, further emphasizing the importance of this largely unrecognized and unappreciated habitat attribute (but see Martin & Roper 1988; Martin 1993).

Our results should be particularly useful for assessing habitat attributes that reflect habitat quality at differing spatial scales to allow effective management in preventing further declines of the focal species. Shrub steppe habitats have experienced widespread destruction and alteration, and the Brewer's sparrow is one of the obligate shrub steppe bird species showing marked population declines throughout its range (Rotenberry, Patten & Preston 1999; Knick *et al.* 2003). We suggest land managers focus on maintaining large tracts of tall, high-cover, sagebrush habitat, given the extent to which such attributes appear to form an important basis for habitat preferences. While nest predation rates may sometimes be higher in such landscapes, the benefits accrued through higher resource availability may help to counterbalance such losses and permit exceptional reproductive output during lower nest predation years. Moreover, taller shrub cover areas support larger numbers of breeding pairs. Maintaining at least some areas within these landscapes that contain high densities of potential nest substrates (A. Chalfoun & T. Martin, unpublished) may also be critical to maximizing reproductive success. Managers must pay particular attention to the eradication of cheatgrass (and other non-native annuals) in sagebrush systems, which increases fire frequency and intensity and so limits the availability of taller, high-cover shrub patches (Rotenberry 1998; Rotenberry, Patten & Preston 1999; Knick *et al.* 2003).

In conclusion, our study elucidates several important concepts applicable to the study of any animal species in the wild. First, habitat preferences are scale-dependent (Orians & Wittenberger 1991; Luck 2002). Apparent mismatches between habitat preferences and fitness outcomes can occur when preferences and resulting fitness consequences 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 food availability and refugia from predators) may vary in importance across spatial scales and may manifest in different (but potentially equally important) ways in terms of fitness consequences. Our study emphasizes the utility of integrating multiple spatial scales and resulting fitness components into studies of habitat selection towards understanding overall habitat selection strategies. Ideally, for any species of concern, researchers should attempt to identify the habitat attributes that affect fitness outcomes at each relevant spatial scale on which to base management prescriptions. Understanding which habitat characteristics are important across different, ecologically relevant, scales will help elucidate the factors truly underlying habitat choices, and will lead to improved assessments of habitat quality for the successful maintenance of animal populations.

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References

- Allen, T.F.H. & Starr, T.B. (1982) *Hierarchy: Perspectives for Ecological Diversity*. University of Chicago Press, Chicago, IL.
- Arcese, P. & Smith, J.N.M. (1988) Effects of population density and supplemental food on reproduction in song sparrows. *Journal of Animal Ecology*, **57**, 119–136.
- Battin, J. (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, **18**, 1482–1491.
- Bock, C.E. & Jones, Z.F. (2004) Avian habitat evaluation: should counting birds count? *Frontiers in Ecology and the Environment*, **2**, 403–410.
- Bolton, M., Monaghan, P. & Houston, D.C. (1993) Proximate determination of clutch size in lesser black-backed gulls: the roles of food supply and body condition. *Canadian Journal of Zoology*, **71**, 273–279.
- Chalfoun, A.D., Thompson, F.R. III & Ratnaswamy, M.J. (2002) Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology*, **16**, 306–318.
- Clark, C.W. & Mangel, M. (2000) *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford University Press, Oxford, UK.
- Clark, R.G. & Shuttler, D. (1999) Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology*, **80**, 272–287.

- Clark, W.R., Schmitz, R.A. & Bogenschutz, T.R. (1999) Site selection and nest success of ring-necked pheasants as a function of location in Iowa landscapes. *Journal of Wildlife Management*, **63**, 976–989.
- Cody, M.L. (1974) *Competition and the Structure of Bird Communities*. Princeton University Press, Princeton, NJ.
- Crowder, L.B. & Cooper, W.E. (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, **63**, 1802–1813.
- Davis, S.E., Nager, R.G. & Furness, R.W. (2005) Food availability affects adult survival as well as breeding success of parasitic Jaegers. *Ecology*, **86**, 1047–1056.
- Eggers, S., Griesser, M., Anderson, T. & Ekman, J. (2005) Nest predation and habitat change interact to influence Siberian jay numbers. *Oikos*, **111**, 150–158.
- Fretwell, S.D. & Lucas, H.L. Jr (1970) On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, **19**, 16–36.
- Garshelis, D.L. (2000) Delusions in habitat evaluation: measuring use, selection and importance. *Research Techniques in Animal Ecology: Controversies and Consequences* (eds L. Boitani & T. Fuller), pp. 111–161. Columbia University Press, New York, NY.
- Grzybowski, J.A. & Pease, C.M. (2005) Renesting determines seasonal fecundity in songbirds. What do we know? What should we assume? *Auk*, **122**, 280–291.
- Heithaus, M.R. & Dill, L.M. (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, **83**, 480–491.
- Hildén, O. (1965) Habitat selection in birds. *Annales Zoologici Fennici*, **2**, 53–75.
- Holmes, R.T., Sherry, T.W., Marra, P.P. & Petit, K.E. (1992) Multiple brooding and productivity of a neotropical migrant, the black-throated blue warbler (*Dendroica caerulescens*) in an unfragmented temperate forest. *Auk*, **109**, 321–333.
- Houston, A.I. & McNamara, J.M. (1999) *Models of Adaptive Behavior: An Approach Based on State*. Cambridge University Press, Cambridge, UK.
- Hutto, R.L. (1985) Habitat selection by non-breeding, migratory land birds. *Habitat Selection in Birds* (ed. M. L. Cody), pp. 455–476. Academic Press, New York, NY.
- Jaenike, J. & Holt, R.D. (1991) Genetic variation for habitat preference: evidence and explanations. *American Naturalist*, **137**, S67–S90.
- Jones, J. (2001) Habitat selection studies in avian ecology: a critical review. *Auk*, **118**, 557–562.
- Jones, J., Doran, P.J., Nagy, L.R. & Holmes, R.T. (2005) Relationship between Mayfield nest-survival estimates and seasonal fecundity: a cautionary note. *Auk*, **122**, 306–312.
- Knick, S.T., Dobkin, D.S., Rotenberry, J.T., Schroeder, M.A., Vander Haegen, W.M. & van Riper, C. III (2003) Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor*, **105**, 611–634.
- Kokko, H. & Sutherland, W.J. (2001) Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evolutionary Ecology Research*, **3**, 537–551.
- Kolbe, J.J. & Janzen, F.J. (2002) Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology*, **83**, 269–281.
- Leber, K.M. (1985) The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology*, **66**, 1951–1964.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.
- Lindström, J. (1999) Early development and fitness in birds and mammals. *Trends in Ecology and Evolution*, **14**, 343–348.
- Lloyd, P., Martin, T.E., Redmond, R.L., Langner, U. & Hart, M.M. (2005) Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. *Ecological Applications*, **15**, 1504–1514.
- Luck, G.W. (2002) The habitat requirements of the rufous treecreeper (*Climacteris rufa*). I. Preferential habitat use demonstrated at multiple spatial scales. *Biological Conservation*, **105**, 383–394.
- MacArthur, R.H., Recher, H. & Cody, M. (1966) On the relation between habitat selection and species diversity. *American Naturalist*, **100**, 319–332.
- Martin, T.E. (1987) Food as a limit of breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics*, **18**, 453–487.
- Martin, T.E. (1988) Habitat and area effects on forest bird assemblages: is nest predation an influence? *Ecology*, **69**, 74–84.
- Martin, T.E. (1993) Nest predation and nest sites. *Bioscience*, **43**, 523–532.
- Martin, T.E. (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, **65**, 101–127.
- Martin, T.E. (1998) Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology*, **79**, 656–670.
- Martin, T.E. & Geupel, G.R. (1993) Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology*, **64**, 507–519.
- Martin, T.E. & Roper, J.J. (1988) Nest predation and nest site selection in a western population of the hermit thrush. *Condor*, **90**, 51–57.
- Martin, T.E., Bassar, R.D., Bassar, S.K., Fontaine, J.J., Mathewson, H.A., Niklison, A.M. & Chalfoun, A.D. (2006) Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. *Evolution*, **60**, 390–398.
- Martin, T.E., Paine, C., Conway, C.J., Hochachka, W.M., Allen, P. & Jenkins, J. (1997) *BBIRD Field Protocol*. University of Montana, Missoula, Montana.
- Mayfield, H.F. (1975) Suggestions for calculating nest success. *Wilson Bulletin*, **87**, 456–466.
- Mayhew, P.J. (1997) Adaptive patterns of host-plant selection by phytophagous insects. *Oikos*, **79**, 417–428.
- Menge, B.A. & Olson, A.M. (1990) Role of scale and environmental factors in the regulation of community structure. *Trends in Ecology and Evolution*, **5**, 52–57.
- Misenhelter, M.D. & Rotenberry, J.T. (2000) Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology*, **81**, 2892–2901.
- Morrison, S.A. & Bolger, D.T. (2002) Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. *Oecologia*, **133**, 315–324.
- Nagy, L.R. & Holmes, R.T. (2004) Factors influencing fecundity in migratory songbirds: is nest predation the most important? *Journal of Avian Biology*, **35**, 487–491.
- Orians, G.H. & Wittenberger, J.F. (1991) Spatial and temporal scales in habitat selection. *American Naturalist*, **137**, S29–S49.
- Petit, L.J. & Petit, D.R. (1996) Factors governing habitat selection by prothonotary warblers: field tests of the Fretwell–Lucas models. *Ecological Monographs*, **66**, 367–387.
- Pribil, S. & Picman, J. (1997) The importance of using the proper methodology and spatial scale in the study of habitat selection by birds. *Canadian Journal of Zoology*, **75**, 1835–1844.
- Robertson, B.A. & Hutto, R.L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, **87**, 1075–1085.
- Roff, D.E. (1992) *Evolution of Life Histories*. Chapman & Hall, New York, NY.
- Rotenberry, J.T. (1998) Avian conservation research needs in western shrublands: exotic invaders and the alteration of ecosystem processes. *Avian Conservation: Research and Management* (eds J.M. Marzluff & R. Sallabanks), pp. 261–272. Island Press, Covelo, CA.

- Rotenberry, J.T. & Wiens, J.A. (1989) Reproductive biology of shrubsteppe passerine birds: geographical and temporal variation in clutch size, brood size, and fledging success. *Condor*, **91**, 1–14.
- Rotenberry, J.T. & Wiens, J.A. (1991) Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. *Ecology*, **72**, 1325–1335.
- Rotenberry, J.T. & Wiens, J.A. (1998) Foraging patch selection by shrubsteppe sparrows. *Ecology*, **79**, 1160–1173.
- Rotenberry, J.T., Patten, M.A. & Preston, K.L. (1999) Brewer's sparrow (*Spizella breweri*). *The Birds of North America No. 390* (eds A. Poole & F. Gill). The Birds of North America Inc., Philadelphia, PA. DOI: 10.2173/bna.390.
- Saab, V. (1999) Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications*, **9**, 135–151.
- Saab, V.A. & Rich, T.D. (1997) *Large-Scale Conservation Assessment for Neotropical Migratory Land Birds in the Interior Columbia River Basin*. General Technical Report PNW-GTR-399. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Salamolard, M., Butet, A., Leroux, A. & Bretagnolle, V. (2000) Responses of an avian predator to variations in prey density at a temperate latitude. *Ecology*, **81**, 2428–2441.
- Sinervo, B. (1990) The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effect on offspring performance. *Evolution*, **44**, 279–294.
- Söderström, B. (2001) Seasonal change in red-backed shrike *Lanius collurio* territory quality: the role of nest predation. *Ibis*, **143**, 561–571.
- Tewksbury, J.J., Garner, L., Garner, S., Lloyd, J.D., Saab, V. & Martin, T.E. (2006) Alternative hypotheses of landscape influence on nest predation and brood parasitism in fragmented ecosystems. *Ecology*, **87**, 759–768.
- Thompson, J.N. (1988) Evolutionary ecology of the relationship between oviposition preference and performance in offspring of phytophagous insects. *Entomologia Experimentalis et Applicata*, **47**, 3–14.
- Valladares, G. & Lawton, J.H. (1991) Host-plant selection in the holly leaf-minor: does mother know best? *Journal of Animal Ecology*, **60**, 227–240.
- Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893–901.
- Weatherhead, P.J. & Blouin-Demers, G. (2004) Understanding avian nest predation: why ornithologists should study snakes. *Journal of Avian Biology*, **35**, 185–190.
- Wheatley, M., Larsen, K.W. & Boutin, S. (2002) Does density reflect habitat quality for North American red squirrels during a spruce-cone failure? *Journal of Mammalogy*, **83**, 716–727.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.
- Wiens, J.A. & Rotenberry, J.T. (1981) Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs*, **51**, 21–41.
- Wiens, J.A., Van Horne, B. & Rotenberry, J.T. (1987) Temporal and spatial variations in the behavior of shrubsteppe birds. *Oecologia*, **73**, 60–70.
- Willson, M.F. (1974) Avian community organization and habitat structure. *Ecology*, **55**, 1017–1029.
- Zanette, L., Clinchy, M. & Smith, J.N.M. (2006) Food and predators affect egg production in song sparrows. *Ecology*, **8**, 2459–2467.

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