

**HABITAT SELECTION OF THE SAGEBRUSH BREWER'S SPARROW *SPIZELLA
BREWERI BREWERI* IN BRITISH COLUMBIA**

by

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ABSTRACT

When animals cluster their territories within larger patches of seemingly appropriate habitat it could mean that they have additional, finer scale habitat requirements or that non-habitat cues play a role in their selection decisions. Sagebrush Brewer's Sparrows (*Spizella breweri breweri*) cluster their territories throughout their breeding range. I examined territory-scale selection by the species using two approaches: observation of individual selection for vegetation characteristics, and an experimental test of conspecific attraction. Within a suitable range of shrub cover (where clustering occurs), vegetation characteristics did not predict individual selection decisions or breeding success. However, more males established territories in response to playbacks than untreated controls, indicating that conspecific attraction may play a role in Brewer's Sparrow habitat selection. These results suggest that traditional habitat models, which consider only resource distributions and not social factors, may be inadequate for the conservation of this and similar species.

Keywords: habitat selection; conspecific attraction; Brewer's Sparrow; territory clustering

Subject Terms: Brewer's Sparrow; sparrows; birds - habitat; birds - behaviour

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TABLE OF CONTENTS

Approval.....	ii
Abstract.....	iii
Acknowledgements.....	iv
Table of Contents	v
List of Figures.....	vi
List of Tables	vii
Chapter 1: GENERAL INTRODUCTION	1
Chapter 2: VEGETATION INFLUENCES PATCH OCCUPANCY BUT NOT SETTLEMENT AND DISPERSAL DECISIONS IN A DECLINING MIGRATORY SONGBIRD.....	5
2.1 Abstract.....	5
2.2 Introduction	6
2.3 Methods	10
2.4 Results.....	17
2.5 Discussion.....	31
Chapter 3: CONSPECIFIC ATTRACTION INFLUENCES BREEDING HABITAT SELECTION OF A DECLINING MIGRATORY SONGBIRD	38
3.1 Abstract.....	38
3.2 Introduction	39
3.3 Methods	41
3.4 Results.....	45
3.5 Discussion.....	47
Chapter 4: CONCLUSIONS	54
Reference List.....	57

LIST OF FIGURES

- Figure 1** Brewer's Sparrow detections from Ministry of Environment surveys within habitat classed as suitable for the species in the South Okanagan region of British Columbia (location shown on inset map). 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).....9
- Figure 2** The proportion of point count plots occupied by Brewer's Sparrows across the three study years (2003-2005) presented according to the mean % cover of big sage within the plots (n = 144). The numbers above the bars represent the number of plots within each sage cover category.20

LIST OF TABLES

Table 1	A summary of the studies that have examined habitat associations of Brewer’s Sparrows across the species’ breeding range. I distinguish between studies that based associations on the occupancy (presence/absence) and relative abundance of Brewer’s Sparrows across sites. (+) and (-) indicate the direction of habitat associations. Ranges in vegetation variables are given when the associations were highest within an intermediate range.	4
Table 2	Groupings of sub-variables into more general terms for incorporation into models that predict fine-scale habitat selection in Brewer’s Sparrows.	15
Table 3	Means and 95% confidence intervals for vegetation characteristics within point count plots that were occupied and unoccupied by Brewer’s Sparrow between 2003 and 2005. Sample sizes are shown in brackets.	17
Table 4	AIC ranking (by w_i) of candidate models that predict patch occupancy (from point counts) of Brewer’s Sparrows in the South Okanagan, British Columbia between 2003 and 2005.	18
Table 5	The parameter likelihood, weighted estimate and unconditional standard error of every parameter included in the candidate model set predicting patch occupancy in Brewer’s Sparrows.	19
Table 6	Means and 95% confidence intervals of vegetation characteristics within territories settled by Brewer’s Sparrows in 2007 (n = 79).	21
Table 7	AIC ranking (by w_i) of candidate models that predict settlement order of Brewer’s Sparrows in the South Okanagan, British Columbia in 2007.	22
Table 8	The parameter likelihood, weighted estimate and unconditional standard error of every parameter included in the candidate model set predicting settlement order in Brewer’s Sparrows.	23
Table 9	Means and 95% confidence intervals of vegetation characteristics within territories of Brewer’s Sparrows that were successful (fledged one or more young) and within territories of birds that experienced reproductive failure in 2007. Sample sizes are in brackets.	25
Table 10	AIC ranking (by w_i) of candidate models that predict reproductive success of Brewer’s Sparrows in the South Okanagan, British Columbia in 2007.	26
Table 11	The parameter likelihood, weighted estimate and unconditional standard error of every parameter included in the candidate model set predicting reproductive success in Brewer’s Sparrows.	27

Table 12	Means and 95% confidence intervals of vegetation characteristics within territories of Brewer’s Sparrows that stayed in the same territory from year to year (2006 to 2007 or 2007 to 2008) and within the initial territories of birds that dispersed to a new territory. Sample sizes are shown in brackets.....	29
Table 13	AIC ranking (by w_i) of candidate models that predict territory fidelity of Brewer’s Sparrows in the South Okanagan, British Columbia between 2006 and 2008.	29
Table 14	The parameter likelihood, weighted estimate and unconditional standard error of every parameter included in the candidate model set predicting Brewer’s Sparrow territory fidelity.....	30
Table 15	Means and 95% confidence intervals for vegetation characteristics within previous (1) and subsequent (2) territories for Brewer’s Sparrows that dispersed to new territories in the second year they were monitored (n = 20).	30
Table 16	A summary of the response of Brewer’s Sparrows to playback treatments versus controls within the ASY and SY settlement periods. The response of the birds is split into three components: # of birds that visited plots during the treatment period, # of males that established territories, and # of pairs. Sample sizes were insufficient to test for statistical differences in the reproductive success of attracted birds.	46
Table 17	A summary of the response of territorial songbirds to playbacks in eight studies where playbacks were used to test for social attraction. The response of the birds is split into three components: visitation of playbacks plots, establishment of territories, and attraction of females or pairs.	48

CHAPTER 1: GENERAL INTRODUCTION

Habitats are often heterogeneous, causing animals to congregate within suitable patches rather than distribute themselves evenly across their environment (Fretwell and Lucas 1970). However, in some species this congregation seems to occur independently of key habitat variables, with groups of individuals aggregating in one area and leaving adjacent apparently suitable habitat unoccupied (Danchin and Wagner 1997; Alonso et al. 2004). From an individual-based habitat selection perspective, two main hypotheses have been put forth to explain this behaviour. The most traditional hypothesis is that individuals are clustering around a previously unidentified limited resource or at an optimal distance between several important resources (Brown et al. 1992; Clark and Shuttler 1999). Under this hypothesis, it is assumed that animals have the capacity to individually assess each of these resources and then settle either around or at an optimal distance between them. This belief has been at the heart of theories such as the Ideal Free Distribution (Fretwell and Lucas 1970), which assume that individuals are able to gather a perfect set of information about all available habitats before choosing the one that will maximize their survival. Under this assumption, a careful survey of resources would allow us to identify key variables, or the spatial distributions of several variables that should predict where individuals would choose to settle and potentially where clustering would occur.

While direct assessment is the most reliable way to assess habitat suitability, it is now recognized that individual evaluation of all resources leading to site selection can be extremely time-consuming, potentially leading to delayed breeding (in the case of breeding habitat selection) or reduced survival (due to energetic costs or increased risk

of predation; Danchin et al. 2001). For this reason, animals may elect to use integrative cues, such as the presence or reproductive success of conspecifics in their habitat selection decisions (Danchin et al. 1998). A second hypothesis has thus emerged, suggesting that individuals choose to settle in close vicinity to conspecifics, thereby forming aggregations, because the presence or reproductive success of a conspecific indicates a high likelihood of reproductive success for a later arriving individual (Boulinier and Danchin 1997; Danchin et al. 1998). It is widely recognized that many species use their own reproductive success from previous breeding experiences to determine where they will breed in subsequent attempts, leading to either breeding site dispersal (following failure) or philopatry (following success; Porneluzi 2003; Sedgwick 2004). In addition, a great deal of work has shown that animals use the actions of conspecifics to direct their own decisions on such matters as foraging (Templeton and Giraldeau 1996; Galef and White 2000; Valone and Templeton 2002), predator escape (Lima 1995), and mate choice (Nordell and Valone 1998; Galef and Giraldeau 2001). It is not surprising, therefore, that there is now considerable evidence that many species also use the presence or success of conspecifics to direct their own habitat selection decisions (Stamps 1988; Danchin et al. 1998; Ward and Schlossberg 2001; Ahlering et al. 2006; Donahue 2006; Hahn and Silverman 2006; Nocera et al. 2006).

The Sagebrush Brewer's Sparrow (*Spizella breweri breweri*) is a sagebrush-steppe obligate, relying on these habitats during both breeding and wintering periods (Rotenberry et al. 1999). The species breeds largely within the Great Basin region of the United States and Canada, inhabiting sagebrush-dominated habitats from the Okanagan Valley in British Columbia in the North, to New Mexico in the South, and from California in the West, to Montana in the East (Rotenberry et al. 1999). Brewer's Sparrows overwinter between southwestern California and northern Mexico (Rotenberry et al. 1999).

Breeding Bird Survey data from 1966-2007 showed that Brewer's Sparrows have been experiencing a range-wide average decline of approximately 2.1% per year (Sauer et al. 2008). Due to this decline and continued conversion of sagebrush habitats for agriculture and residential development, the species is now listed as vulnerable or at-risk in both the United States and Canada. However, while habitat destruction is one of the factors that have been implicated in the Brewer's Sparrow's range-wide decline, the sparrows cluster their breeding territories into small areas within larger patches, leaving much apparently suitable habitat unoccupied (Wiens et al. 1985; Cannings et al. 1987; Sarell and McGuinness 1996; Hobbs 2001). This territory clustering has been observed in other songbird species, and is a sign that there are additional factors in the species' habitat selection that have not yet been identified (Perry and Anderson 2003; Tarof and Ratcliffe 2004; Mills et al. 2006; Roth and Islam 2007). Substantial effort has been directed towards habitat selection research in Brewer's Sparrows; however, the results that have been found have been highly variable (Table 1), leaving uncertainty about the factors leading to territory clustering in the species.

In this thesis I examined fine-scale (territory-level) habitat selection in Brewer's Sparrows using two approaches. In **Chapter 2**, I employed previously unused direct measures of habitat preference to determine whether the uneven distributions of sparrows can be explained by vegetation patterns. I coupled this approach with a more traditional patch occupancy analysis, using data collected over several seasons. In **Chapter 3**, I assessed the potential for social attraction in the species by conducting a call-playback experiment in physically suitable but previously unoccupied areas. In **Chapter 4**, I discuss the relevance of the results for Brewer's Sparrow conservation in the South Okanagan and suggest one avenue of research that warrants further exploration.

Table 1 A summary of the studies that have examined habitat associations of Brewer's Sparrows across the species' breeding range. I distinguish between studies that based associations on the occupancy (presence/absence) and relative abundance of Brewer's Sparrows across sites. (+) and (-) indicate the direction of habitat associations. Ranges in vegetation variables are given when the associations were highest within an intermediate range.

		Shrubs		Grasses	Forbs
		<i>Cover/Density</i>	<i>Size</i>	<i>Cover</i>	<i>Cover</i>
New Mexico	Larson and Bock (1986) <i>Occupancy</i>	15-45% shrub cover	20-60cm tall	10-40% cover	
Nevada / Oregon	Olson (1974) <i>Relative abundance</i>	12-49% sage cover			
	Wiens et al. (1987) <i>Occupancy</i>	23-37% shrub cover			
	McAdoo et al. (1989) <i>Relative abundance</i>	17-21% shrub cover	35-52cm tall	(-) crested wheat grass	
	Rotenberry and Wiens (1980) <i>Occupancy</i>			(-) all grass	
Washington	Dobler et al. (1996) <i>Relative abundance</i>	3-19% shrub cover			
Montana / Wyoming	Walcheck (1970) <i>Relative abundance</i>	53% shrub cover			
	Bock and Bock (1987) <i>Relative abundance</i>	3425 shrubs/ha			
	Chalfoun and Martin (2007) <i>Occupancy</i> <i>Relative abundance and timing of settlement</i>	(+) shrub cover/density (+) shrub cover and density of potential nest shrubs			
British Columbia	Sarell and McGuinness (1996) <i>Relative abundance</i>	10-30% shrub cover			
	Paczek (2002) <i>Relative abundance</i>	(+) sage cover		(+) junegrass	(+) lupine and buckwheat

CHAPTER 2: VEGETATION INFLUENCES PATCH OCCUPANCY BUT NOT SETTLEMENT AND DISPERSAL DECISIONS IN A DECLINING MIGRATORY SONGBIRD

2.1 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. I examined breeding territory selection in the Sagebrush Brewer's Sparrow (*Spizella breweri breweri*) at the northern extent of its range to test for influences on fine-scale habitat selection. I used an information theoretic approach to evaluate models relating a suite of vegetation characteristics to breeding habitat selection. I employed two methods: 1) assessment of patch occupancy at a territory scale, and 2) examination of individual decisions relating to settlement and dispersal. I found that patch occupancy was best predicted by models that included the cover of big sage (*Artemisia tridentata*) with the greatest likelihood of occupancy at 20-25% cover. However, vegetation characteristics did not predict individual territory selection decisions, providing little support for the idea that vegetation influences territory settlement or fidelity. 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 settlement or dispersal decisions on vegetation cover.

2.2 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. 2005, Winter et al. 2005). It is therefore important to study the cues used in habitat selection in order 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 characterising 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 factors can result in density differences among patches that are not related to differences in inherent patch quality (reflected in productivity; 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 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 particular, 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 Anderson 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. When species exhibit territory clustering, simple habitat suitability modelling based on patch occupancy data may fail to accurately define the habitat requirements of the species, and lead to the identification of target conservation areas that do not address the species' needs. 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 breweri*) has been described as a loosely colonial species throughout its breeding range (Wiens et al. 1985; Cannings et al. 1987; Sarell and McGuinness 1996), and recent surveys within the northern extent

of the range lend empirical support to those observations (Hobbs 2001, Figure 1). A recent study by Chalfoun and Martin (2007) examined multi-scale habitat selection in Brewer's Sparrows closer to the core of the species' range. At a landscape scale, they found that increased density and earlier settlement correlated with higher shrub cover and shrub density. At a finer scale, they found that Brewer's Sparrows select territories with high shrub cover and high density of potential nest shrubs. However, they did not examine vegetation characteristics outside the shrub layer, and used 'use' versus 'non-use' as a preference metric at the territory scale, which may miss more subtle factors that can be elucidated by investigating individual settlement decisions (Johnson 1980). In addition, Walker (2004) showed that the habitat associations that have been found for Brewer's Sparrows are region-specific (see Table 1), indicating that habitat selection must be investigated throughout the species' range. An understanding of habitat selection mechanisms may be particularly important at the northern periphery of species' ranges, where climatic variability may alter the breeding strategies and demography of populations (Järvinen 1989; Maurer and Brown 1989; La Sorte and Thompson 2007).

I examined breeding territory selection in the Sagebrush Brewer's Sparrow at the northern extent of its range to test for influences on fine-scale habitat selection. I used an information theoretic approach to evaluate models relating a suite of vegetation characteristics to habitat choice. My study approached the question of territory-level habitat selection in Brewer's Sparrows from two directions. I first assessed potential factors that could predict patch occupancy at a territory scale. Patch occupancy in this case referred to whether birds were present or absent at plots reflecting a range of vegetation characteristics during a given breeding season. I then tested whether habitat factors could predict territory settlement and dispersal (or territory fidelity) decisions in

banded individuals. In addition, I assessed the consequences of habitat selection decisions on reproductive success by monitoring nesting birds.

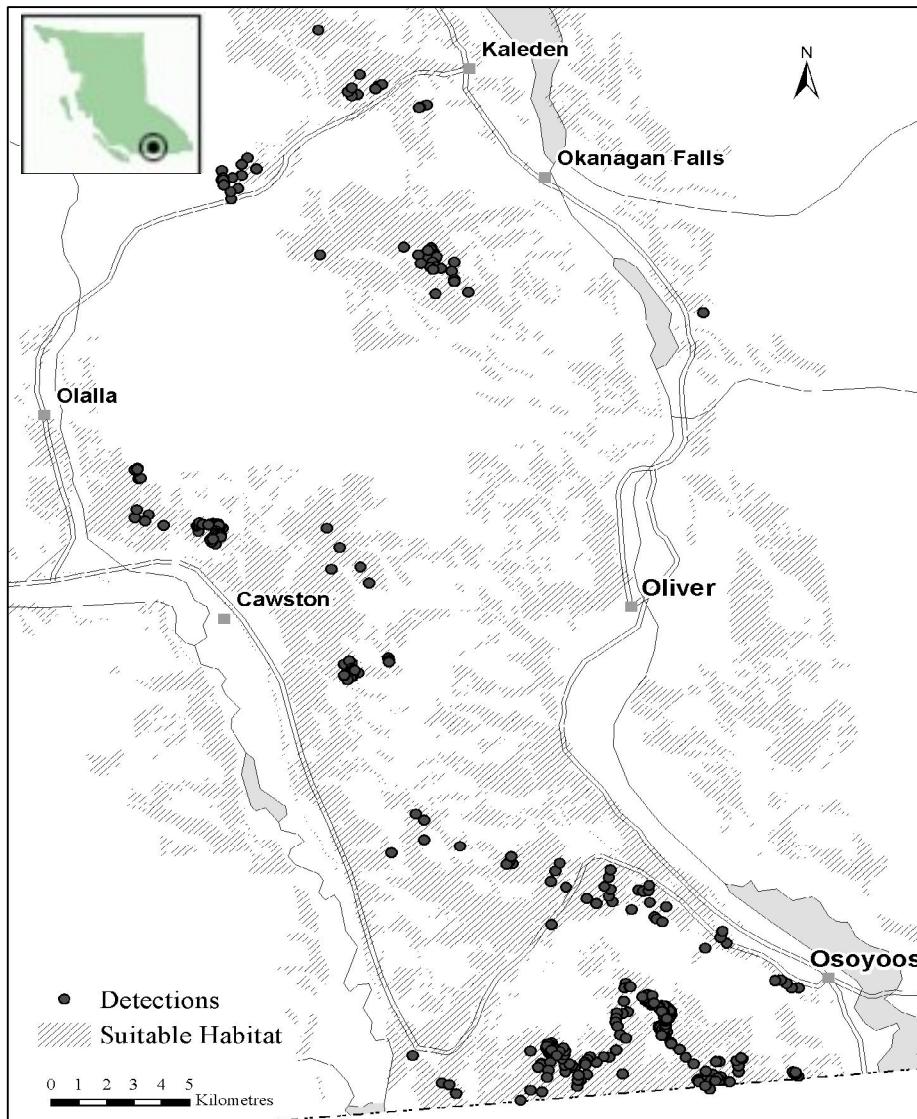


Figure 1 Brewer's Sparrow detections from Ministry of Environment surveys within habitat classed as suitable for the species in the South Okanagan region of British Columbia (location shown on inset map). Terrestrial Ecosystem Mapping (TEM) provided the basis for the suitability classification, with relative cover of dominant vegetation classes as the primary classification factor (Warman et al. 1998).

2.3 Methods

Focal species and study area

The Sagebrush Brewer's Sparrow is a neotropical migrant that inhabits sagebrush-steppe habitats during both wintering and breeding periods (Paige and Ritter 1999; Rotenberry et al. 1999). Breeding Bird Survey data shows that the species has been declining across its entire range at an average rate of 2.1% per year (Sauer et al. 2008). Due to this decline and continued conversion of sagebrush habitats for agricultural and residential development (Knick et al. 2003), the species is now listed as vulnerable or at-risk in 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 McGuinness 1996; Paczek and Krannitz 2004). Studies at a coarse scale have suggested that the sparrows are more abundant at sites with intermediate (10-30%) cover of shrubs (Harvey 1992; Sarell and McGuinness 1996). Paczek and Krannitz (2004) also examined factors that influence sparrow density at a fine scale, and argued that sparrow densities were positively correlated with sagebrush (*Artemisia* spp.), two species of robust forbs (parsnip-flowered buckwheat *Eriogonum heracleoides* and silky lupine *Lupinus sericeus*), and junegrass (*Koeleria macrantha*). However, their study was conducted in a year defined by abnormally high spring precipitation, and their analysis treated density as a categorical rather than continuous variable and accepted variables as significant with p-values of less than 0.1. These issues limit the reliability of their results as realistic measures of Brewer's Sparrow habitat associations in the South Okanagan. Because the territory clustering that has been observed in the species is most likely to be explained by factors that influence selection at a fine scale, additional attention is needed to assess fine-scale habitat selection in this species.

I studied fine-scale habitat selection decisions in the South Okanagan region of British Columbia (Figure 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. 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, and Kilpoola - KIL). Dominant vegetation on all sites is big sage (*Artemisia tridentata*) with a mixed understory of native and non-native grass species and a sparse forb layer dominated by lupine and parsnip-flowered buckwheat. 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 three hours 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 birds were observed at the majority of the plots (i.e., 76% of plots were unoccupied). I therefore classified plots as either occupied or unoccupied in any year for analyses.

Banding and monitoring of reproductive success

I 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. The majority of the males (>80%) within the research plots were banded in 2006 and 2007. Less than 10% of the females were banded because our objective was to study territory selection, which is done by males. In 2008, we focused primarily on the activities of returning, previously banded birds. Sites were monitored every two to four days throughout the breeding season to re-sight 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 three to four 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 nine days (Rotenberry and Wiens 1991). In the absence of observations of fledglings, nests were assumed to have fledged if the nest was empty no fewer than eight 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.

Settlement monitoring

The precise order in which territories were settled by males was monitored at all three sites in 2007. I visited each site every two days beginning the first week of April, 2007, to re-sight previously banded individuals, and detect and band new arrivals. To track settlement order, I recorded the first location of each bird that was defending an area through song. Un-marked 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 (four days) of commencing territorial behaviour. I then

recorded the locations of each individual using a GPS daily from April 14th to July 1st, and calculated a territory centre based on the average 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 average 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

I used the daily re-sighting 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 greater than 50 m (the average 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 re-settled within 50 m of their previous territory.

Vegetation assessment

Once breeding was complete, I 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 in order to avoid disturbing the birds during settlement and nesting and potentially influencing their territory selection decisions or reproductive success. I 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. I also recorded the height of each shrub. At the 5, 15 and 25 m points along each of four the transects, I estimated the percent cover of individual forb and grass species using standard 20 cm x 50 cm Daubenmire plots (Daubenmire 1959).

Statistical analysis

I 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. I considered four different categories of vegetation cover, each of which contained multiple variables (Table 2). Where previous findings indicated selection for intermediate measures, I included both linear and squared terms (Wiens and Rotenberry 1985; Petersen and Best 1985; Larson and Bock 1986; Howe et al. 1996; Sarell and McGuinness 1996; Mahony 2003). The robust forbs grouping included species found by Pazcek and Krannitz (2004) to influence Brewer's Sparrow density plus species of similar growth form. Grass cover was split into two variables: native and non-native species, to allow for detection of their potentially contrasting effects. 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*shrubs cover interactions were included because I expected the value of forbs in providing food sources to become apparent only when sufficient shrub cover was present to support nesting. It also included a year term and interactions between year and each of the vegetation terms. The shrub size term was not included in the patch occupancy analysis because size measurements were not collected prior to 2007. 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 overparameterising models fitted to the smaller territory fidelity dataset, I included only the shrub cover and forb cover terms, which had received some support in previous analyses (i.e., $\Delta AIC_c < 4$; Burnham and Anderson 1998).

Table 2 Groupings of sub-variables into more general terms for incorporation into models that predict fine-scale habitat selection in Brewer's Sparrows.

Group term	Component variables
Shrub cover	mean big sage cover + mean cover of other shrub species + mean big sage cover ²
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 (<i>Balsamorhiza sagittata</i> , <i>Eriogonum heracleoides</i> , <i>Lithospermum ruderales</i> , <i>Lupinus sericeus</i> , <i>Lupinus sulphureus</i> , <i>Verbascum thapsus</i>)
Grass cover	mean cover of non-native grass species + mean cover of native grass species

Within each candidate model set, I tested the relative support for each of the models using an information theoretic approach (Burnham and Anderson 1998). Akaike Information Criterion values for small sample sizes (AICc) were derived for each model using the output of general linear models (settlement order analysis), or logistic regressions (presence-absence, territory fidelity, and reproductive success analyses) computed in SAS version 9.1. AICc values were used in all analyses because the sample sizes divided by the number of models in the candidate sets were always less than 40 (Burnham and Anderson 1998). QAICc values (AICc for over-dispersed data)

were used for the presence-absence (patch occupancy) analysis because the calculated variance inflation factor (\hat{c}) exceeded 1.0 (Burnham and Anderson 1998). AICc and QAICc values give a measure of the level of fit of the data to the model weighted by the number of variables in the model. Low AICc or QAICc values reflect both better fit of the data to the model and a low likelihood of model overfitting. $\Delta(Q)AICc$ values were calculated as the differences between the (Q)AICc of each model and that of the most parsimonious model. (Q)AICc 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 $\Delta(Q)AICc$ values and used to assess the relative support for each of the models. Models with high w_i values were the best-supported by the data. Parameter likelihoods and parameter estimates and their associated unconditional standard errors were also computed to assess the relative influences of the parameters present in the best-supported models. An AIC parameter likelihood is the sum of the w_i of all models in which the parameter was included. An AIC 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. An AIC unconditional standard error is defined as the standard error of each parameter weighted by the AICc weight of each model in which the parameter was included.

A discriminant function analysis (DFA) was used to determine whether old and new territories of dispersing birds could be distinguished on the basis of vegetation parameters. Only three of the of the vegetation parameters, big sage cover, other shrub cover, and forb cover, were used in the DFA because the analysis could not be run with greater than three terms due 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 $\Delta(Q)AICc < 4$, Burnham and Anderson 1998) in the AIC analyses.

2.4 Results

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). Only one of the 19 models examining the influence of habitat characteristics on the occupancy of Brewer's Sparrows received strong support ($\Delta\text{QAIC}_C < 2$), with a further two models receiving moderate support ($\Delta\text{QAIC}_C < 4$, Burnham and Anderson 1998, Table 4). The best-supported model included only the term, shrub cover, and received more than three times the level of support of the next best-supported model ($w_i = 0.62$ vs. 0.17, respectively). Shrub cover was included in the top nine models and had the highest parameter likelihood of any explanatory variable (0.99, Table 5). Model averaged parameter estimates for big sage cover and big sage cover squared indicate that Brewer's Sparrows are more likely to occur in areas with intermediate (20-25%) sage cover (Figure 2). The parameter likelihoods associated with all other variables were low and the variability surrounding their model estimates was high (Table 5). The absence of support for interactive terms indicates that shrub effects occur independently of forb cover, and that habitat does not vary across years.

Table 3 Means and 95% confidence intervals for vegetation characteristics within point count plots that were occupied and unoccupied by Brewer's Sparrow between 2003 and 2005. Sample sizes are shown in brackets.

Variable	Occupied (35)		Unoccupied (109)	
	Mean	95% C.I.	Mean	95% C.I.
Big sage cover (%)	19.9	17.1 - 22.7	9.5	7.5 - 11.6
Other shrub cover (%)	5.7	4.1 - 7.2	6.1	4.7 - 7.5
Forb cover (%)	4.8	3.1 - 6.6	3.7	2.8 - 4.5
Native grass cover (%)	12.1	9.6 - 14.7	12.4	11.0 - 13.7
Non-native grass cover (%)	2.0	0.8 - 3.2	3.2	2.2 - 4.1

Table 4 AIC ranking (by w_i) of candidate models that predict patch occupancy (from point counts) of Brewer's Sparrows in the South Okanagan, British Columbia between 2003 and 2005.

Model	N	K ^a	QAICc	ΔAICc	w_i	Pseudo r^{2b}
occupancy = shrub cover	144	5	86.869	0.000	0.620	0.33
occupancy = shrub cover + forb cover + shrub cover*forb cover	144	9	89.436	2.567	0.172	0.39
occupancy = shrub cover + grass cover	144	7	90.841	3.972	0.085	0.31
occupancy = year + shrub cover	144	7	91.137	4.267	0.073	0.33
occupancy = shrub cover + forb cover + shrub cover*forb cover + grass cover	144	11	93.766	6.897	0.020	0.32
occupancy = year + shrub cover + forb cover + shrub cover*forb cover	144	11	93.985	7.116	0.018	0.39
occupancy = year + shrub cover + grass cover	144	9	95.291	8.422	0.009	0.31
occupancy = year + shrub cover + forb cover + shrub cover*forb cover + grass cover	144	13	98.510	11.641	0.002	0.33
occupancy = year + shrub cover + year*shrub cover	144	13	101.188	14.319	0.001	0.34
occupancy = forb cover	144	3	101.521	14.652	0.000	0.02
occupancy = null	144	2	102.512	15.643	0.000	0.00
occupancy = grass cover	144	4	103.418	16.549	0.000	0.02
occupancy = forb cover + grass cover	144	5	104.648	17.779	0.000	0.04
occupancy = year + forb cover	144	5	105.737	18.868	0.000	0.02
occupancy = year	144	4	106.668	19.799	0.000	0.00
occupancy = year + grass + year*grass cover	144	10	107.685	20.816	0.000	0.04
occupancy = year + grass cover	144	6	107.706	20.837	0.000	0.02
occupancy = year + forb cover + grass cover	144	7	109.016	22.147	0.000	0.04
occupancy = year + forb cover + year*forb cover	144	7	109.140	22.271	0.000	0.02

^a The number of estimated parameters in the model including the variance

^b Nagelkerke's pseudo r^2

Table 5 The parameter likelihood, weighted estimate and unconditional standard error of every parameter included in the candidate model set predicting patch occupancy in Brewer's Sparrows.

Parameter	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Intercept	1.000	4.376	1.347
2003	0.092	-0.009	0.044
2004	0.092	0.012	0.047
big sage cover	0.988	-0.354	0.133
big sage cover ²	0.988	0.007	0.003
other shrub cover	0.988	-0.001	0.047
forb cover	0.211	-0.071	0.119
non-native grass cover	0.110	-0.002	0.009
native grass cover	0.110	-0.002	0.006
forb cover*big sage cover	0.211	0.008	0.014
forb cover*big sage cover ²	0.211	0.000	0.000
forb cover*other shrub cover	0.211	-0.002	0.004
2003*big sage cover	0.000	0.000	0.000
2004*big sage cover	0.000	0.000	0.000
2003*big sage cover ²	0.000	0.000	0.000
2004*big sage cover ²	0.000	0.000	0.000
2003*other shrub cover	0.000	0.000	0.000
2004*other shrub cover	0.000	0.000	0.000
2003*forb cover	0.000	0.000	0.000
2004*forb cover	0.000	0.000	0.000
2003*non-native grass cover	0.000	0.000	0.000
2004*non-native grass cover	0.000	0.000	0.000
2003*native grass cover	0.000	0.000	0.000
2004*native grass cover	0.000	0.000	0.000

^{Note} Negative parameter estimates actually represent positive effects.

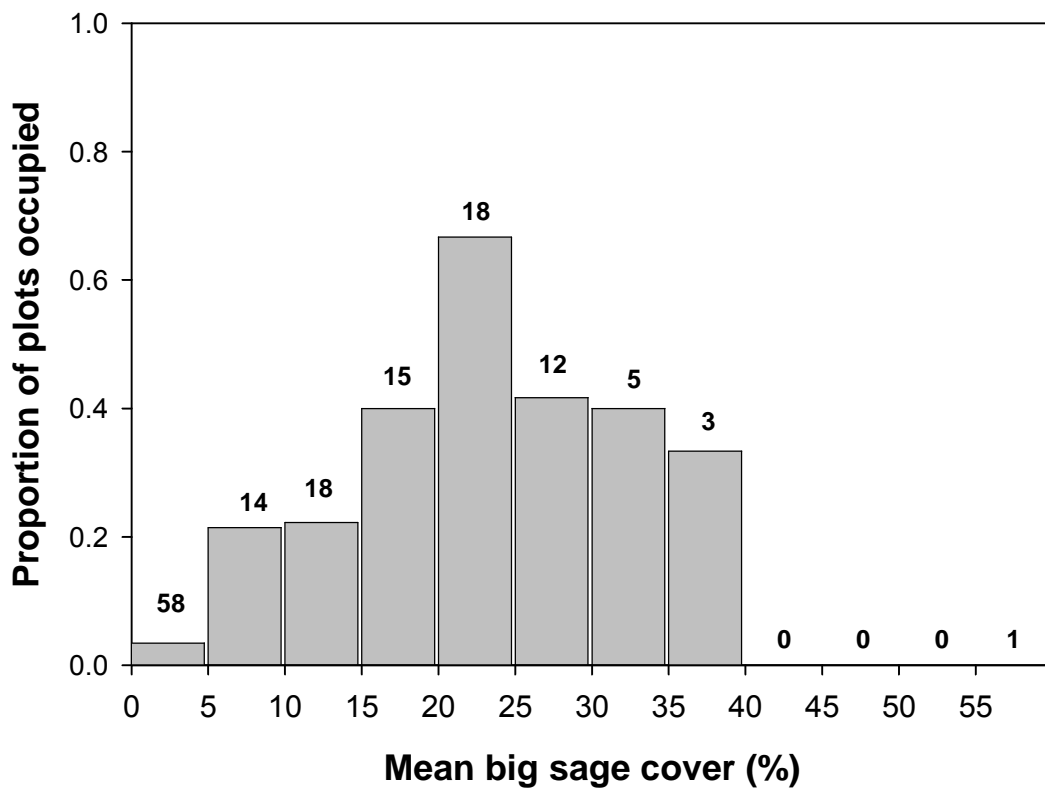


Figure 2 The proportion of point count plots occupied by Brewer's Sparrows across the three study years (2003-2005) presented according to the mean % cover of big sage within the plots (n = 144). The numbers above the bars represent the number of plots within each sage cover category.

Settlement order

The vegetation characteristics within territories settled by Brewer's Sparrows in 2007 are summarized in Table 6. Males settled on territories over a six-week period spanning April 14th – June 1st. 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 two of the 16 models examined received strong AIC support ($\Delta AICc < 2$): the null model, and the model that included forb cover ($w_i = 0.451$ and 0.177 , respectively; Table 7). However, while the model with forb cover received strong AIC support, the parameter likelihood for forb cover was low, and its parameter estimate was both low and had an unconditional SE that bounded zero (Table 8). 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 re-run with male age as a base variable, although there is strong support for the model with age only, indicating that ASY (after second year) birds established territories earlier than SY (second year) birds (results not presented).

Table 6 Means and 95% confidence intervals of vegetation characteristics within territories settled by Brewer's Sparrows in 2007 (n = 79).

Variable	Mean	95% C.I.
Big sage cover (%)	24.3	22.2 - 25.6
Other shrub cover (%)	10.1	8.5 - 11.7
Shrub width (m)	59.3	56.0 - 62.2
Shrub height (m)	75.1	72.2 - 77.9
Forb cover (%)	7.1	5.2 - 8.5
Native grass cover (%)	13.9	11.3 - 16.0
Non-native grass cover (%)	11.5	9.1 - 14.1

Table 7 AIC ranking (by w_i) of candidate models that predict settlement order of Brewer's Sparrows in the South Okanagan, British Columbia in 2007.

Model	N	K ^a	AICc	ΔAICc	w_i	r^2
settlement rank = null	75	2	317.432	0.000	0.451	0.00
settlement rank = forb cover	75	3	319.309	1.877	0.177	0.17
settlement rank = shrub size	75	5	319.812	2.380	0.137	0.40
settlement rank = grass cover	75	4	320.934	3.501	0.078	0.20
settlement rank = shrub size + forb cover	75	6	322.130	4.698	0.043	0.40
settlement rank = shrub cover	75	5	322.610	5.177	0.034	0.30
settlement rank = grass cover + forb cover	75	5	322.896	5.463	0.029	0.22
settlement rank = shrub size + grass cover	75	7	323.687	6.255	0.020	0.40
settlement rank = shrub size + shrub cover	75	8	323.977	6.544	0.017	0.41
settlement rank = shrub size + grass cover + forb cover	75	8	326.014	8.582	0.006	0.39
settlement rank = shrub cover + grass cover	75	7	326.813	9.380	0.004	0.29
settlement rank = shrub size + shrub cover + grass cover	75	10	328.423	10.991	0.002	0.39
settlement rank = forb cover + shrub cover + forb cover*shrub cover	75	9	330.474	13.042	0.001	0.36
settlement rank = shrub size + shrub cover + forb cover + forb cover*shrub cover	75	12	332.907	15.475	0.000	0.38
settlement rank = shrub cover + grass cover + forb cover + forb cover*shrub cover	75	11	335.451	18.019	0.000	0.35
settlement rank = shrub size + shrub cover + grass cover + forb cover + forb cover*shrub cover	75	14	337.705	20.272	0.000	0.37

^a The number of estimated parameters in the model including the variance

Table 8 The parameter likelihood, weighted estimate and unconditional standard error of every parameter included in the candidate model set predicting settlement order in Brewer's Sparrows.

Parameter	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Intercept	1.000	11.120	16.212
big sage cover	0.058	0.053	0.078
big sage cover ²	0.058	-0.001	0.001
other shrub cover	0.058	-0.015	0.026
shrubs width	0.226	-0.001	0.024
shrubs height	0.226	0.142	0.416
shrubs height ²	0.226	-0.001	0.003
forb cover	0.256	0.065	0.098
non-native grass cover	0.140	-0.006	0.024
native grass cover	0.140	-0.012	0.029
forb cover*big sage cover	0.001	-0.005	0.005
forb cover*big sage cover ²	0.001	0.000	0.000
forb cover*other shrub cover	0.001	0.001	0.001

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. Failure of nesting attempts was due entirely to predation. There was no evidence of partial brood loss, abandonment or total brood mortality due to extreme climatic events. The average number of fledglings produced per nest across the three sites in 2007 was 1.45 ± 0.36 (95% C.I.). The vegetation characteristics within territories of Brewer's Sparrows that were successful and within those of birds that were unsuccessful are summarized in Table 9. 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 ($\Delta AICc < 2$) and an additional three models received moderate support ($\Delta AICc < 4$; Table 10). 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 (Table 10). Parameter likelihoods for all terms were also low and the model averaged parameter estimates for all habitat variables had large standard errors (Table 11), providing little support for a relationship between habitat variables and reproductive success.

Table 9 Means and 95% confidence intervals of vegetation characteristics within territories of Brewer’s Sparrows that were successful (fledged one or more young) and within territories of birds that experienced reproductive failure in 2007. Sample sizes are in brackets.

Variable	Success (33)		Failure (26)	
	Mean	95% C.I.	Mean	95% C.I.
Big sage cover (%)	23.82	21.6 - 26.1	23.31	19.7 - 26.9
Other shrub cover (%)	11.79	9.3 - 14.3	7.55	5.4 - 9.7
Shrub width (m)	59.92	54.8 - 65.0	56.73	53.0 - 60.4
Shrub height (m)	74.65	69.5 - 79.8	74.57	70.5 - 78.6
Forb cover (%)	8.23	5.5 - 11.0	4.59	2.6 - 6.6
Native grass cover (%)	15.53	12.1 - 19.0	12.28	8.9 - 15.6
Non-native grass cover (%)	9.11	6.0 - 12.2	13.50	9.1 - 17.9

Table 10 AIC ranking (by w_i) of candidate models that predict reproductive success of Brewer's Sparrows in the South Okanagan, British Columbia in 2007.

Model	N	K ^a	AICc	ΔAICc	w _i	Pseudo r ^{2b}
success = shrub cover	57	5	90.095	0.000	0.279	0.35
success = forb cover	57	3	90.103	0.008	0.277	0.24
success = null	57	2	91.207	1.112	0.160	0.00
success = grass cover + forb cover	57	5	93.000	2.905	0.065	0.28
success = grass cover	57	4	93.130	3.035	0.061	0.26
success = shrub size	57	5	93.804	3.708	0.044	0.34
success = shrub size + shrub cover	57	8	94.353	4.258	0.033	0.46
success = shrub cover + grass cover	57	7	94.448	4.353	0.032	0.39
success = shrub size + forb cover	57	6	94.519	4.424	0.031	0.35
success = shrub size + grass cover	57	7	97.487	7.392	0.007	0.35
success = shrub size + grass cover + forb cover	57	8	97.919	7.824	0.006	0.36
success = forb cover + shrub cover + forb cover*shrub cover	57	9	98.449	8.354	0.004	0.41
success = shrub size + shrub cover + grass cover	57	10	100.003	9.907	0.002	0.46
success = shrub cover + grass cover + forb cover + forb cover*shrub cover	57	11	104.119	14.024	0.000	0.45
success = shrub size + shrub cover + forb cover + forb cover *shrub cover	57	12	105.123	15.028	0.000	0.50
success = shrub size + shrub cover + grass cover + forb cover + forb cover*shrub cover	57	14	111.704	21.608	0.000	0.51

^a The number of estimated parameters in the model including the variance

^b Nagelkerke's pseudo r²

Table 11 The parameter likelihood, weighted estimate and unconditional standard error of every parameter included in the candidate model set predicting reproductive success in Brewer's Sparrows.

Parameter	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Intercept	1.000	4.642	3.844
big sage cover	0.350	-0.070	0.099
big sage cover ²	0.350	0.001	0.001
other shrub cover	0.350	0.033	0.045
shrub width	0.122	0.002	0.006
shrub height	0.122	-0.035	0.085
shrub height ²	0.122	0.000	0.001
forb cover	0.383	0.034	0.048
non-native grass cover	0.173	-0.006	0.013
native grass cover	0.173	-0.002	0.008
forb cover*big sage cover	0.005	0.000	0.000
forb cover*big sage cover ²	0.005	0.000	0.000
forb cover*other shrub cover	0.005	0.000	0.000

^{Note} Negative parameter estimates actually represent positive effects.

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 12. 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 ($\Delta AICc < 2$); one other model received moderate support ($\Delta AICc < 4$; Table 13). The only strongly supported model was the one with the term, previous reproductive success ($w_i = 0.652$; Table 13). 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 parameter estimate for that term was low and the error surrounding it high (Table 14), indicating that it does not have a real influence on territory fidelity. The remaining models, which included the null model, and the models with shrub cover and shrub*forb cover interactions, were weakly supported ($\Delta AICc > 4$). For individuals that did establish new territories, a discriminant function analysis could discern no differences between the old and new territories on the basis of big sage cover, other shrub cover, and shrub height (Table 14; $F_{3,36} = 0.49$, $p = 0.69$). 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.

Table 12 Means and 95% confidence intervals of vegetation characteristics within territories of Brewer's Sparrows that stayed in the same territory from year to year (2006 to 2007 or 2007 to 2008) and within the initial territories of birds that dispersed to a new territory. Sample sizes are shown in brackets.

Variable	Stayed (19)		Moved (20)	
	Mean	95% C.I.	Mean	95% C.I.
Big sage cover (%)	25.0	21.9 - 28.2	22.2	18.4 - 26.0
Other shrub cover (%)	9.6	7.1 - 12.1	7.8	5.0 - 10.7
Forb cover (%)	7.3	3.7 - 11.0	5.5	3.4 - 7.7

Table 13 AIC ranking (by w_i) of candidate models that predict territory fidelity of Brewer's Sparrows in the South Okanagan, British Columbia between 2006 and 2008.

Model	N	K ^a	AICc	Δ AICc	w_i	Pseudo r^{2b}
fidelity = previous success	28	3	12.025	0.000	0.652	0.23
fidelity = forb cover + previous success	28	4	14.185	2.160	0.222	0.26
fidelity = null	39	2	17.054	5.029	0.053	0.00
fidelity = shrub cover + previous success	28	6	17.246	5.221	0.048	0.39
fidelity = forb cover	39	3	18.873	6.848	0.021	0.03
fidelity = shrub cover	39	5	22.279	10.254	0.004	0.10
fidelity = forb cover + shrub cover + forb cover*shrub cover	39	9	29.201	17.176	0.000	0.29
fidelity = forb cover + shrub cover + forb cover*shrub cover + previous success	28	10	30.042	18.017	0.000	0.51

^a The number of estimated parameters in the model including the variance

^b Nagelkerke's pseudo r^2

Table 14 The parameter likelihood, weighted estimate and unconditional standard error of every parameter included in the candidate model set predicting Brewer's Sparrow territory fidelity.

Parameter	Parameter likelihood	Weighted parameter estimate	Unconditional SE
Intercept	1.0000	1.4423	1.4396
big sage cover	0.0520	-0.0478	0.0997
big sage cover ²	0.0520	0.0009	0.0018
other shrub cover	0.0520	0.0034	0.0099
forb cover	0.2430	-0.0005	0.0005
forb cover*big sage cover	0.0002	0.0000	0.0000
forb cover*big sage cover ²	0.0002	0.0000	0.0000
forb cover*other shrub cover	0.0002	0.0000	0.0000
success	0.9220	-1.7246	0.9188

Note Negative parameter estimates actually represent positive effects.

Table 15 Means and 95% confidence intervals for vegetation characteristics within previous (1) and subsequent (2) territories for Brewer's Sparrows that dispersed to new territories in the second year they were monitored (n = 20).

Variable	Territory 1		Territory 2	
	Mean	95% C.I.	Mean	95% C.I.
Big sage cover (%)	22.2	18.4 – 26.0	25.6	21.8 – 29.5
Other shrub cover (%)	7.8	5.0 – 10.7	7.5	4.5 – 10.6
Forb cover (%)	5.5	3.4 – 7.7	5.3	2.3 – 8.2

2.5 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 McGuinness 1996; Chalfoun and Martin 2007). This study adds to evidence that shrub cover is also important at a finer scale (Paczek and Krannitz 2004; Chalfoun and Martin 2007). In a single-year study conducted in the South Okanagan, Paczek and Krannitz (2004) found that Brewer's Sparrows were more abundant within territory-scale plots that had higher cover of sage (*Artemisia* spp.). In a multiple-year study conducted in the core of the Brewer's Sparrow breeding range, Chalfoun and Martin (2007) found that the sparrows are more likely to use territories with high shrub cover and density of potential nest shrubs. This 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), consistently predicts the occupancy patterns of Brewer's Sparrows. The results of these studies indicate that shrub cover can be used as a reliable criterion for the identification of suitable Brewer's Sparrow habitat throughout the species' range. This study also provides evidence that there is selection for an intermediate range of shrub cover. This pattern is supported by previous studies conducted at a broader scale throughout the Brewer's Sparrow's range (Wiens and Rotenberry 1985; Petersen and Best 1985; Larson and Bock 1986; Harvey 1992; Howe et al. 1996; Sarell and McGuinness 1996). Managers may therefore need to limit or eliminate grazing at sites selected for conservation of the species, since grazing has been found to increase shrub density in sagebrush-steppe habitats, possibly to a level that is unsuitable to support breeding Brewer's Sparrows (Harvey 1992; Paige and Ritter 1999).

I found little evidence to suggest that cover of forbs or grasses influence patch occupancy by Brewer's Sparrows. This is in contrast with the results of a one-year study conducted within the South Okanagan (Paczek and Krannitz 2004), which found that the cover of two robust forb and one grass species influenced the relative density of Brewer's Sparrows within occupied plots (evaluated using point counts). The two robust forbs found by Paczek and Krannitz (2004) to influence habitat use (silky lupine and parsnip-flowered buckwheat) were primary components of my robust forbs grouping. However, I found little support for the inclusion of a robust forb term in habitat occupancy models, either alone or as interactions with shrub cover or year. While the robust forb layer does support a population of arthropods that could serve as a potential food source for Brewer's Sparrows (Krannitz unpublished data), most foraging observations conducted for the species suggest that this activity occurs primarily in the shrub layer (Wiens et al. 1987; Rotenberry and Wiens 1998). My data suggests that robust forbs are not of great importance in providing food for Brewer's Sparrows, since multi-year patch occupancy patterns are not associated with the presence of those species. Since data collection for the Paczek and Krannitz (2004) study occurred during a year with abnormally high spring precipitation, resulting in an unusually well-developed forb community, the patterns found in that study are likely a consequence of anomalous environmental conditions.

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; Sedgwick 2004; Sergio and Newton 2003). 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 ASY and SY birds (10 days). Vegetation characteristics of the territories of later-arriving SY birds did not differ from those in the territories of more experienced conspecifics. Further, birds that dispersed did not select territories that differed, in any vegetation characteristics, from their previous ones. It is possible that my 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, due 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, since my results did not change when I included age as a base variable, and I also found no evidence for an influence of vegetation on territory selection decisions when following the fidelity/dispersal of returning birds, it is unlikely that the absence of a relationship between vegetation and settlement order is due to a methodological inadequacy. My 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 to 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 remarkable 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 I 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 McGuinness 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 on the basis of vegetation because reproductive success is unrelated to floristic cover or structure. Reproductive success is unrelated to vegetation characteristics because the primary factor influencing success in this study area is predation (this study; Welstead et al. 2003; Mahony 2003), and the success of the primary predators in the area in detecting and accessing Brewer's Sparrows' nests does not seem to be restricted by vegetation within breeding territories (Welstead et al. 2003). Potential predators in the South Okanagan include several species of snakes (gopher snake *Pituophis catenifer*, racer *Coluber constrictor mormon*, wandering garter snake *Thamnophis elegans*), corvids (American Crow *Corvus brachyrhynchos*, Common Raven *Corvus corax*, Black-billed Magpie *Pica hudsonia*), and small mammals (long-tailed weasel *Mustela frenata* and several rodent species). 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. A similar analysis of my data also found no evidence that nest shrub characteristics influenced breeding success (data not shown). Welstead et al. (2003) gave two primary explanations for their findings. First, they suggested that the shrub cover above Brewer's Sparrow nests was sufficient to preclude visual detection of nests by corvids, meaning that nesting birds were protected against predation by avian predators (see Sullivan and Dinsmore 1990). Second, they interpreted the lack of influence of shrub characteristics on actual predation to mean that avian predation is actually less significant in this study area than predation by mammals and snakes, which are less restricted by vegetation structure. A third explanation for the absence of a link between shrub characteristics and actual predation that Welstead et al. (2003) did not mention is that Brewer's Sparrow parents may be able to behaviourally compensate for reduced nest concealment by altering their daily activities to limit their chances of being detected by predators (Remeš 2005). However, regardless of whether the absence of a link between vegetation and predation is a consequence of predators' detection capabilities or parental compensation, the evidence from this study and Welstead et al. (2003) suggests that selection for certain vegetation characteristics within the range of vegetation cover represented in breeding clusters is not adaptive from a predation avoidance perspective. My finding that individuals are more likely to move to a new territory if they are unsuccessful does suggest, however, that birds may be able to reduce their chances of future predation by leaving areas where they have experienced predation in the past.

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

Conspecific attraction could be an alternative explanation for territory clustering in Brewer's Sparrows. Territorial individuals have been shown to cluster due to conspecific attraction in Collared Flycatchers *Ficedula albicollis* (Doligez et al. 2002), Least Flycatchers (Mills et al. 2006), Black-throated Blue Warblers (Hahn and Silverman 2007; Betts et al. 2008), Bobolinks *Dolichonyx oryzivorus* (Nocera et al. 2006), Black-capped Vireos *Vireo atricapilla* (Ward and Schlossberg 2004), and Baird's Sparrows *Ammodramus bairdii* (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 (Ward and Schlossberg 2004; Doligez et al. 2002; Ahlering et al. 2006; Hahn and Silverman 2007; Nocera et al. 2006).

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 Anderson (2003) suggested that clustering could act as a means of predator deterrence in Least Flycatchers (*Empidonax minimus*) because birds in clusters suffered less reproductive failure due to predation than birds outside clusters. Using broad-scale surveys (between six well-spaced sites), Welstead (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 characterised by high predator densities. When examined over the short term, it would lead to territory selection decisions that have no apparent link to habitat characteristics. I will assess the role of conspecific attraction in Brewer's Sparrow territory selection in the following chapter.

CHAPTER 3: CONSPECIFIC ATTRACTION INFLUENCES BREEDING HABITAT SELECTION OF A DECLINING MIGRATORY SONGBIRD

3.1 Abstract

The Sagebrush Brewer's Sparrow (*Spizella breweri breweri*) is a vulnerable species that breeds in small clusters within larger areas of suitable habitat. Clustered breeding that is unrelated to the distribution of resources may be explained by social attraction (conspecific cueing). I used a call-playback experiment to test the conspecific cueing hypothesis in this species. Playbacks were conducted during the spring settlement period in habitat that was physically suitable for breeding but had not been occupied during the previous two breeding seasons. Treatments were split between two periods that reflected peak settlement of experienced and first time breeders. In both periods, more males established and defended territories at plots where conspecific song was broadcast than at corresponding untreated controls. Breeding pairs were not, however, more abundant at treatment than at control plots. This could mean that males attracted to playbacks are lower quality than males in established breeding clusters, and thus less attractive to females, or that females require a threshold male group size in order to settle. These results lend support to the conspecific cueing hypothesis in this species, indicating that social attraction may play a role in Brewer's Sparrow habitat selection. They also suggest that traditional habitat models, which consider only resource distributions and not social factors, may be insufficient tools for the conservation of this and similar species. I discuss the utility of playbacks as a potential tool for the management of territorial songbirds.

3.2 Introduction

Habitat models that identify the suitability of management units based on the occupancy patterns of a species are a traditional approach to wildlife management (Jones 2001; Johnson 2007). However, there is increasing evidence that non-habitat cues may be equally or more important in directing settlement decisions, and scientists are advocating for the inclusion of these additional components in wildlife management planning (Campomizzi et al. 2008). The non-habitat cues that have most frequently been shown to influence individual settlement decisions include the locations or behaviour of predators and competitors. Predator distributions have been recognized as an important factor in the habitat use of prey in numerous species (Longland and Price 1991; Dickman 1992; Werner and Anholt 1996; Brown 1999; Fontaine and Martin 2006). Similarly, the distributions of heterospecific competitors have been shown to alter habitat selection across a broad range of taxa (Pimm and Rosenzweig 1981; Grossman et al. 1998; Durant 2000). Both predators and competitors alter species' distributions by causing them to avoid certain areas. However, recent research has shown that non-habitat cues can also work in the opposite direction. Social attraction (both conspecific and heterospecific) has been identified as a primary habitat selection cue in a number of species (conspecifics: Stamps 1988; Danchin et al. 1998; Doligez et al. 2002; Nocera et al. 2006; Donahue 2006; Parejo et al. 2006, heterospecifics: Thomson et al. 2003; Parejo et al. 2004; Fletcher 2007; Forsman et al. 2008). Individuals may choose to settle in close vicinity to conspecifics or heterospecifics because the presence of those individuals reflects habitat quality, or because group formation creates individual benefits (e.g., increased likelihood of mate attraction, extra-pair mating or predator detection) that exceed the potential costs (e.g., competition) of settling close to others. Conspecific

attraction, in particular, is a likely explanation for territorial clustering that is seemingly unrelated to the distribution of key habitat features.

The importance of conspecific attraction in the settlement of territorial songbirds has typically been demonstrated through the use of call-playback experiments (Ward and Schlossberg 2004; Ahlering et al. 2006; Hahn and Silverman 2006 and 2007; Mills et al. 2006; Nocera et al. 2006; Fletcher 2007; Betts et al. 2008). These studies showed that individuals were attracted to and established territories in areas where conspecific song was broadcast. In some cases, individuals could even be convinced to settle in areas where habitat was unsuitable for breeding, demonstrating the strength of social attraction relative to other potential cues (Nocera et al. 2006; Betts et al. 2008). These results have led some scientists to suggest that call-playbacks could be used as a management tool, allowing managers to establish populations in habitats where individuals were previously absent (Ahlering and Faaborg 2006; Hahn and Silverman 2007). This method of population re-establishment has already had some success in colonial species (Kress 1983; Jeffries and Brunton 2001; Parker et al. 2007). For species of conservation concern, it may be useful to test the potential for attraction to call-playbacks in order to determine whether it can be used as a viable management tool.

The Sagebrush Brewer's Sparrow (*Spizella breweri breweri*) is a sagebrush-steppe obligate, relying on these habitats during both breeding and wintering periods (Rotenberry et al. 1999). Breeding Bird Survey (BBS) data from 1966-2007 showed range-wide declines in Brewer's Sparrows of 2.1% per year (Sauer et al. 2008), and due to this decline and continued conversion of sagebrush habitats for agriculture and residential development, the species is now listed as vulnerable or at-risk in both the United States and Canada. However, while habitat loss is one of the factors that have been implicated in the Brewer's Sparrow's range-wide decline, individuals have been

shown to cluster their territories into small areas within larger expanses of seemingly suitable habitat, leaving much 'suitable' habitat unoccupied (Wiens et al. 1985; Cannings et al. 1987; Sarell and McGuinness 1996; Hobbs 2001). This clustering has thus far been unexplained by studies focusing on preference for certain vegetation characteristics (Chapter 2), and may be a consequence of social attraction.

I tested the conspecific cueing hypothesis by investigating the response of Brewer's Sparrows to playback of conspecific song during the settlement period. Response to playback during the post-breeding period was not assessed since fledglings move to riparian areas during post-breeding (Yu 1999) suggesting that prospecting by juveniles is unlikely. Playbacks were conducted at two periods associated with the arrival of older, experienced breeders (after second year – ASY) and first time breeders (second year – SY). I examined whether playback sites both attracted and retained more territorial males than untreated control sites, whether playback sites yielded more breeding pairs, and whether the response to playbacks varied with the period and hence age of the birds returning to the breeding grounds.

3.3 Methods

Study area

This study was conducted in the South Okanagan region of British Columbia between April 27th and June 9th, 2008. Experimental plots were established at two sites: on land holdings managed by the Nature Trust of British Columbia (White Lake - WL), and in the East Chopaka region of the Okanagan Grasslands Protected Area (International Grasslands - ING). Dominant vegetation on all plots was big sage (*Artemisia tridentata*) with a mixed understory of native and non-native grass species and a sparse forb layer dominated by lupine (*Lupinus sulphureus* and *L. sericeus*) and

parsnip-flowered buckwheat (*Eriogonum heracleoides*). All study plots were located within larger expanses of unconverted sagebrush.

Experimental design

I selected 44 plots at two sites (ING and WL), confirmed by point count data as having no occupants during the previous two breeding seasons but by vegetation assessments as being suitable for breeding. All plots were between 200 and 350 m from their nearest neighbour, and between 200 and 1190 m from the core Brewer's Sparrow breeding cluster. Point count observations were conducted twice per season during the breeding period and consisted of 15 min of audio and visual observations where all birds within a 100 m radius were noted. Sites were considered suitable for breeding if they had 10-30% cover of big sage (*Artemisia tridentata*). Big sage is the primary nesting, foraging and perching shrub for the species (Rotenberry et al. 1999) and 10-30% cover was selected as the suitable range based on Harvey (1992), Sarell and McGuiness (1996), and Chapter 2. I randomly assigned the 44 plots as either controls or treatments (playbacks) in one of two periods, so that each period had 10 control and 12 playback plots. The two periods reflected peak settlement for experienced (ASY) birds, and inexperienced (SY) birds. Peak settlement for the two age groups was determined based on settlement observations from a related study conducted in 2007 (Chapter 2).

Treatments consisted of playing songs of local males for six hours per day once every two days for an 18-day period. The first period, reflecting peak settlement for ASY birds, was between April 27th and May 14th, and the second period, reflecting peak settlement of SY birds, was between May 15th and June 1st. Each playback system included two Nexxtech portable amplified speakers powered by four C-batteries, and one Centrios 2GB mp3 player. These systems projected sound with sufficient amplitude

for song to be detectable by human observers standing 75 m from the source. Each mp3 player was loaded with 10 song tracks: four long song recordings and six short songs (40-150 seconds), and four silence tracks (60 seconds), which were played at random. At each plot, three speaker systems were installed for each day of playback, emulating a group of three singing birds. The first speaker system was located 75 m from the centre of the plot, at a random compass bearing. The other two systems were also located 75 m from the plot centre, at 120° from the random bearing. Speaker systems were suspended from sage shrubs to imitate perched, singing males. Since treatments occurred at two sites, each plot received a treatment every second day. I chose to use three speakers per plot and conduct playbacks for six hours per day following a small-scale pilot study conducted in 2007. In the pilot study, I had only one speaker per plot and conducted playbacks at each plot for only one hour per day (following the methods of Nocera et al. 2006), and found that plot visitation rates were too low to conclude that birds had been able to detect the playbacks.

Each plot (treatment and control) was monitored for two 1 h intervals during the playback treatments to record visitation rates, and then for six days immediately following the playback period to determine whether significantly more males established territories, attracted mates and attempted to breed on plots where conspecific song was broadcast than on untreated controls. Any males attracted to treatment plots were captured with mist-nets and colour-banded. Birds were assigned to the ASY and SY age-classes at the time of banding based on patterns of wear in their primary and tail feathers (Mattias Leu, personal communication; Pyle 1997). They were also sexed at the time of banding based on the development of the cloacal protuberance. I succeeded in catching all of the males that established territories in the ASY settlement period and five of the seven males from the SY period, and the ages of all individuals corresponded correctly with the 'peak settlement period' they responded in. I did not capture and age

females. Plots were revisited every four to six days in order to monitor banded birds and breeding pairs, locate nests and determine breeding success.

Vegetation sampling

Once breeding was complete, I conducted vegetation sampling at each plot to gather data on key vegetation characteristics that have predicted coarse-scale Brewer's Sparrow habitat occupancy in other studies (Harvey 1992; Sarell and McGuinness 1996; Paczek et al. 2004; Chalfoun and Martin 2007; Chapter 2), and that could confound the response of birds to playback treatments. I established two 50 m transects intersecting the centre of the plot. The first transect was established at a random bearing, and the second was established at a 90° angle from the first. On each transect I recorded the intersection points (to derive percent cover), height and species of each shrub.

Statistical analyses

I first confirmed that plots randomly assigned to the two periods and experimental treatment did not differ in their mean percent cover of big sage and shrub height using two-factor analyses of variance (ANOVAs). I subsequently examined whether the experimental treatment in playback period one or two influenced three response variables: the number of males attracted to playback plots during two hours of observation, the numbers of males that established territories, and the number of breeding pairs. Playbacks typically elicited either no response or attracted one male Brewer's Sparrow (very few plots attracted greater than one male). I therefore analysed the data with a yes/no response using general linear models (GLMs) with a binomial distribution and a logit link. In all analyses I initially fitted a full model including treatment, period and the treatment*period interaction. I then sequentially removed non-significant terms beginning with the interaction and then the main effects until only

significant terms remained. Significance was evaluated using the change deviance (equivalent to χ^2) associated with dropping the term of interest from a fuller model. All statistical analyses were conducted in GenStat v10 (VSN International Ltd., 2007).

3.4 Results

Big sage cover and shrub height did not differ between control and playback plots or between plots within the two periods (Table 16). Playbacks had a significant effect on the number of males attracted to plots and the number of males that established territories on the plots during both periods (Table 16). Males visited playback plots over six times more frequently than control plots. The rate of territory establishment was over four times greater on playback plots than on controls. Neither the numbers attracted nor the numbers establishing territories varied with the playback period (Table 16). Playback did not have a significant influence on the number of pairs that formed in either period (Table 16). Four pairs attempted to breed, three from the ASY settlement period (one on a treatment plot, and two on a control plot) and one from the SY period (treatment plot). All three pairs from the ASY period were successful in fledging young; the pair from the SY period was unsuccessful (Table 16).

Table 16 A summary of the response of Brewer's Sparrows to playback treatments versus controls within the ASY and SY settlement periods. The response of the birds is split into three components: # of birds that visited plots during the treatment period, # of males that established territories, and # of pairs. Sample sizes were insufficient to test for statistical differences in the reproductive success of attracted birds.

			Period 1 (ASY)		Period 2 (SY)		Statistics		
			Control	Treatment	Control	Treatment	Treatment (T)	Period (P)	T*P
<i>N (plots)</i>			10	12	10	12			
Habitat	Big sage cover	<i>mean (%)</i>	11.8	15.4	20.2	16.6	$F_{3,43} = 1.34$ $p = 0.25$	$F_{3,43} = 2.47$ $p = 0.12$	$F_{3,43} = 1.51$ $p = 0.23$
	Shrub height	<i>mean (m)</i>	60.9	69.1	70.0	70.3	$F_{3,43} = 0.42$ $p = 0.52$	$F_{3,43} = 3.03$ $p = 0.09$	$F_{3,43} = 0.14$ $p = 0.72$
Birds	Visitation	<i>total # visits</i>	2	12	1	10			
		<i># plots with visits</i>	1	8	1	7	$\chi^2_3 = 13.95$ $p < 0.001$	$\chi^2_3 = 0.13$ $p = 0.71$	$\chi^2_3 = 0.04$ $p = 0.84$
	Territorial males	<i>total # males</i>	2	8	1	7			
		<i># plots with males</i>	1	6	1	5	$\chi^2_3 = 7.31$ $p = 0.007$	$\chi^2_3 = 0.13$ $p = 0.72$	$\chi^2_3 = 0.04$ $p = 0.84$
	Pairs	<i>total # pairs</i>	2	2	0	4			
		<i># plots with pairs</i>	1	2	0	3	$\chi^2_3 = 2.55$ $p = 0.11$	$\chi^2_3 = 0.00$ $p = 1.00$	$\chi^2_3 = 1.69$ $p = 0.19$
	Reproductive success	<i>% of pairs initiating nests</i>	100.0	50.0	n/a	25.0			
		<i>% of pairs fledging > 1 young</i>	100.0	50.0	n/a	0.0			

3.5 Discussion

Conspecific attraction has been found to play a major role in the habitat selection decisions of species within several taxonomic groups (lizards - Stamps 1988; crabs - Donahue 2006; birds - Danchin et al. 1998; Doligez et al. 2002; Nocera et al. 2006; Parejo et al. 2006). My study, which demonstrates that male Brewer's Sparrows use conspecific song as a cue when making settlement decisions during the pre-breeding period, adds to the mounting evidence that conspecific attraction can be an important habitat selection cue in territorial songbirds. Seven songbird species have now been shown to use conspecific song in settlement (Table 17). Conspecific attraction may therefore play a role in the clustering of territories observed in this (Cannings et al. 1987; Sarell and McGuinness 1996) and other species (Perry and Anderson 2003, Tarof and Ratcliffe 2004, Mills et al. 2006).

Call-playback treatments in my study were effective in attracting male Brewer's Sparrows during the peak settlement periods of both ASY and SY birds. This finding was in contrast with the results of Ward and Schlossberg (2004) and Nocera et al. (2006), who found greater conspecific cue use by first time breeders than by adults in their studies of conspecific attraction in Black-capped Vireos (*Vireo atricapilla*) and Bobolinks (*Dolichonyx oryzivorus*). Betts et al. (2008) also had a greater response of SY than ASY birds to playbacks at unsuitable plots in their study of conspecific attraction in Black-throated Blue Warblers (*Dendroica caerulescens*). However, Ward and Schlossberg (2004) suggested that this pattern was a reflection of younger birds simply making up a greater proportion of the population settling in new sites, and was not necessarily an indicator of greater conspecific cue use in younger birds. Since the age ratios in the core populations at the two sites in this study are biased towards ASYs

Table 17 A summary of the response of territorial songbirds to playbacks in eight studies where playbacks were used to test for social attraction. The response of the birds is split into three components: visitation of playbacks plots, establishment of territories, and attraction of females or pairs.

Species	Reference		Visitation	Territories	Pairs / Females	Timing of playback
American Redstart <i>Setophaga ruticilla</i>	Hahn and Silverman	2006	Yes	Yes	No	settlement
	Fletcher	2007	Yes	Yes	Yes*	entire breeding season
Baird's Sparrow <i>Ammodramus bairdii</i>	Ahlering et al.	2006	Yes	Yes	No	entire breeding season
Black-capped Vireo <i>Vireo atricapilla</i>	Ward and Schlossberg	2004	Yes	Yes	Yes	entire breeding season
Black-throated Blue Warbler <i>Dendroica caerulescens</i>	Betts et al.	2008	Yes	Yes	Yes	post-breeding
	Hahn and Silverman	2007	Yes	Yes	No	settlement
Bobolink <i>Dolichonyx oryzivorus</i>	Nocera et al.	2006	Yes	Yes	Yes	pre- and post-breeding
Least Flycatcher <i>Empidonax minimus</i>	Mills et al.	2006	Yes	No	No	settlement
	Fletcher	2007	Yes	Yes	Yes*	entire breeding season
Nelson's Sharp-tailed Sparrow <i>Ammodramus nelsoni</i>	Nocera et al.	2006	No	No	No	pre- and post-breeding

*Surveys were conducted throughout the season, and males and females were distinguished in the observations, so a female response is assumed.

(approximately 3:1, ASY:SY), and nest failure is high enough in these populations to result in significant dispersal of failed breeders (Chapter 2), I would not expect to have significantly more SYs than ASYs at our treatment plots. Both Nocera et al. (2006) and Betts et al. (2008) found an SY-biased response to playbacks at plots that were unsuitable for breeding, suggesting that younger birds that have no previous breeding experience are more likely to be tricked into occupying poor quality habitats than are experienced adults. Since playbacks occurred only on plots with suitable habitat in this study, I would not expect differentiation between ASY and SY responses on the basis of previous experience with habitat. Since the criteria for plot selection was 'suitable but unoccupied during the previous two seasons', I also know that the ASYs in this study had not held territories in the playback plot locations in the previous years. If ASYs are not relying on past experience, either with habitat quality, or with breeding success (i.e. returning to their previous territory), they are just as likely to respond to playbacks as are younger, inexperienced birds.

Although I found that call-playbacks had an effect on the number of males that were attracted to and established territories in previously unoccupied plots, these treatments did not have a detectable influence on the number of pairs that subsequently formed. There are four possible explanations for this finding. The first is that these previously unoccupied plots are not as attractive to female Brewer's Sparrows as other sites where sparrows have settled before, because they differed in terms of some characteristic not considered. A second explanation is that an insufficient number of females returned in the 2008 breeding season to allow for all the males that responded to playbacks to attract mates. A third possibility is that attracted males were poor quality, so females chose to settle elsewhere. Finally, a fourth explanation is that female Brewer's Sparrows require a threshold male group size to be present before they will settle.

Females may be more reliant on habitat cues in site selection and these characteristics could have differed between the playback plots and the areas with established breeding clusters. However, a concurrent study that examined territory-level habitat selection and subsequent reproductive success in relation to a suite of vegetation parameters found no evidence that Brewer's Sparrows select habitat on the basis of anything beyond shrub-level characteristics (Chapter 2). A study of nest-site and nest-patch selection by Mahony (2003) also demonstrated that female Brewer's Sparrows select habitats primarily on the basis of shrub-level characteristics. Since there has been no evidence for fine- or coarse-scale selection for habitat features beyond those used in the selection of plots for this study and males arrive first at breeding sites, establish territories and sing to attract females (Rotenberry et al. 1999), it is unlikely that females are relying on alternative cues. This is also supported by Betts et al. (2008), who found that female Black-throated Blue Warblers responded directly to male presence as opposed to habitat or signs of previous success in a territory.

The second explanation: that pair formation at playback plots was limited by the number of returning females, can be tested by comparing the pairing rates of playback responders to those of birds within established breeding clusters (data from Chapter 2). Eighty percent of males within established clusters were successful in attracting mates, as compared with 40% at playback plots, indicating that the lack of success of playback plot males in attracting females was not due to a population-level absence of females. The lower pairing rates at playback plots compared to the core breeding clusters could indicate that the males that settle in response to playbacks are lower quality and thus less desirable to females. However, it could also mean that females require a threshold male group size in order to settle, and that the group sizes within playback plots were simply inadequate to elicit female settlement.

Despite the success of playbacks in attracting Brewer's Sparrow males to previously unoccupied sites, there remains some uncertainty about the utility of playbacks as a management tool. Three main issues must be resolved before managers can seriously consider implementing playbacks to establish or manipulate populations. The first issue is that there has been limited success in promoting female settlement within the majority of the call-playback experiments that have been attempted (Table 17). In fact, only four studies found evidence for preferential settlement of pairs (and not just males) in response to playback treatments (Ward and Schlossberg 2004, Nocera et al. 2006, Fletcher 2007, Betts et al. 2008). These results highlight the importance of carrying experiments through to the point of female settlement to determine the true significance of conspecific attraction in the population as a whole. If females truly cannot be enticed to settle following call-playbacks, then a viable population cannot be established. This thus limits the extent to which call-playbacks can be used as a tool for population management.

In addition to the issue surrounding female attraction, another limitation to the utility of call-playbacks as a management tool is that playbacks are restricted in their capacity to attract individuals to habitats without existing populations nearby. All of the nine studies (including this one) that have tested conspecific attraction using playbacks occurred in close vicinity to existing populations. This means that the evidence in support of the utility of playbacks as a management tool can only be applied to cases where the objective is to move some individuals from an existing population to an adjacent, more desired area. This could be useful if a disturbance was planned or predicted in the existing population location, but would be of little use to managers who would like to establish or restore populations in isolated areas.

In addition to the limitations of playbacks in creating new populations in remote areas, there is also potential to over-ride other cues and draw individuals into areas that

are unsuitable for breeding (Nocera et al. 2006; Betts et al. 2008), creating an ecological trap (Ahlering and Faaborg 2006). Higher predator and competitor densities and conflicting adjacent land uses (reviewed in Ahlering and Faaborg 2006) limit the suitability of habitats that may otherwise appear appropriate based on physical habitat characteristics. Because it has been demonstrated that playbacks can attract individuals to areas that are actually unsuitable based on habitat (Nocera et al. 2006; Betts et al. 2008) or predator densities (e.g. Ward and Schlossberg 2004), it is imperative that managers consider all aspects of the quality of a target area before implementing call-playbacks as a population establishment tool. As suggested by Ward and Schlossberg (2004), it may be necessary to accompany playback treatments with concurrent predator or competitor control measures to ensure that a population sink is not created. It is also important to include comparisons of reproductive success and other physical or physiological measures between birds on playback plots and within existing populations in pilot projects testing the effectiveness of playbacks. This will allow managers to determine whether playbacks are attracting lower quality individuals or are occurring in habitat that is of lower quality for some reason not previously considered. If the uneven response of females to playbacks that we have seen in this and other studies (Table 17) is a sign that males that settle in response to playbacks are actually less desirable or that previously unoccupied areas represent lower quality habitat, it is unlikely that populations established through call-playbacks in these systems will endure over the long-term.

While there is still uncertainty about the use of playbacks as a tool to manipulate the distributions of populations (Ahlering and Faaborg 2006), playback experiments are undoubtedly useful for testing the importance of social attraction in a population, and can provide valuable insight into the reasons for territory clustering within larger areas of seemingly appropriate habitat (Campomizzi et al. 2008). Playbacks have provided

evidence that Brewer's Sparrows use social cues in settlement, which, combined with previous evidence that habitat plays little role in fine-scale settlement decisions in the northern population of this species (Chapter 2), indicates that management decisions for this population must incorporate non-habitat components (Campomizzi et al. 2008). Welstead et al. (2003) found that site choice in this population was related to the distributions of avian predators, suggesting that predator distributions should be a component in future Brewer's Sparrow conservation planning. This study shows that the locations of existing populations are critical in predicting where new Brewer's Sparrow immigrants will settle, so models that incorporate long-term occupancy data in conjunction with habitat data may be better identifiers of critical conservation target areas than models that include habitat data alone. I suggest that intensive surveys for Brewer's Sparrows and their predators be included in conservation efforts for the species in the northern periphery of its range, to improve the process for prioritizing areas for conservation. Playback studies that test the influence of conspecific attraction in settlement are valuable precursors to the improvement of habitat prioritization processes for species that exhibit territorial clustering.

CHAPTER 4: CONCLUSIONS

Determining which habitat selection strategies are behind the distributions of breeding populations will be vital in providing proper management and in understanding how populations will respond to changes in the structure and stability of their environments. For example, Fletcher (2006) found that populations using primarily conspecific cueing may be more sensitive to habitat fragmentation than those using other habitat selection strategies. Similarly, Alonso et al. (2004) suggested that the clustering created by conspecific cueing could cause groups of individuals to be more susceptible to disturbance than if they were more widely distributed. In their review of the possible mechanisms behind the evolution of coloniality, Danchin and Wagner (1997) also suggest that individuals using different strategies will respond differently to temporal changes in the quality of their breeding habitats, with those using conspecific attraction or prior individual success likely tracking changes in their environments more slowly than those using more direct cues. With knowledge of the primary selection strategies being used in a population, managers can determine the likely responses of populations to proposed or predicted changes in their habitats, and identify necessary measures that must be taken to negate population declines.

The results of this study, in combination with those of Chalfoun and Martin (2007), provide solid evidence that shrub-level characteristics are critical in initial site- and patch-selection decisions in Brewer's Sparrows across the species' range. In contrast with the results of Paczek and Krannitz (2004), our study showed that forb and grass characteristics do not predict Brewer's Sparrow patch occupancy when examined over several years. The results of this study indicate that, within a certain range of shrub

cover, the factors driving individual decisions (e.g. territory selection) are not related strongly to vegetation. Within that suitable range of vegetation characteristics, I suggest that a combination of previous experience of returning birds and attraction to conspecifics dictates where birds will choose to establish territories.

The results from the patch occupancy analysis showing the importance of sage cover in predicting occupancy patterns supports the use of shrub-level characteristics as baseline criteria for the identification of suitable Brewer's Sparrow habitat. However, the evidence that previous success (dictated by predators) and conspecific attraction 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. Since 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 re-occupy areas that are suitable due to 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 non-habitat 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.

Future research must be undertaken to assess the potential role of predators in shaping the distributions of Brewer's Sparrows, from the landscape to the territory level. If predators are as influential as it would appear in driving the dispersal decisions of

experienced birds (and through conspecific attraction, the distributions of inexperienced birds), they could be a major factor affecting the population dynamics and eventual persistence of breeding clusters. I alluded to the potential influence of predators in this thesis, but have not explicitly tested the relationship between predator distributions and sparrow habitat choice. Welstead et al. (2003) examined site-level effects of predator distributions on Brewer's Sparrow densities and found evidence that sparrows avoid nesting in sites with high concentrations of avian predators, but the relatively low level of replication in that study leaves a measure of uncertainty about the influence of predators in sparrows' habitat selection decisions. A multi-year, landscape-level assessment of Brewer's Sparrow habitat selection in conjunction with predator surveys would be valuable in determining with greater certainty the factors involved in the species' habitat selection decisions and population dynamics in the South Okanagan.

REFERENCE LIST

- Ahlering, M.A. and J. Faaborg. 2006. Avian habitat management meets conspecific attraction: if you build it, will they come? *The Auk* 123:301-312.
- Ahlering, M.A., Johnson, D.G. and J. Faaborg. 2006. Conspecific attraction in a grassland bird: the Baird's Sparrow. *Journal of Field Ornithology* 77: 365-371.
- Alonso, J.C., Martin, C.A., Alonso, J.A., Palacin, C., Magana, M. and S.J. Lane. 2004. Distribution dynamics of a great bustard metapopulation throughout a decade: influence of conspecific attraction and recruitment. *Biodiversity and Conservation* 13:1659-1674.
- Arlt, D. and T. Pärt. 2007. Nonideal breeding habitat selection: a mismatch between preference and fitness. *Ecology* 88:792-801.
- Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology* 18:1482-1491.
- Betts, M.G., Hadley, A.S., Rodenhouse, N. and J.J. Nocera. 2008. Social information trumps vegetation site structure in breeding site-selection by a migrant songbird. *Proceedings of the Royal Society B* 275:2257-2263.
- Bock, C.E. and J.H. Bock. 1987. Avian habitat occupancy following fire in a Montana shrubsteppe. *Prairie Naturalist* 19:153-158.
- Bock, C.E. and J.F. Jones. 2004. Avian habitat evaluation: should counting birds count? *Frontiers in Ecology and the Environment* 2:403-410.
- Boulinier, T. and E. Danchin. 1997. The use of conspecific reproductive success for breeding patch selection in territorial migratory species. *Evolutionary Ecology* 11: 505-517.

- Brower, J. E., Zar, J. H. and C. N. von Ende. 1989. Field and laboratory methods for general ecology. 3rd ed. Wm C. Brown Publishers, Dubuque, Iowa.
- Brown, J.S. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary Ecology Research* 1:49-71.
- Brown, C.R., Bomberger-Brown, M.B. and A.R. Yves. 1992. Nest placement relative to food and its influence on the evolution of avian coloniality. *The American Naturalist* 139:205-217.
- Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Campomizzi, A.J., Butcher, J.A., Farrell, S.L., Snelgrove, A.G., Collier, B.A., Gutzwiller, K.J., Morrison, M.L. and R.N. Wilkins. 2008. Conspecific attraction is a missing component in wildlife habitat modeling. *Journal of Wildlife Management* 72:331-336.
- Cannings, R. A., Cannings, R. J. and S. G. Cannings. 1987. Birds of the Okanagan Valley, British Columbia. First edition. Royal British Columbia Museum, Victoria, British Columbia.
- Chalfoun, A.D. and T.E. Martin. 2007. Assessments of habitat quality and preference depend on spatial scale and metrics of fitness. *Journal of Applied Ecology* 44:983-992.
- Clark, R. and D. Shutler. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology* 80:272–287.
- Danchin, E., Boulinier, T. and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79:2415-2428.

- Danchin, E. and R. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* 12:342-347.
- Daubenmire, R. F. 1959. A canopy coverage method of vegetational analysis. *Northwest Science* 35:43-64.
- Dickman, C.R. 1992. Predation and habitat shift in the house mouse *Mus domesticus*. *Ecology* 73:313-322.
- Dobler, F.C., Eby, J., Perry, C., Richardson, S. and W.M. Vander Haegen. 1996. Status of Washington's shrubsteppe ecosystem: extent, ownership, and wildlife/vegetation relationships. Research Report. Washington Department of Fish and Wildlife, Olympia, Washington.
- Doligez, B., Danchin, E. and J. Clobert. 2002. Public information and breeding habitat selection in a wild bird population. *Science* 297:1168-1170.
- Donahue, M.J. 2006. Allee effects and conspecific cueing jointly lead to conspecific attraction. *Oecologia* 149:33-43.
- Durant, S.M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology* 11:624-632.
- Fletcher, R. 2006. Emergent properties of conspecific attraction in fragmented landscapes. *The American Naturalist* 168:207-219.
- Fletcher, R. 2007. Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology* 76:598-606.
- Fontaine, J.J. and T.E. Martin. 2006. Habitat selection responses of parents to offspring predation risk: an experimental test. *The American Naturalist* 168:811-818.

- Forsman, J.T., Hjernquist, M.B., Taipale, J. and L. Gustafsson. 2008. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. *Behavioral Ecology* 19:539-544.
- Fretwell, S.D. and H.L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I Theoretical development. *Acta Biotheoretica* 19:19–36.
- Galef, B. and L. Giraldeau. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour* 61:3–15.
- Galef, B. and D. White. 2000. Evidence of social effects on mate choice in vertebrates. *Behavioural Processes* 51:167–175.
- Grossman, G.D., Ratajczak, R.E., Crawford, C. and M. C. Freeman. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecies interactions. *Ecological Monographs* 68:395-420.
- Gunnarsson, T.G., Gill, J.A., Atkinson, P.W., Gelinaud, G., Potts, P.M., Croger, R.E., Gudmundsson, G.A., Appleton, G.F. and W.J. Sutherland. 2005. Population-scale drivers of individual arrival times in migratory birds. *Journal of Animal Ecology* 75:1119-1127.
- Hahn, B.A. and E.D. Silverman. 2006. Social cues facilitate habitat selection: American Redstarts establish breeding territories in response to song. *Biology Letters* 2:337–340.
- Hahn, B.A. and E.D. Silverman. 2007. Managing breeding forest songbirds with conspecific song playbacks. *Animal Conservation* 10:436-441.
- Harvey, D.H. 1992. The distribution, density and habitat of Brewer's Sparrows (*Spizella breweri*) in the South Okanagan valley of British Columbia. Prepared for the British Columbia Ministry of Environment, Victoria, British Columbia.

- Hobbs, J. 2001. An inventory of Brewer's Sparrow in the grasslands of Southern and Central British Columbia. Ministry of Water, Land and Air Protection, Habitat Branch, Victoria, British Columbia.
- Howe, F. P., Knight, R. L., McEwen, L. C. and T. L. George. 1996. Direct and indirect effects of insecticide applications on growth and survival of nestling passerines. *Ecological Applications* 6:1314-1324.
- Järvinen, A. 1989. Geographical variation in temperature variability and predictability and their implications for the breeding strategy of the Pied Flycatcher (*Ficedula hypoleuca*). *Oikos* 54:331-336.
- Jeffries, D. and D. Brunton. 2001. Attracting endangered species to 'safe' habitats: responses of fairy terns to decoys. *Animal Conservation* 4:301-305.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Johnson, M.D. 2007. Measuring habitat quality: a review. *The Condor* 109:489-504.
- Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. *The Auk* 118:557-562.
- Krebs, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major*. *Ecology* 52:2-22.
- Kress, S. W. 1983. The use of decoys, sound recording, and gull control for reestablishing a tern colony in Maine. *Journal of Field Ornithology* 59:161-170.
- Lambrechts, M.M., Caro, S., Charmantier, A., Gross, N., Galan, M., Perret, P., Cartanson, M., Dias, P.C., Blondel, J. and D.W. Thomas. 2004. Habitat quality as a predictor of spatial variation in blue tit reproductive performance a multi-plot analysis in a heterogeneous landscape. *Oecologia* 141:555-561.

- Lanyon, S.M. and C.F. Thompson. 1986. Site fidelity and habitat quality as determinants of settlement pattern in male Painted Buntings. *The Condor* 88:206-210.
- Larson, D. L. and C. E. Bock. 1986. Determining avian habitat preference by bird-centered vegetation sampling. Pages 37-43 in J. Verner, J. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin.
- La Sorte, F.A. and Thompson, F.R. 2007. Poleward shifts in winter ranges of North American birds. *Ecology* 88:1803-1812.
- Lima, S. 1995. Collective detection of predatory attack by social foragers: fraught with ambiguity? *Animal Behaviour* 50:1097-1108.
- Longland, W.S. and M.V. Price. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology* 72:2261-2273.
- Mahony, N. A. 2003. Reproductive ecology and population viability of Brewer's Sparrows at the northern edge of the range. Ph.D thesis. University of British Columbia, Vancouver, British Columbia.
- Mahony, N., Krannitz, P.G. and K. Martin. 2006. Seasonal fecundity of the Sagebrush Brewer's Sparrow (*Spizella breweri breweri*) at the northern edge of its breeding range. *The Auk* 123:512-523.
- Maurer, B.A. and J.H. Brown. 1989. Distributional consequences of spatial variation in local demographic processes. *Annals Zoologica Fennici* 26:121-131.
- McAdoo, J.K., Longland, W.S. and R.A. Evans. 1989. Nongame bird community responses to sagebrush invasion of crested wheatgrass seedings. *Journal of Wildlife Management* 53:494-502.

- Mills, A.M., Rising, J.D. and D.A. Jackson. 2006. Conspecific attraction during establishment of Least Flycatcher clusters. *Journal of Field Ornithology* 77:34-38.
- Misenhelter, M.D. and J.T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology* 81:2892-2901.
- Nocera, J.J., Forbes, G.J. and L-A. Giraldeau. 2006. Inadvertent social information in breeding habitat selection of natal dispersing birds. *Proceedings of the Royal Society B* 273:349–355.
- Nordell, S. and T. Valone. 1998. Mate choice copying as public information. *Ecology Letters* 1:74–76.
- Olson, R.A. 1974. Bird populations in relation to land use in Curlew Valley, Idaho and Utah. M.S. thesis. Idaho State University, Pocatello, Idaho.
- Paczek, S., and P. Krannitz. 2004. The importance of floristics to sagebrush breeding birds of the South Okanagan and Similkameen Valleys, British Columbia. USDA Forest Service Gen. Tech. Rep. PSW-GTR-191.
- Paige, C. and S. A. Ritter. 1999. Birds in a sagebrush sea: managing sagebrush for bird communities. *Partners in Flight Western Working Group*, Boise, Idaho.
- Parejo, D., Danchin, E. and J.M. Aviles. 2004. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? *Behavioral Ecology* 16:96-105.
- Parejo, D., Oro, D. and E. Danchin. 2006. Testing habitat copying in breeding habitat selection in a species adapted to variable environments. *Ibis* 148:146-154.

- Parker, M.W., Kress, S.W., Golightly, R.T., Carter, H.R., Parsons, E.B., Schubel, S.E., Boyce, J.A., McChesney and S.M. Wisely. 2007. Assessment of social attraction techniques used to restore a Common Murre colony in central California. *Waterbirds* 30:17-28.
- Perry, E.F. and D.E. Anderson. 2003. Advantages of clustered nesting for least flycatchers in north-central Minnesota. *The Condor* 105:756-770.
- Petersen, K.L., and L.B. Best. 1985. Brewer's Sparrow nest-site characteristics in a sagebrush community. *Journal of Field Ornithology* 56:23-27.
- Pimm, S.L. and M.L. Rosenzweig. 1981. Competitors and habitat use. *Oikos* 37:1-6.
- Porneluzi, P.A. 2003. Prior breeding success affects return rates of territorial male ovenbirds. *Condor* 105:73-79.
- Pyle, P. 1997. Identification guide to North American birds, Part 1, Columbidae to Ploceidae. Slate Creek Press, Bolinas, California.
- Remeš, V. 2003. Effects of exotic habitat on nesting success, territory density and settlement patterns in the Blackcap (*Sylvia atricapilla*). *Conservation Biology* 17:1127–1133.
- Remeš, V. 2005. Nest concealment and parental behavior interact in affecting nest survival in the Blackcap (*Sylvia atricapilla*): an experimental evaluation of the parental compensation hypothesis. *Behavioral Ecology and Sociobiology* 58:326-333.
- Rotenberry, J.T., Patten, M.A. and K.L. Preston. 1999. Brewer's Sparrow (*Spizella breweri*). A. Poole and F. Gill, editors. The birds of North America, No. 390. The Birds of North America, Inc., Philadelphia, Pennsylvania.
- Rotenberry, J.T. and J.A. Wiens. 1980. Temporal variation in habitat structure and shrubsteppe bird dynamics. *Oecologia* 47:1-9.

- Rotenberry, J.T., and J.A. Wiens. 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. and J.A. Wiens. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. *Ecology* 72:1325-1335.
- Rotenberry, J.T. and J.A. Wiens. 1998. Foraging patch selection by shrubsteppe sparrows. *Ecology* 79:1160-1173.
- Roth, K.L. and K. Islam. 2007. Do Cerulean Warblers (*Dendroica cerulean*) exhibit clustered territoriality? *American Midland Naturalist* 157:345-355.
- Sarell, M.J. and K.P. McGuinness. 1996. Status of the Brewer's Sparrow in British Columbia. Wildlife Working Report No. WR-77. Ministry of Environment, Lands, and Parks, Wildlife Branch, Victoria, British Columbia.
- Sauer, R.J., Hines, J. E. and J. Fallon. 2004. The North American Breeding Bird Survey, Results and Analysis 1966–2007. Version 2008.1. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.
- Sedgwick, J.A. 2004. Site fidelity, territory fidelity, and natal philopatry in Willow Flycatchers (*Empidonax traillii*). *The Auk* 121:1103-1121.
- Sergio, F. and I. Newton. 2003. Occupancy as a measure of territory quality. *Journal of Animal Ecology* 72:857–865.
- Stamps, J.A. 1988. Conspecific attraction and aggregation in territorial species. *The American Naturalist* 131:329-347.
- Sullivan, B.D. and J.J. Dinsmore. 1990. Factors affecting egg predation by American Crows. *Journal of Wildlife Management* 54:433-437.

- Tarof, S.A. and L.M. Ratcliffe. 2004. Habitat characteristics and nest predation do not explain clustered breeding in Least Flycatchers (*Empidonax minimus*). *The Auk* 121:877-893.
- Templeton, J.J. and L-A. Giraldeau. 1996. Vicarious sampling: the use of personal and public information by starlings foraging in a simply patchy environment. *Behavioral Ecology and Sociobiology* 38:105-114.
- Thomson, R.L., Forsman, J.T. and M. Mönkkönen. 2003. Positive interactions between migrant and resident birds: testing the heterospecific attraction hypothesis. *Oecologia* 134:431-438.
- Valone, T.J. and J.J. Templeton. 2002. Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions of the Royal Society B* 357:1549–1557.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*. 47:893-901.
- Vickery, P.D., Hunter, M.L. and J.V. Wells. 1992. Is density an indicator of breeding success? *The Auk* 109:706-710.
- Walcheck, K.C. 1970. Nesting bird ecology of four plant communities in the Missouri River Breaks, Montana. *Wilson Bulletin* 82:370-382.
- Walker, B. 2004. Effects of management practices on grassland birds: Brewer's Sparrow. Northern Prairie Wildlife Research Center, Jamestown, ND. Northern Prairie Wildlife Research Center Online.
[http://www.npwrc.usgs.gov/resource/literatr/grasbird/Brewer's Sparrow/Brewer's Sparrow.htm](http://www.npwrc.usgs.gov/resource/literatr/grasbird/Brewer's%20Sparrow/Brewer's%20Sparrow.htm) (Version 12AUG2004).
- Ward, M.P. and S. Schlossberg. 2004. Conspecific attraction and the conservation of territorial songbirds. *Conservation Biology* 18:519–525

- Warman, L., Robertson, S., Haney, A. and M. Sarell. 1998. Using terrestrial ecosystem mapping (1:20,000) in the South Okanagan and Lower Similkameen study area and forest cover mapping (1:20,000) in the Penticton Forest District. Prepared for the Wildlife Branch, Ministry of Environment, Lands and Parks, Penticton, British Columbia.
- Welstead, K., Krannitz, P, and N. Mahony. 2003. Using survival analysis of artificial and real Brewer's Sparrow (*Spizella breweri breweri*) nests to model site level and nest site factors associated with nest success in the South Okanagan region of Canada. USDA Forest Service Gen. Tech. Rep. PSW-GTR-191.
- Werner, E.E. and B.R. Anholt. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. *Ecology* 77:157-169.
- Wiens, J.A. and J.T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs* 51:21-41.
- Wiens, J.A. and J.T. Rotenberry. 1985. Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. *Journal of Applied Ecology* 22:655-668.
- Wiens J. A., Rotenberry, J.T. and B. Van Horne. 1985. Territory size variations in shrubsteppe birds. *The Auk*. 102:500-505.
- Wiens, J.A., Van Horne, B. and J.T. Rotenberry. 1987. Temporal and spatial variations in the behavior of shrubsteppe birds. *Oecologia* 73:60-70.
- Winter, M., Johnson, D.H. and J.A. Shaffer. 2005. Variability in vegetation effects on density and nesting success of grassland birds. *Journal of Wildlife Management* 69:185-197.
- Yu, J.H.Y. 1999. Postfledging habitat use and movements of Brewer's Sparrows (*Spizella breweri breweri*) in the South Okanagan region. M.Sc. thesis. University of British Columbia, Vancouver, British Columbia.