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

M.L. Harrison and D.J. Green

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 set-

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.

Location	Basis of habitat associations	Shrubs		Grasses (cover)	Forbs (cover)	Reference
		Cover or density	Size			
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		(+) Junegrass		Sarell and McGuiness 1996
	Relative abundance	(+) Big sage cover			(+) 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.

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 un-occupied 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

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^*	$K^†$	$AIC_c^‡$	$\Delta AIC_c^§$	$w_i^{\|}$	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)						

(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 ($\Delta AIC_c < 2$): 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

(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 ($\Delta AIC_c < 2$) and an additional three models received moderate support ($\Delta AIC_c < 4$; 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

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

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

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

rows, 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 ini-
icJ 1 Tf 78i7b1 0 1.4eL7i8ori1 Tf zivorusAm-

References

Ahlering, M.A., Johnson, D.G., and Faaborg, J. 2006. Conspecific attraction in a grassland bird: the Baird's Sparrow. J. Field Ornithol. **77**(4): 365–371. doi:10.1111/j.1557-9263.2006.00066.x.

Arlt, D., and Pärt, T. 2007. Nonideal breeding habitat selection: a mismatch between preference and fitness. Ecology, **88**(3): 792–801. doi:10.1890/06-0574. PMID:17503606.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conserv. Biol. **18**(6): 1482–1491. doi:10.1111/j.1523-1739.2004.00417.x.

Betts, M.G., Hadley, A.S., Rodenhouse, N., and Nocera, J.J. 2008.

Nocera, J.J., Forbes, G.J., and Giraldeau, L.-A. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. Proc. R. Soc. Lond. B Biol. Sci. **273**(1584): 349–355. doi:10.1098/rspb.2005.3318.

Olson, R.A. 1974. Bird populations in relation to land use in Curlew Valley, Idaho and Utah. M.S. thesis, Idaho State University, Pocatello.

Paczek, S. 2002. Effects of fine-scale and landscape-level habitat features on sagebrush breeding birds of the southern Okanagan and Similkameen valleys, British Columbia. M.Sc. thesis, University of British Columbia, Vancouver.

Paige, C., and Ritter, S.A. 1999. Birds in a sagebrush sea: managing sagebrush habitats for bird communities. Partners in Flight Western Working Group, Boise, Idaho.

Perry, E.F., and Andersen, D.E. 2003. Advantages of clustered nesting for least flycatchers in north-central Minnesota. Condor, **105**(4): 756–770. doi:10.1650/7162.

Petersen, K.L., and Best, L.B. 1985. Brewer's Sparrow nest-site characteristics in a sagebrush community. J. Field Ornithol. **56**(1): 23–27.

Remeš, V. 2003. Effects of exotic habitat on nesting success, territory density and settlement patterns in the Blackcap (*Sylvia atricapilla*). Conserv. Biol. **17**(4): 1127–1133. doi:10.1046/j.1523-1739.2003.01611.x.

Rotenberry, J.T., and Wiens, J.A. 1980. Temporal variation in habitat structure and shrubsteppe bird dynamics. Oecologia (Berl.), **47**(1): 1–9. doi:10.1007/BF00541768.

Rotenberry, J.T., and 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): 1–14. doi:10.2307/1368142.

Rotenberry, J.T., and Wiens, J.A. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. Ecology, **72**(4): 1325–1335. doi:10.2307/1941105.

Rotenberry, J.T., Patten, M.A., and Preston, K.L. 1999. Brewer's Sparrow (*Spizella breweri*). *In* The birds of North America. No. 390. *Edited by* A. Poole and F. Gill. The Birds of North America, Inc., Philadelphia, Pa.

Roth, K.L., and Islam, K. 2007. Do Cerulean Warblers (*Dendroica cerulean*) exhibit clustered territoriality? Am. Midl. Nat. **157**(2): 345–355. doi:10.1674/0003-0031(2007)157[345:DCWDCE]2.0.CO;2.

Safran, R.J. 2004. Adaptive site selection rules and variation in group size of barn swallows: individual decisions predict popu-