Vegetation influences patch occupancy but not settlement and dispersal decisions in a declining migratory songbird

M.L. Harrison and D.J. Green

Abstract: Territorial clustering within larger, continuous patches of seemingly appropriate habitat could indicate that a species has additional, finer scale habitat requirements. Studying fine-scale (e.g., territory-level) habitat selection using methods that elucidate individual preferences may allow us to identify resources that influence species distributions. We examined breeding territory selection in the sagebrush Brewer's Sparrow (*Spizella breweri* Cassin, 1856) at the northern extent of its range to test for influences on fine-scale habitat selection. We used an information–theoretic approach to evaluate models relating a suite of vegetation characteristics to breeding habitat selection. We employed two methods: (1) assessment of patch occupancy at a territory scale and (2) examination of individual decisions relating to settlement and dispersal. We found that patch occupancy was most consistently predicted by models that included the cover of big sagebrush (*Artemisia tridentata* Nutt.) with the greatest likelihood of occupancy at 20%–25% cover. However, assessment of settlement and dispersal decisions did not identify additional fine-scale preferences for other vegetation characteristics. Vegetation cover also did not influence breeding success, indicating that within the vegetation range found in Brewer's Sparrow territory clusters, there is little benefit in basing individual settlement or dispersal decisions on vegetation cover.

Résumé : Le regroupement d'un territoire avec des taches d'habitat en apparence appropriées, mais plus grandes et continues, pourrait indiquer qu'une espèce possède des besoins additionnels d'habitat à une échelle plus fine. L'étude de la sélection d'habitat à échelle fine (par ex., au niveau du territoire) en utilisant des méthodes qui mettent en lumière les préférences individuelles permet peut-être d'identifier les ressources qui influencent la répartition des espèces. Nous examinons la sélection du territoire de reproduction chez le bruant de Brewer des armoises (*Spizella breweri* Cassin, 1856) à la limite boréale de son aire de répartition afin de vérifier les influences sur la sélection d'habitat à échelle fine. Nous utilisons une approche basée sur la théorie de l'information afin d'évaluer des modèles qui relient une série de caractéristiques de la végétation à la sélection de l'habitat de reproduction. Nous employons deux méthodes, (1) une évaluation de l'occupation des taches à l'échelle du territoire et (2) un examen des décisions individuelles concernant l'établissement et la dispersion. Ce sont les modèles qui incluent la couverture de la grande armoise (*Artemisia tridentata* Nutt.) qui prédisent l'occupation des taches de la façon la plus constante; la plus grande probabilité d'occupation se situe à une couverture de 20 % – 25 %. L'évaluation des décisions d'établissement et de dispersion n'a pas, cependant, identifié de préférences additionnelles à échelle fine pour d'autres caractéristiques de la végétation. De plus, la couverture végétale n'influence pas le succès de la reproduction, ce qui indique que, dans la gamme de végétation retrouvée dans les groupements de territoires des bruants de Brewer, il y a peu d'avantages à baser les décisions individuelles concernant l'établissement ou la dispersion sur la couverture végétale.

[Traduit par la Rédaction]

Introduction

In heterogeneous environments, animals congregate within suitable habitat patches rather than distributing themselves evenly across their environment (Fretwell and Lucas 1970). The patches that individuals choose and the densities at which they settle have important implications for individual fitness and thus the population dynamics and long-term persistence of the species (Misenhelter and Rotenberry 2000; Lambrechts et al. 2004; Gunnarsson et al. 2006; Winter et al. 2005). It is therefore important to study the cues used in habitat selection to define preferred habitat characteristics and to predict how individuals will settle across and be affected by changing landscapes.

Habitat selection has been well studied in avian ecology (reviewed in Jones 2001 and Johnson 2007). However, research that attempts to identify key habitats often examines habitat selection at a very coarse scale. Landscape-scale studies are important for characterizing broad habitat associations, and are a vital first step in identifying critical habitat for a species; however, they may overlook finer scale patterns of habitat selection. In addition, many habitat selection studies use potentially unreliable measures, such as relative density, as metrics for selection (Van Horne 1983; Vickery et al. 1992; Battin 2004; Bock and Jones 2004). These measures can generate misleading results because numerous

Received 22 July 2009. Accepted 19 October 2009. Published on the NRC Research Press Web site at cjz.nrc.ca on 20 January 2010.

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doi:10.1139/Z09-125

factors that are not related to differences in inherent patch quality (reflected in productivity) can result in density differences among patches (Van Horne 1983; Vickery et al. 1992; Battin 2004; Bock and Jones 2004).

Tracking individual decision-making is a way to gather direct information about habitat preference and is a potentially more reliable alternative to assessing habitat preference than using measures of relative density. Several studies have demonstrated the value of using direct measures of preference as indicators of habitat selection in birds, successfully identifying preferred habitat characteristics for their species (Lanyon and Thompson 1986; Remeš 2003; Sergio and Newton 2003; Arlt and Pärt 2007). In migratory birds, the order of settlement of individuals arriving at a habitat patch is often used to elucidate preferred habitat characteristics, because the first territory settled should be selected for its possession of the optimal characteristics to support breeding (Krebs 1971). Because population-level processes are often an emergent property of individual decision rules, the study of individual habitat selection decisions may allow us to develop an understanding of the mechanisms that drive the larger scale distributions of species (Safran 2004).

Territorial species that choose to settle in dense clusters within habitat patches, rather than spreading out more evenly and predictably in accordance with resource distributions, can provide interesting models for the examination of factors that explain fine-scale variation in habitat selection (Perry and Andersen 2003; Tarof and Ratcliffe 2004; Mills et al. 2006; Roth and Islam 2007). This “territory clustering” may indicate the presence of additional factors in habitat selection beyond the general vegetation-class-based parameters traditionally used by land managers to identify suitable habitat. Such clustering could be explained by previously unidentified habitat features that are being selected for at a fine scale, or by nonhabitat factors such as conspecific attraction. Understanding the mechanisms behind territory clustering will allow us to determine whether seemingly appropriate but not evenly distributed habitat patches are truly suitable for a species and worthy of conservation, or whether the smaller areas where individuals cluster possess some additional critical factor that increases their suitability.

The sagebrush Brewer’s Sparrow (*Spizella breweri* Cassin, 1856) has been described as a loosely colonial species at the northern extent of its breeding range (Cannings et al. 1987; Sarell and McGuiness 1996), and recent surveys lend empirical support to those observations (Hobbs 2001; Fig. 1). Compelling evidence has been found for conspecific attraction as a driver of individual habitat selection in the northern population of this species (Harrison et al. 2009); however, selection for habitat characteristics at a fine scale may also play a role in territory selection and clustering. The purpose of this study was to answer two questions: (1) do fine-scale vegetation characteristics explain the territory clustering observed in Brewer’s Sparrows at the northern extent of their range and (2) do the vegetation characteristics used in fine-scale habitat selection explain subsequent reproductive success? If fine-scale habitat selection based on vegetation characteristics explains the territory clustering observed in Brewer’s Sparrows, we expected that while patch occupancy would be predicted by broad-scale habitat requirements, settlement order and dispersal decisions of individuals would be predicted by additional finer scale habitat preferences. We also predicted that the reproductive success of an individual would be correlated with any fine-scale habitat preferences. We tested these predictions by comparing how vegetation predicted occupancy patterns (from point-count surveys), individual territory settlement, fidelity and dispersal decisions, and subsequent reproductive success of Brewer’s Sparrows breeding at the northern extent of their range.

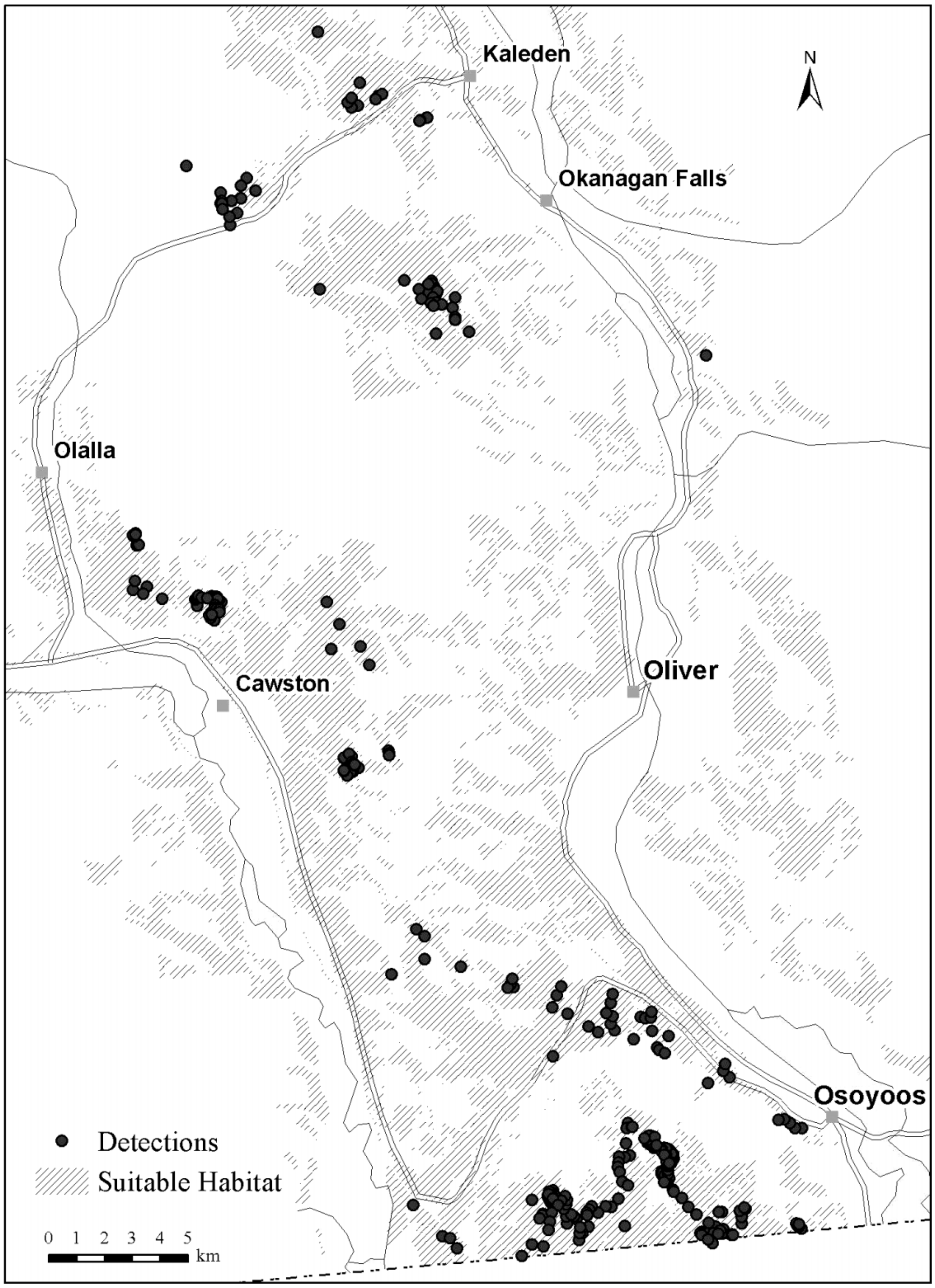
Materials and methods

Focal species and study area

The sagebrush Brewer’s Sparrow is a neotropical migrant that inhabits shrub–steppe habitats during both wintering and breeding periods (Paige and Ritter 1999; Rotenberry et al. 1999). Breeding Bird Survey data show that the species has been declining across its entire range at a mean rate of 2.1% per year (Sauer et al. 2008). Because of this decline and continued conversion of sagebrush habitats for agricultural and residential development (Knick et al. 2003), the species is now been identified as vulnerable or at-risk within both the United States and Canada. Within the South Okanagan region of British Columbia, several Brewer’s Sparrow habitat selection studies have been conducted (Harvey 1992; Sarell and McGuiness 1996; Paczek 2002). Studies at a coarse scale (multiple hectare site level) have suggested that the sparrows are more abundant at sites with intermediate (10%–30%) cover of shrubs (Harvey 1992; Sarell and McGuiness 1996). Paczek (2002) also examined factors that influence sparrow density at a fine scale (100 m point-count station), and argued that sparrow densities were positively correlated with big sagebrush (*Artemisia tridenta* Nutt.; subsequently referred to as big sage), two species of robust forbs (parsnip-flowered buckwheat (*Eriogonum heracleoides* Nutt.) and silky lupine (*Lupinus sericeus* Pursh)), and junegrass (*Koeleria macrantha* (Ledeb.) J.A. Schultes). The Paczek study was unique in its finding that Brewer’s Sparrows select habitats based on the presence of specific forb and grass species (Table 1). Given the potential importance of such a novel finding in improving habitat models and explaining clustering in the species, it is important to evaluate the strength of support for that finding by evaluating fine-scale Brewer’s Sparrow habitat selection in the South Okanagan over multiple years and using multiple methods.

We studied fine-scale (territory-level) habitat selection decisions in the South Okanagan region of British Columbia (Fig. 1) between 2003 and 2008. Patch occupancy at a territory scale was evaluated using point counts within three regions, on private land holdings near the town of Keremeos and in the Okanagan Grasslands and White Lake Grasslands Protected Areas. A “patch” was sampled using a 100 m radius point count. Monitoring of individual settlement, breeding success, and dispersal was investigated at one site within White Lakes Grassland Protected Area (White Lake, WL) and at two sites within Okanagan Grasslands Protected Area (International Grasslands, ING; Kilpoola, KIL). Dominant vegetation on all sites is big sage with a mixed understory of native and non-native grass species and a sparse forb layer dominated by lupine and parsnip-flowered buckwheat.

Fig. 1. Brewer's Sparrow (*Spizella breweri*) detections from Ministry of Environment surveys within habitat classed as suitable for the species in the South Okanagan region of British Columbia (UTMs: 10N 714150 5483106 to 11N 326455 5431123). Terrestrial Ecosystem Mapping (TEM) provided the basis for the suitability classification, with relative cover of dominant vegetation classes as the primary classification factor (Warman et al. 1998).



All study plots were located within larger expanses of unconverted sagebrush.

Patch occupancy

Data on patch occupancy for Brewer's Sparrows came from point-count observations at 48 stations, conducted twice per year during the 2003, 2004, and 2005 breeding seasons. All observations were conducted within 3 h of sunrise, the order in which plots were visited was randomized, and the observations were made by the same individual throughout the season. Point-count observations lasted 15 min during which the number and locations of all birds within 100 m of the plot centre were recorded. No Brewer's Sparrows were observed at the majority of the plots (i.e., 76% of plots were unoccupied) and occupied plots rarely contained more than one singing male. We therefore classified plots as either occupied or unoccupied in any year for analyses.

Table 1. A summary of studies that have examined habitat associations of Brewer's Sparrows (*Spizella breweri*) across the breeding range of the species.

		Shrubs				
Location	Basis of habitat associations	Cover or density	Size	Grasses (cover)	Forbs (cover)	Reference
New Mexico	Occupancy	15%–45% shrub cover	20–60 cm tall	10%–40% cover		Larson and Bock 1986
Nevada, Oregon	Relative abundance	12%–49% sage cover				Olson 1974
	Occupancy	23%–37% shrub cover				Wiens et al. 1987
	Relative abundance	17%–21% shrub cover	35–52 cm tall	(–) Crested wheat grass		McAdoo et al. 1989
	Occupancy			(–) All grass		Rotenberry and Wiens 1980
Washington	Relative abundance	3%–19% shrub cover				Dobler et al. 1996
Montana, Wyoming	Relative abundance	53% shrub cover				Walcheck 1970
	Relative abundance	3425 shrubs/ha				Bock and Bock 1987
	Occupancy	(+) Shrub cover or density				Chalfoun and Martin 2007
	Relative abundance and timing of settlement	(+) Shrub cover and density of potential nest shrubs				
British Columbia	Relative abundance	10%–30% shrub cover				Sarell and McGuiness 1996
	Relative abundance	(+) Big sage cover		(+) Junegrass	(+) Lupine and buckwheat	Paczek 2002

Note: We distinguish between studies that based associations on the occupancy (presence or absence) and relative abundance of sparrows across sites. Plus and minus indicate the direction of habitat associations. Ranges in vegetation variables are given when the associations were highest within an intermediate range.

Banding and monitoring of reproductive success

We monitored breeding pairs on 10 ha plots at three sites (WL, KIL, and ING) between 2007 and 2008. Territorial birds were captured in mist nets with the aid of call playbacks, and marked with a metal Canadian Wildlife Service (CWS) band and three coloured leg bands. In 2006, extensive banding occurred at the three sites in preparation for this study, but nesting success was not closely monitored. Over 80% of the males within the research plots were banded in 2006 and 2007. In 2008, we focused primarily on the activities of returning, previously banded birds. Sites were monitored every 2–4 days throughout the breeding season to resight banded birds, search for nests, and monitor nesting success. Nests were located through systematic searches of known territories or behavioural observations. They were then monitored every 3–4 days to track development and determine fledge rates. Where observational data on a nest was incomplete, dates for clutch initiation, hatching, and fledging were calculated based on an assumed incubation period of 11 days, and nestling period of 9 days (Rotenberry and Wiens 1991). In the absence of observations of fledglings, nestlings were assumed to have fledged if the nest was empty no fewer than 8 days after hatching, there were no signs of predation, and parents could be observed carrying food or heard making contact calls with mates or fledglings. Seasonal reproductive success (i.e., whether or not an individual successfully fledged one or more young) was assessed for each male territory holder based on the observed outcomes of all identified nests.

Settlement monitoring

The precise order in which territories were settled by males was monitored at all three sites in 2007. We visited each site every 2 days beginning the first week of April 2007, to resight previously banded individuals, and detect and band new arrivals. To track settlement order, we recorded the first location of each bird that was defending an area through song. Unmarked individuals were drawn in with call playbacks, and then captured and banded using standard procedures (see above). All individuals were banded within two site visits (4 days) of commencing territorial behaviour. We then recorded the locations of each individual using a GPS daily from 14 April to 1 July, and calculated a territory centre based on the mean of each bird's locations. No males appeared to be displaced from their original settlement locations by later arriving individuals. The majority of the birds remained in the same territory throughout the season, so a single mean represented an accurate territory centre. Four birds (out of 75) moved to a new territory following an initial reproductive failure. For those birds, two territory centres were calculated, and the centre of the first territory was used in analyses.

Territory fidelity

We used the daily resighting locations to calculate the territory centre for all breeding birds at the three sites between 2006 and 2008. Birds that returned in 2007 or 2008 were considered to have moved (dispersed) if the centre of their subsequent territory was >50 m (the mean diameter of a Brewer's Sparrow territory on our study plots) from the centre of their previous territory. They were considered to have stayed (exhibited fidelity) if they resettled within 50 m of their previous territory.

Vegetation assessment

Once breeding was complete, we conducted vegetation sampling within each of the territories in our main study plots (ING, WL, and KIL), and on each point-count station. Vegetation sampling was conducted following breeding rather than at the time of settlement to avoid disturbing the birds during settlement and nesting, and potentially influencing their territory selection decisions or reproductive success. We established two 50 m transects intersecting the centre of the territory or the centre of the point-count station. The first transect was established at a random bearing, and the second was established at a 90° angle from the first. The intersection of the two 50 m transects created four 25 m transects at right angles from each other. The line-intercept method (Brower et al. 1989) was used to measure percent linear cover of sagebrush and other shrubs. We also recorded the height of each shrub. At the 5, 15, and 25 m points along each of four the transects, we estimated the percent cover of individual forb and grass species using standard 20 cm × 50 cm Daubenmire plots (Daubenmire 1959).

Statistical analysis

We developed a set of candidate models that related a suite of vegetation characteristics to the occupancy of Brewer's Sparrows at point-count plots, and to the order of territory establishment (i.e., settlement order), territory fidelity, and reproductive success of birds within the three 10 ha plots. We considered four different categories of vegetation cover, each of which contained multiple variables (Table 2). Where previous findings indicated selection for intermediate measures, we included both linear and squared terms (Petersen and Best 1985; Wiens and Rotenberry 1985; Larson and Bock 1986; Howe et al. 1996; Sarell and McGuiness 1996; Mahony 2003). Big sage was highlighted in the shrub-cover term because sage is the most dominant shrub in Brewer's Sparrow habitats, is used almost exclusively for nesting, and has been the site of most foraging observations in the species (Rotenberry et al. 1999). The robust forbs grouping included species found by Paczek (2002) to influence Brewer's Sparrow density plus other species of similar growth form. Robust forbs have been associated with high abundance of invertebrates used by Brewer's Sparrows to feed nestling (P.G. Krannitz, unpublished data), so were expected to be associated with both habitat choice and success. Grass cover was split into two variables (native and nonnative species), to allow for detection of their potentially contrasting effects. Grasses are the primary nest substrate for Brewer's Sparrows (Rotenberry et al. 1999). The patch occupancy analysis included all combinations of the shrub cover, forb cover, and grass cover terms plus interactions between shrub cover and forb cover (in any model where both terms were included). Forb cover × shrub cover interactions were included because we expected the value of forbs in providing food sources to become apparent only when sufficient shrub cover was present to support nesting. A shrub-size term was not included in the patch occupancy analysis because size measurements were not collected prior to 2007. Separate analyses were performed for each year within the patch occupancy data set (2003, 2004, and 2005). The settlement order and reproductive success analyses included all combinations of the shrub-cover, shrub-size, forb-cover and, grass-cover terms plus interactions between shrub cover and forb cover (in any model where both terms were included). To avoid overparamaterising models fitted to the smaller territory fidelity data set, we included only the shrub-cover and forb-cover terms, which had received some support in the patch occupancy and settlement analyses (i.e., $\Delta\mathrm{AIC_c} < 4$; Burnham and Anderson 2002). Following Chalfoun and Martin (2007, 2009), we prepared a "density of potential nest shrubs" measure based on the density of shrubs that fell within the same width and height range as shrubs previously used for nesting (12–200 and 30–240 cm, respectively). However, this measure was correlated with both big sage cover and cover of other shrubs ($r > 0.65$), so it was not included in analyses.

Within each candidate model set, we tested the relative support for each of the models using an information–theoretic approach (Burnham and Anderson 2002). Akaike's information criterion values corrected for small sample sizes ($\mathrm{AIC_c}$) were derived for each model using the output of general linear models (settlement order analysis), or logistic regressions (presence and absence, territory fidelity, and reproductive success analyses) computed in SAS version 9.1 (SAS Institute Inc., Cary, North Carolina, USA). $\mathrm{AIC_c}$ values were used in all analyses because the sample sizes divided by the number of models in the candidate sets were always <40 (Burnham and Anderson 2002). $\mathrm{AIC_c}$ values give a measure of the level of fit of the data to the model weighted by the number of variables in the model (Burnham and Anderson 2002). Low $\mathrm{AIC_c}$ values reflect both better fit of the data to the model and a low likelihood of model overfitting. $\Delta\mathrm{AIC_c}$ values were calculated as the differences between the $\mathrm{AIC_c}$ of each model and that of the most parsimonious model (Burnham and Anderson 2002). $\mathrm{AIC_c}$ weights (w_i), which indicate the likelihood of the model given the data, relative to the other models in the candidate set, were calculated from the $\Delta\mathrm{AIC_c}$ values and used to assess the relative support for each of the models (Burnham and Anderson 2002). Relative levels of support were illustrated with evidence ratios, which are values derived from dividing the w_i of a model by the w_i of the next highest ranked model in the candidate set. Variable weights and weighted parameter estimates and their associated unconditional standard errors (SE) were also computed to assess the relative influences of the parameters present in the best supported models. An $\mathrm{AIC_c}$ variable weight is the sum of the w_i of all models in which the parameter was included, a weighted parameter estimate is defined as the mean estimate (across all models in the candidate set) of each parameter weighted by the w_i of each model in which the parameter was included, and an unconditional SE is defined as the SE of each parameter weighted by the $\mathrm{AIC_c}$ weight of each model in which the parameter was included (Burnham and Anderson 2002).

A discriminant function analysis (DFA) was used to determine whether old and new territories of dispersing birds could be distinguished based on vegetation parameters. Only three of the vegetation parameters (i.e., big sage cover, other shrub cover, and forb cover) were used in the DFA be-

Table 2. Groupings of subvariables into more general terms for incorporation into models that predict fine-scale habitat selection in Brewer's Sparrows (*Spizella breweri*).

Group term	Component variables
Shrub cover	Mean big sage cover + mean big sage cover^2 + mean cover of other shrub species
Shrub size	Mean shrub width + mean shrub height + mean shrub height^2
Forb cover	Mean cover of species with robust growth forms that are present during both settlement and nesting (arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.), *Eriogonum heracleoides*, western stoneseed (*Lithospermum ruderale* Dougl. ex Lehm.), *Lupinus sericeus*, sulphur lupine (*Lupinus sulphureus* Dougl. ex Hook.), mullein (*Verbascum thapsus* L.))
Grass cover	Mean cover of non-native grass species + mean cover of native grass species

cause the analysis could not be run with greater than three terms owing to a small sample size (N = 40). The three terms that were chosen had received at least moderate support (present in a model with a $\Delta AIC_c < 4$; Burnham and Anderson 2002) in the AIC analyses.

Results[2]

Patch occupancy

There was considerable variation in vegetation characteristics between point-count plots that were occupied and unoccupied by Brewer's Sparrows between 2003 and 2005 (Table 3). Two of the nine models examining the influence of habitat characteristics on the occupancy of Brewer's Sparrows in 2003 received strong support ($\Delta AIC_c < 2$); no models received moderate support ($\Delta AIC_c < 4$; Table 4; Burnham and Anderson 2002). The best supported model, which had an evidence ratio over the next best supported model of 2.0 (w_i = 0.619 vs. 0.293, respectively; Table 4), included only shrub cover. Shrub cover was included in the top four models and its component variables had the highest variable weights (1.000). Model averaged parameter estimates for big sage cover and big sage cover squared were 0.790 ± 0.478 (unconditional SE) and –0.015 ± 0.011, respectively, indicating that Brewer's Sparrows were more likely to occur in areas with intermediate sage cover in 2003 (Fig. 2*a*). Other shrub cover was also positively associated with Brewer's Sparrow occupancy with a parameter estimate of 0.147 ± 0.134. The other strongly supported model included grass cover; however, the variable weights associated with all other variables (including the two grass-cover terms) were far lower than those for the shrub-cover terms (below 0.354) and the variability surrounding their model estimates was high (bounded zero), indicating that Brewer's Sparrow occupancy was not related to nonshrub variables in 2003. The absence of support for interactive terms indicated that shrub effects occurred independently of forb cover.

Four of the nine models examining the influence of habitat characteristics on the occupancy of Brewer's Sparrows in 2004 received strong support ($\Delta AIC_c < 2$); one other model received moderate support ($\Delta AIC_c < 4$; Table 4; Burnham and Anderson 2002). All three of the vegetation-cover terms (shrub, forb, and grass) were present in the top four models, which received similar support (w_i: 0.192–0.257; Table 4). The null model received moderate support (Table 4); however, the models with vegetation terms all had evidence ratios over the null model of >3.8. The differences in the AIC_c values of the top four models was related more to the number of parameters present in the vegetation terms (K), than to differences in model support (–2 log likelihoods), with the terms containing the fewest parameters (i.e., forb cover) ranking higher than the terms with more components (Table 4). Forb cover, big sage cover, and invasive grass cover were all positively associated with Brewer's Sparrow occupancy with weighted estimates of 0.061 ± 0.084, 0.074 ± 0.127, and 0.183 ± 0.186, respectively. The error for all other variables was over twice that of the weighted estimates, indicating no association with Brewer's Sparrow occupancy. Given the error surrounding the weighted parameter estimates for all vegetation variables, and the similar AIC support for models containing all three of the vegetation terms, we can conclude that there was no clear or dominant association between Brewer's Sparrow occupancy and any of the vegetation variables in 2004.

Three of the nine models examining the influence of habitat characteristics on the occupancy of Brewer's Sparrows in 2005 received strong support ($\Delta AIC_c < 2$); two other models received moderate support ($\Delta AIC_c < 4$; Table 4; Burnham and Anderson 2002). Grass cover and shrub cover were present in the top three models and had variable weights of 0.641 and 0.414, respectively. Within the grass-cover term, invasive grass cover was negatively associated with Brewer's Sparrow occupancy with a weighted estimate of –0.227 ± 0.239. Within the shrub-cover term, big sage cover was positively associated with Brewer's Sparrow occupancy with an estimate of 0.118 ± 0.164, and big sage cover squared had a negative estimate (–0.0025 ± 0.0039), indicating selection for intermediate sage cover (Fig. 2*c*). The error for all other variables was over twice that of the weighted estimates, indicating that there were no associations between Brewer's Sparrow occupancy and any of the other vegetation variables in 2005. Despite the error surrounding the weighted parameter estimates for sage cover, sage cover squared, and invasive grass, the high evidence ratios for models containing these variables over the null model (>2.0) indicates that sage cover and invasive grass were associated with Brewer's Sparrow occupancy in 2005.

Sage cover was the most consistently supported parameter over the 3 years, with Brewer's Sparrows most frequently occupying plots within the 20%–25% cover range

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[2] Supplementary tables for this article are available on the journal Web site (http://cjz.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5340. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

Table 3. Means and 95% confidence intervals (in parentheses) of vegetation characteristics within point-count plots or territories used to tive success, and territory fidelity.

	Patch occupancy					
	2003		2004		2005	
	Occupied (N = 12)	Unoccupied (N = 36)	Occupied (N = 11)	Unoccupied (N = 37)	Occupied (N = 12)	Unoccupied (N = 36)
Big sage cover (%)	21.7 (18.4 to 25.0)	8.7 (5.0 to 12.4)	19.6 (13.3 to 25.9)	10.9 (7.2 to 14.6)	18.5 (13.6 to 23.3)	9.0 (5.7 to 12.3)
Other shrub cover (%)	5.4 (2.4 to 8.5)	4.2 (2.2 to 7.2)	6.1 (3.6 to 8.5)	6.6 (4.4 to 8.9)	5.5 (2.6 to 8.3)	6.8 (4.3 to 9.3)
Shrub width (cm)						
Shrub height (cm)						
Forb cover (%)	4.0 (2.0 to 6.0)	4.4 (2.8 to 6.0)	5.0 (1.7 to 8.4)	2.6 (1.1 to 3.9)	5.5 (1.8 to 9.1)	3.9 (2.4 to 5.3)
Native grass cover (%)	15.0 (11.0 to 19.0)	12.3 (10.2 to 14.5)	8.9 (5.5 to 12.2)	10.5 (8.4 to 12.5)	12.3 (7.0 to 17.7)	14.0 (11.2 to 16.8)
Invasive grass cover (%)	1.2 (–0.1 to 2.4)	2.7 (1.5 to 3.9)	3.9 (0.6 to 7.3)	1.1 (0.4 to 1.8)	1.0 (0.2 to 1.8)	5.4 (3.1 to 7.7)

Table 4. AIC ranking (by w_i) of candidate models that predict four measures of Brewer's Sparrow (*Spizella breweri*) habitat selection: patch occupancy, order of territory settlement, reproductive success, and territory fidelity.

Model	N*	K[†]	AIC_c[‡]	ΔAIC_c[§]	w_i[‖]	Pseudo r^2[¶]
Occupancy = (9 models)						
2003						
1. Occupancy = shrub cover	48	6	42.563	0.000	0.619	0.61
2. Occupancy = shrub cover + grass cover	48	8	44.060	1.498	0.293	0.68
5. Occupancy = null	48	3	60.529	17.967	0.000	0.00
2004						
1. Occupancy = forb cover	48	4	54.957	0.000	0.257	0.17
2. Occupancy = grass cover	48	5	55.018	0.060	0.249	0.24
3. Occupancy = forb cover + grass cover	48	6	55.377	0.420	0.208	0.29
4. Occupancy = shrub cover + grass cover	48	8	55.539	0.582	0.192	0.43
5. Occupancy = null	48	3	58.219	3.262	0.050	0.00
2005						
1. Occupancy = grass cover	48	5	57.001	0.000	0.381	0.24
2. Occupancy = shrub cover	48	6	57.902	0.901	0.243	0.28
3. Occupancy = shrub cover + grass cover	48	8	58.970	1.970	0.142	0.39
5. Occupancy = null	48	3	60.529	3.529	0.065	0.00
Settlement rank = (16 models)						
1. Settlement rank = null	75	2	317.432	0.000	0.451	0.00
2. Settlement rank = forb cover	75	3	319.309	1.877	0.177	0.17
Success = (16 models)						
1. Success = shrub cover	57	5	90.095	0.000	0.279	0.35
2. Success = forb cover	57	3	90.103	0.008	0.277	0.24
3. Success = null	57	2	91.207	1.112	0.160	0.00
Fidelity = (8 models)						
1. Fidelity = previous success	28	3	12.025	0.000	0.652	0.23
3. Fidelity = null	39	2	17.054	5.029	0.053	0.00

Note: Listed are models that received strong support ($\Delta\text{AIC}_c < 2.0$), plus the null models.

*The sample size.

[†] The number of estimated parameters in the model including the variance.

[‡] A measure of the level of fit of the data to the model weighted by the number of variables in the model, corrected for small sample sizes.

[§] The difference between the AICc of each model and that of the most parsimonious model.

[‖] The likelihood of the model given the data, relative to the other models in the candidate set.

[¶] The proportion of variability in the data that is accounted for by the model. Pseudo r^2 = Nagelkerke's r^2.

(Figs. 2*a*–2*c*). The level of support for all vegetation terms varied from year to year (Table 4). The association between Brewer's Sparrow occupancy and invasive grass cover varied most widely, from no association in 2003, to a positive association in 2004, to a negative association in 2005 (Table 4). The forb-cover term received the least consistent support over the 3 years (Table 4).

Settlement order

The vegetation characteristics within territories settled by Brewer's Sparrows in 2007 are summarized in Table 3. Males settled on territories over a 6-week period spanning 14 April – 1 June. However, despite this broad range in settlement dates, the AIC model comparison showed little support for an influence of vegetation characteristics on settlement order. Only 2 of the 16 models examined received strong AIC support ($\Delta\text{AIC}_c < 2$): the null model and the model that included forb cover (w_i = 0.451 and 0.177, respectively; Table 4). However, while the model with forb cover received strong AIC support, the variable weight for forb cover was low (0.256) and its parameter estimate was both low and had an unconditional SE that bounded zero examine four measures of Brewer's Sparrow (*Spizella breweri*) habitat selection: patch occupancy, order of territory settlement, reproduc-

	Reproductive success in 2007		Territory fidelity in 2006–2008			
Territory settlement in 2007 (N = 79)	Successful (N = 33)	Failed (N = 26)	Stayed (N = 19)	Moved (N = 20)	Previous territory (N = 20)	New territory (N = 20)
24.3 (22.2 to 25.6)	23.8 (21.6 to 26.1)	23.3 (19.7 to 26.9)	25.0 (21.9 to 28.2)	22.2 (18.4 to 26.0)	22.2 (18.4 to 26.0)	25.6 (21.8 to 29.5)
10.1 (8.5 to 11.7)	11.8 (9.3 to 14.3)	7.6 (5.4 to 9.7)	9.6 (7.1 to 12.1)	7.8 (5.0 to 10.7)	7.8 (5.0 to 10.7)	7.5 (4.5 to 10.6)
59.3 (56.0 to 62.2)	59.9 (54.8 to 65.0)	56.7 (53.0 to 60.4)				
75.1 (72.2 to 77.9)	74.7 (69.5 to 79.8)	74.6 (70.5 to 78.6)				
7.1 (5.2 to 8.5)	8.2 (5.5 to 11.0)	4.6 (2.6 to 6.6)	7.3 (3.7 to 11.0)	5.5 (3.4 to 7.7)	5.5 (3.4 to 7.7)	5.3 (2.3 to 8.2)
13.9 (11.3 to 16.0)	15.5 (12.1 to 19.0)	12.3 (8.9 to 15.6)				
11.5 (9.1 to 14.1)	9.1 (6.0 to 12.2)	13.5 (9.1 to 17.9)				

(0.065 ± 0.098). The likelihoods for all other parameters were <0.226. Consequently, it is not possible to conclude that there is a link between settlement order and vegetation. This conclusion does not change if all models are rerun with male age as a base variable, although there is strong support for the model with age only, indicating that after-second-year birds established territories earlier than second-year birds (results not presented).

Reproductive success

Fifty-six percent of the Brewer's Sparrow pairs that had known nesting outcomes in 2007 were successful in fledging one or more young over the course of the season. Failure of nesting attempts was due entirely to predation. There was no evidence of partial brood loss, abandonment, or total brood mortality owing to extreme climatic events. The mean (95% confidence intervals) number of fledglings produced per pair (all pairs) across the three sites in 2007 was 2.51 ± 0.56. The vegetation characteristics within territories of Brewer's Sparrows that were successful and within those of birds that were unsuccessful are summarized in Table 3. Three of the 16 models examining the influence of habitat characteristics on reproductive success (i.e., the likelihood of a pair fledging one or more young) received strong AIC support ($\Delta\text{AIC}_c < 2$) and an additional three models received moderate support ($\Delta\text{AIC}_c < 4$; Table 4). The two best supported models included a single term (shrub cover or forb cover), but neither model received substantially more support than the null model (i.e., their evidence ratios over the null model were <2.0; Table 4). Variable weights for all terms were below 0.350 and the model averaged parameter estimates for all habitat variables had standard errors that bounded zero, providing little support for a relationship between habitat variables and reproductive success.

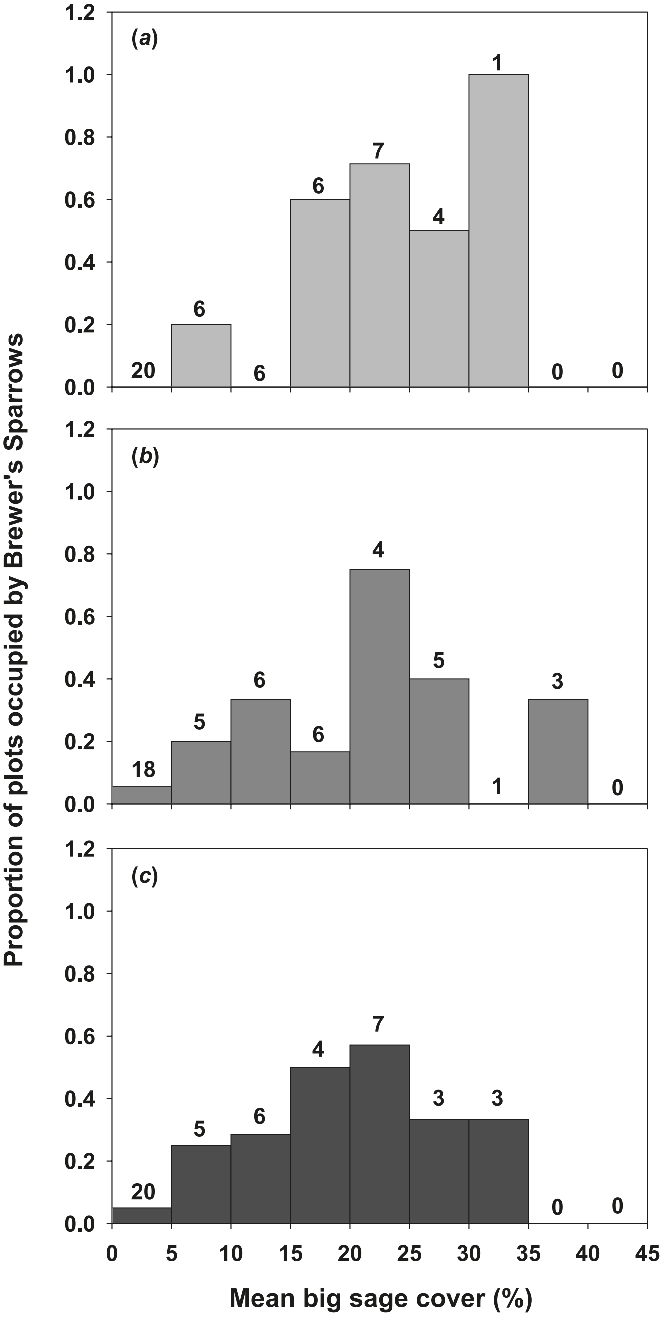
Territory fidelity

The vegetation characteristics within territories of Brewer's Sparrows that stayed in the same territory from year to year (exhibited fidelity) and within territories of birds that dispersed from their original territories to another territory within the study area are summarized in Table 3. Only one of the eight models that predicted territory fidelity as a function of territory vegetation characteristics and reproductive success in the previous season received strong support ($\Delta\text{AIC}_c < 2$); one other model received moderate support ($\Delta\text{AIC}_c < 4$; Table 4). The only strongly supported model was the one with the term, previous reproductive success ($w_i = 0.652$; Table 4). The previous reproductive success parameter had a likelihood of 0.922 and a parameter estimate of 1.725 ± 0.919 (unconditional SE). Seventy-one percent of returning birds that had been successful in the previous year returned to the same territory (N = 15). In contrast, only 28% of birds that had been unsuccessful returned to the territory they had previously held (N = 14). The only other variable that was present in a supported model was robust forb cover; however, the variable weights for all habitat parameters, including forb cover, were below 0.0243 and had estimates and unconditional SE that bounded zero, indicating that vegetation characteristics do not influence territory fidelity. The remaining models, which included the null model, and the models with shrub cover and shrub cover × forb cover interactions, were not supported ($\Delta\text{AIC}_c > 4$). For individuals that did establish new territories, a discriminant function analysis could discern no differences between old and new territories based on big sage cover, other shrub cover, and shrub height (Table 3; $F_{[3,36]} = 0.49$, $p = 0.69$). Only 53% of cases were classified correctly using a "leave-one-out classification" method where each data point was sequentially omitted, the discriminant function recalculated, and the omitted point classified using that function.

Discussion

There has been considerable evidence that shrub cover influences habitat selection by Brewer's Sparrows at a landscape scale (Wiens and Rotenberry 1981; Petersen and Best 1985; Rotenberry and Wiens 1989, 1991; Harvey 1992; Sarell and McGuiness 1996; Chalfoun and Martin 2007, 2009). Our study adds to evidence that shrub cover is also important at a finer scale (Paczek 2002; Chalfoun and Martin 2007, 2009). Paczek (2002), in a single-year study conducted in the South Okanagan, found that Brewer's Sparrows were more abundant within territory-scale plots that had higher cover of big sage. Chalfoun and Martin (2007), in a multiple-year study conducted in the core of the Brewer's Sparrow breeding range, found that the sparrows are more likely to use territories with high shrub cover and density of potential nest shrubs. Our study, conducted over several years and at the periphery of the species' range, shows that shrub cover, specifically big sage (the primary nesting shrub for the species; Rotenberry et al. 1999), most consistently predicts the occupancy patterns of Brewer's Sparrows. Our study also provides evidence that there is selection for an intermediate range of shrub cover. This pattern is sup-

Fig. 2. Proportion of point-count plots occupied by Brewer's Sparrows (*Spizella breweri*) across the three study years: 2003 (*a*), 2004 (*b*), and 2005 (*c*) presented according to the mean percent cover of big sage within the plots ($N = 48$). The numbers above the bars indicate the number of plots within each big sage cover category.



ported by previous studies conducted at a broader scale throughout the Brewer's Sparrow's range (Petersen and Best 1985; Wiens and Rotenberry 1985; Larson and Bock 1986; Harvey 1992; Howe et al. 1996; Sarell and McGuiness 1996).

We found that there was annual variation in both the level of support for and the direction of the associations between the cover of forbs and grasses and patch occupancy in Brewer's Sparrows, indicating that cover of forbs and grasses were not reliable predictors of Brewer's Sparrow occupancy. Paczek (2002) found that the cover of two robust forb and one grass species was positively associated with the density of Brewer's Sparrows within occupied plots (evaluated using point counts) in 1998. The two robust forbs found by Paczek (2002) to influence habitat use (silky lupine and parsnip-flowered buckwheat) were primary components of our robust forbs grouping. Junegrass was a component of our native-grass term. A possible explanation for the inconsistency between our study and Paczek's, which was conducted over a single season, is that there is significant annual variation in the cover of forbs and grasses. Because these variables fluctuate independently of sagebrush, which is the key component that Brewer's Sparrows are tracking, they appear positively related, negatively related, or unrelated to Brewer's Sparrow occupancy patterns in different years when there is no actual selection for these characteristics. The annual variation that we found in the relative support for the grass and forb terms is evidence in support of this explanation.

Previous studies have identified preferred habitat based on settlement order or individual dispersal decisions, leading to the suggestion that the investigation of individual selection decisions may provide insight into fine-scale habitat preference (Lanyon and Thompson 1986; Remeš 2003; Sergio and Newton 2003; Sedgwick 2004). However, monitoring of individual territory settlement and dispersal decisions in Brewer's Sparrows provided little evidence that vegetation cover influences fine-scale habitat selection decisions in this species. Settlement order was found to be unrelated to any of the vegetation parameters examined, despite a broad range in settlement dates (first – last = 48 days), and substantial differences in the mean settlement dates of after-second-year and second-year birds (10 days). Vegetation characteristics of the territories of later-arriving second-year birds did not differ from those in the territories of more experienced conspecifics. Furthermore, birds that dispersed did not select territories that differed, in any vegetation characteristics, from their previous ones. It is possible that our inability to find a link between settlement order and preferred vegetation characteristics is a sign that not all individuals within the study population are using the same criteria for territory selection. If later arriving birds, owing to differences in their requirements or their knowledge of optimal habitat characteristics, are actually assessing potential territories and making decisions based on different selection criteria than are earlier arriving (older) birds, then settlement order will not reflect a uniform gradient between the most to the least preferred characteristics. However, because our results did not change when we included age as a base variable, and we also found no evidence for an influence of vegetation on territory selection decisions when following the fidelity or dispersal of returning birds, it is unlikely that the absence of a relationship between vegetation and settlement order is due to a methodological inadequacy. Our inability to find a relationship with settlement order, or a link between habitat and dispersal decisions, suggests that the primary factors causing variation in territory selection within breeding clusters in this study area are not influenced strongly by vegetation.

Why does vegetation play a limited role in Brewer's Sparrows' individual settlement decisions?

One explanation for there being no link between habitat and territory settlement or dispersal in the individual decision analyses is that there is a critical range of suitability within key vegetation characteristics, and territories that fall within that range are all equally likely to be selected on the basis of habitat. In the patch occupancy analysis, over 75% of the plots that were occupied had big sage cover between 12% and 29% (26 out of 35), with the highest likelihood of occupancy in those with 20%–25% cover. In the individual decision analyses, over 75% of the territories within the plots had big sage cover between 14% and 32%. With the similarity in the sage characteristics between the most highly occupied plots in the patch occupancy analysis and the entire suite of territories examined in the individual decisions analysis, it is possible that we found no influence of vegetation on settlement decisions because most of the territories examined fell within an almost uniformly suitable range. In the South Okanagan, breeding clusters occur frequently within habitat that falls within this critical range of suitability (Sarell and McGuiness 1996; Hobbs 2001), meaning that the majority of the territories occupied within this population may not differ significantly enough to influence Brewer's Sparrow settlement decisions.

A second explanation for the absence of a link between vegetation characteristics and territory selection is that there appears to be little advantage to selecting territories based on vegetation because reproductive success at the northern extent of the Brewer's Sparrow breeding range is unrelated to territory-level vegetation characteristics. The primary factor influencing nest success in the South Okanagan is predation (Mahony 2003; Welstead et al. 2003; this study). Studies that have assessed associations between habitat variables and nest success and predation risk in Brewer's Sparrows in the South Okanagan have found little evidence that there are nest-shrub-level or nest-patch-level vegetation variables that consistently predict success (Mahony 2003; Welstead et al. 2003). Welstead et al. (2003) found that shrub height and width, which are correlated with concealment, affected avian predation on artificial nests, but did not influence actual predation rates on real Brewer's Sparrow nests, indicating that snakes and small mammals are responsible for the majority of the predation on actual nests within breeding clusters. They also found that sites with fewer avian predators had greater Brewer's Sparrow nest densities, indicating selection against avian predation at a broad scale (Welstead et al. 2003). Mahony (2003) found that successful nests were more concealed from the north, but less concealed from the west and overhead than depredated nests, but that there were no consistent differences in nest patch characteristics between successful and depredated nests. There was, however, a difference in aspect between successful and depredated nests, with west-facing slopes containing more successful nests than north-facing slopes, indicating that there is broad-scale variation in the distribution of predators (Mahony 2003). Potential predators in the South Okanagan include several species of snakes (Gopher Snake (*Pituophis catenifer* Blainville, 1835); Western Yellow-bellied Racer (*Coluber mormon* Baird and Girard, 1852); Western Terrestrial Garter Snake (*Thamnophis elegans* (Baird and Girard, 1852))), corvids (American Crow (*Corvus brachyrhynchos* Brehm, 1822), Common Raven (*Corvus corax* L., 1758), Black-billed Magpie (*Pica hudsonia* (Sabine, 1823))), and small mammals (long-tailed weasel (*Mustela frenata* Lichtenstein, 1831) and several rodent species). Together, the results from this study and from Mahony (2003) and Welstead et al. (2003) suggest that (*i*) predation risk is scale-dependent in the South Okanagan, and effective selection for habitats that reduce predation risk occurs at a site, rather than a territory, nest patch, or nest shrub scale, and (*ii*) within Brewer's Sparrow breeding clusters, most predation appears to be by snakes and small mammals, which are incidental rather than target predators of Brewer's Sparrow nests, and less limited by vegetation characteristics than are avian predators.

Our finding that territory-level vegetation characteristics do not influence Brewer's Sparrow reproductive success (caused entirely by predation at our sites) conflicts with the results of Chalfoun and Martin (2009), who found that the density of potential nest shrubs within a nest patch was positively associated with daily survival probability for birds breeding within the core of the species' range. Chalfoun and Martin (2009) suggest that their finding is evidence in support of the "potential prey site" hypothesis, which predicts that a prey individual's likelihood of predation will decrease where a greater number of potential nest sites exist for predators to search. Because a similar "density of potential nest shrubs" measure was found to be highly correlated with shrub cover, and shrub cover was unrelated to reproductive success, it is unlikely that our inability to find a similar pattern was a consequence of density of potential nest shrubs not being included in our analysis. It is also unlikely that the absence of an association between vegetation structure and reproductive success was a function of the scale we examined (territory vs. nest patch), because a study by Mahony (2003) at the same sites showed no consistent associations between nest patch shrub cover and reproductive success. Instead it is more likely that the lower population densities and different predator communities of Brewer's Sparrows breeding at the northern extent of the species' range result in different habitat selection consequences for northern periphery populations.

A third potential explanation for the absence of a link between vegetation characteristics and territory selection in Brewer's Sparrows breeding at the northern extent of their range is that decision rules are selected at the centre of the range where vegetation characteristics and associated predator assemblages differ from those in the north. Because there is a high level of gene flow from the centre to the edge of the range (Croteau et al. 2007), it is possible that decision rules have not become adapted for northern conditions. Given the high level of gene flow, if breeding conditions at the north of the range are suboptimal relative to those in the range centre, resulting in lower relative fitness of northern-bred individuals, adaptation to the northern environment is unlikely to occur under present conditions.

What else could explain individual settlement decisions in Brewer's Sparrows?

This study was meant to determine whether fine-scale vegetation patterns explained territory selection in Brewer's Sparrows, and thus the territory clustering observed in the species at the northern extent of their range. Our results are consistent in their indication that Brewer's Sparrows are not selecting for non-sagebrush vegetation characteristics at a fine scale, indicating that vegetation is not responsible for the observed territory clustering. However, we did find that previous success is an important factor in the settlement decisions of experienced breeders, indicating the importance of the previous year's predator distributions in driving the territory-selection choices of returning birds. Combined with the results from a recent study which showed that conspecific attraction is an important driver of territory selection in the species (Harrison et al. 2009), our result suggests that the territory clustering observed in Brewer's Sparrows is driven primarily by nonhabitat factors.

Conspecific attraction is one potential driver of territory clustering in Brewer's Sparrows at the northern extent of their range. Territorial individuals have been shown to cluster owing to conspecific attraction in Collared Flycatchers (*Ficedula albicollis* (Temminck, 1815)) (Doligez et al. 2002), Least Flycatchers (*Empidonax minimus* (W.M. Baird and S.F. Baird, 1843)) (Mills et al. 2006), Black-throated Blue Warblers (*Dendroica caerulescens* (Gmelin, 1789)) (Hahn and Silverman 2007; Betts et al. 2008), Bobolinks (*Dolichonyx oryzivorus* (L., 1758)) (Nocera et al. 2006), Black-capped Vireos (*Vireo atricapilla* Woodhouse, 1852) (Ward and Schlossberg 2004), and Baird's Sparrows (*Ammodramus bairdii* (Audubon, 1844)) (Ahlering et al. 2006). The benefits of clustering in territorial species may not initially seem apparent, but there are several reasons for an individual to use the presence of conspecifics as a settlement cue rather than using more direct cues such as habitat features or resource distributions. Ahlering et al. (2006) suggested that males may benefit from the presence of other males because of the increased likelihood of mate attraction. Tarof and Ratcliffe (2004) suggested that individuals preferentially settle adjacent to conspecifics to increase their opportunities for extra-pair copulations. Still other studies have suggested that individuals use the presence of conspecifics as an indicator of habitat quality, both in terms of physical habitat characteristics and factors like predation risk (Doligez et al. 2002; Ward and Schlossberg 2004; Ahlering et al. 2006; Nocera et al. 2006; Hahn and Silverman 2007).

Substantial evidence has been found in support of clustering as a strategy for lowering predation risk in songbird species. Fontaine and Martin (2006) found higher nesting densities at sites with fewer predators in their broad-scale survey of 12 species of nesting songbirds. Perry and Andersen (2003) suggested that clustering could act as a means of predator deterrence in Least Flycatchers because birds in clusters suffered less reproductive failure owing to predation than birds outside clusters. Using broad-scale surveys (between six well-spaced sites), Welstead et al. (2003) found that Brewer's Sparrows nest in higher densities in sites with fewer avian predators.

Conspecific attraction, combined with a decision rule to return to a previous territory if successful and disperse following failure, could explain both the avoidance of areas with high avian predator densities and the absence of a relationship between territory vegetation characteristics and individual selection decisions. Individual Brewer's Sparrows that return to a territory have generally avoided predation in the previous season. First time breeders and older birds that have experienced reproductive failure may therefore be able to use the locations of experienced birds to avoid settling in areas with high predation risk. Over time, this would lead to clustering of territories away from areas characterized by consistently high predator densities. When examined over the short term, it would lead to territory selection decisions that have no apparent link to fine-scale habitat characteristics.

Management implications

Because our findings that Brewer's Sparrows' settlement decisions and reproductive success were not linked strongly with habitat differ from those of studies conducted nearer to the centre of the species' range, it appears that habitat selection mechanisms in the species are spatially variable. Therefore, we cannot use our results to postulate on potential reasons behind the species' range-wide decline. However, our results do allow us to discuss the conservation and management of birds breeding at the northern extent of the species' range. The results from the patch occupancy analysis showing the importance of sage cover in predicting occupancy patterns support the use of shrub-level characteristics as baseline criteria for the identification of suitable Brewer's Sparrow habitat in British Columbia. However, the evidence that previous success (dictated by predators) and conspecific attraction (Harrison et al. 2009) are also important in driving Brewer's Sparrow settlement decisions indicates that management of the species will require more than just the identification and preservation of patches of suitable sagebrush. Because northern Brewer's Sparrows cluster their territories rather than spreading out across suitable habitats, they are potentially more susceptible to disturbance than more broadly distributed species. Following disturbance, they may also be less likely to reoccupy areas that are suitable because of the social components of their habitat selection decisions. If increasing climatic variability causes the quality of their habitat to change from year to year, they may fail to respond appropriately because of their reliance on cues like previous experience (and attraction to experienced individuals), which reflect conditions in the previous rather than the current season. Recognition of the importance of nonhabitat components in Brewer's Sparrow habitat selection will be vital in developing models that accurately predict the species' response to proposed or predicted changes in its environment and in enhancing current methods for the identification of potential conservation areas.

Acknowledgements

We would like to acknowledge John Reynolds, Elizabeth Elle, two anonymous reviewers, and the students and faculty within the Simon Fraser University Centre for Wildlife Ecology for their helpful comments on the manuscript, the many members of the Brewer's Sparrow field crews (especially Christine Rock, Camille Andrews, Naira Johnston, and Nathan Hentze) for their dedication to the project, and B.C. Parks and the Nature Trust of B.C. for granting permission to conduct research on their properties. Nancy Mahony (Environment Canada) and Jared Hobbs (B.C. Ministry of Environment) also provided invaluable support in obtaining funding and hiring personnel. Funding for this project was provided by Environment Canada, the Centre for Wildlife Ecology, the Natural Sciences and Engineering Research Council of Canada, the Nature Trust of B.C. (Brink McLean Grassland Conservation Fund), and the Forest Science Program (Graduate Student Pilot Project).

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