POSTFLEDGING HABITAT USE AND MOVEMENTS OF BREWER'S SPARROWS (SPIZELLA BREWERI BREWERI) IN THE SOUTH OKANAGAN REGION

by

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We accept this thesis as conforming to the required standard

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Date _September 19, 2001_
ABSTRACT

The postfledging period is one of the least understood portions of the avian life cycle, yet it may have critical ecological and conservation importance. In many species, independent fledglings are known to disperse from natal sites to form juvenile groups. However, relatively little is known about their movement patterns and the habitats they use, which may be vital pieces of information for habitat conservation. Brewer's Sparrow (*Spizella b. breweri*), a sagebrush obligate, is red-listed in BC due to its limited range. I investigated the movement patterns and habitat use of Brewer's Sparrows during the postfledging period. This study was conducted at four sites in the South Okanagan Valley. In total, 272 nestlings were color-banded. Systematic surveys were conducted at each site from mid-June to mid-July to determine patterns of habitat use and movements of resighted birds. Non-nesting habitats such as young aspen gullies and areas with tall shrub were preferred by juveniles and adults during the postfledging period at two sites. At the other two sites, these habitats were poorly represented. By mid-July, few individuals remained in sites where sagebrush was the dominant vegetation, while activity remained high at sites where deciduous vegetation was present. Radio telemetry was conducted at one site in August. Fifteen radio-tagged birds (12 juveniles and 3 adults) also spent most of their time along aspen gullies. The extensive use of non-nesting habitats by postfledging juveniles and postbreeding adults suggests that protection of homogeneous sagebrush nesting habitats alone may not be adequate to protect Brewer's Sparrows in the summer breeding grounds.
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My study is built upon a foundation of knowledge established from previous research on the Brewer’s Sparrow-grassland system in the South Okanagan. Research closely tied to my projects include Nancy Mahony’s four-year demographic study (1997-2000) provided me with a solid background knowledge of nest site selection, local population dynamics and inter-annual dispersal of adults and juveniles. In the South Okanagan grasslands, Susan Paczek examined landscape habitat selection and Pam Krannitz investigated local habitat selection.

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INTRODUCTION

Populations of Neotropical migrant birds can be limited by events and circumstances at all times of the year (Sherry and Holmes 1993). In their winter quarters, on their summer breeding grounds and at migratory stop-over sites, migrants can be limited by habitat loss, predation, or competition for high quality resources (Hutto 1985, Moore and Yong 1991, Moore and Simons 1992). Therefore, conservation efforts must be informed by life history information throughout the year. For some migrant species, the most significant limitations may occur on the summer breeding ground. During the breeding season, reproductive success is affected by multiple factors, and determined by a series of events from nesting to the time that young became independent. While suitable nesting habitat is essential to reproductive success, the availability of postfledging habitats may be important to the viability of a population.

The postfledging period begins when young birds leave the nests and lasts until juvenile migrants begin their southbound migration, or until juvenile residents settle in a winter or permanent home range. This period is the least known and understood portion of the passerine life cycle (Pärt 1990, Morton 1991, Baker 1993). The scarcity of information on the postfledging period is due mainly to the difficulties of observing the young before and after independence. Before fledglings become independent, they are cryptic and difficult to detect; after they become independent, they may move considerable distances from their natal site (Smith 1978).

Previous studies on postfledging period covered a range of issues which have both ecological significance and conservation implications. One issue is the low survivorship during postfledging period, especially for small passerines. Postfledging mortality can be so high that it affects population dynamics more than other factors such as over winter survival or nesting success, as in the case for Great Tits (Parus major L.) (McCleery and Perrins
Survival during this stage is an important determinant for the breeding population size in the next year (Arcese et al. 1992). In Yellow-eyed Juncos (Junco phaeonotus), juvenile mortality changes dramatically over the different stages of the postfledging period (Sullivan 1989). Survivorship is low for fledglings before they can fly proficiently, but increases once they can fly. It then decreases when parental care ceases and increases again when juveniles become more experienced. Other factors also affect postfledging survival. They include: body size and condition of fledglings (Hochachka and Smith 1991, Ringsby et al. 1998), predation and vigilance (Sullivan 1989), food availability (Morton 1991), foraging proficiency (Weathers and Sullivan 1991), social foraging (Sullivan, 1988), and social dominance (Leary et al. 1999, Arcese and Smith 1985). For many migrating species, the postfledging period is also a time for postjuvenal molt when specific habitat and energetic requirements need to be met (Young 1991, Morton & Morton 1990).

Movements, dispersal, and habitat use are also critical during the postfledging period. Fledglings move to seek food (Morton 1991, Vega Rivera et al. 1998), to avoid predation (Anders et al. 1998), to orient themselves with the local landscape (Baker 1993), to prospect for future breeding areas (Gluck 1984, Pärt 1990), and to seek conspecific to socialize and migrate with (Morton et al. 1991). Juveniles of many species are known to disperse from natal sites to other areas after they become independent. For some species, juveniles may prefer habitats that differ from nesting habitats. For example, Powell et al. (1995) and Vega Rivera et al. (1998) found that Wood Thrush (Hylocichla mustelina) fledglings dispersed from natal territories and settled in habitats with less canopy cover, fewer mature trees, and a denser understory. While Yellow-eyed Juncos breed in both forested and open habitats, the juveniles congregate in open, park-like areas (Sullivan, 1989). In fragmented landscape, juveniles have to decide on the safest route to take when moving away from natal sites (Desrochers and Hannon, 1997). While some fledglings
remain in the area they disperse to until migration (Anders et al. 1998), others disperse again and explore other areas (Vega Rivera et al. 1998, Baker 1993).

Brewer’s Sparrow (Spizella breweri breweri) is Nearctic-Neotropical migrant that winters in Sonoran and Chihuahuan deserts of southwestern United States, western Mexico, and Mexican Plateau (Rappole et al. 1993) and breeds in and around Great Basin. It reaches the northern limit of its breeding range in the Southern Okanagan and Similkameen Valleys. It is restricted to sagebrush shrub-steppe habitat (Fleischner 1994, Dobler et al. 1996), and its populations have been undergoing a decline of 3 to 6%/year throughout their range over the past three decades (BBS: Sauer et al. 1997, Rotenberry et al. 1999).

*Spizella b. breweri* is red-listed in B.C. due to its small range.

The habitat associations, habitat selection during breeding season, and the reproductive biology of Brewer’s Sparrow are well-known (Rotenberry et al. 1999). Brewer’s Sparrows breed in shrublands dominated by big sagebrush (*Artemisia tridentata*) (Best 1972, Rich 1980, Wiens and Rotenberry 1981) and select for patches of high shrub vigor (Knopf et al. 1990, Petersen and Best 1985). Reproductive success is variable, being higher in wetter, more biologically productive years (Rotenberry and Wiens 1989, Rotenberry and Wiens 1991). As it is for most open-cup nesting passerines, nest predation is the major factor that affects fledging success (Rotenberry and Wiens 1989). Females perform the majority of incubation, and both parents brood and feed nestlings (Reynolds 1981).

Significant gaps in knowledge of the species include local and regional population dynamics (Rotenberry et al, 1999). In the Okanagan/Similkameen region of B.C., a four-year demographic study (1997-2000) has been conducted (N. Mahony, pers. comm.).

Little is known about habitat use and movement patterns during the postfledging period in Brewer's Sparrows, and it is possible that the observed population decline may in part be attributable to losses at this critical stage. The Brewer's Sparrow is only one of several shrub-steppe birds of conservation concern in B. C. In response to this concern,
areas of shrub-steppe grassland are being purchased and managed as reserves (British Columbia, 1998). Such areas, however, may not include the full spectrum of limiting habitats for all species of concern. If, for example, postfledging juveniles and postbreeding adults disperse from nesting sites to other "designated" sites with specific characteristics, protection of the nesting habitats alone may not be sufficient to protect the summer breeding ground of the species. In this thesis, I test the hypothesis that postfledging juveniles disperse from natal sites to other non-nesting habitats to exploit resources like food and shelter that are lacking on nesting sites. I characterize the habitat use of Brewer's Sparrow juveniles during the postfledging period and compare habitat use to availability. I also investigate the temporal and spatial movement patterns of juveniles prior to their southward migration.

Finally, I discuss the conservation implications of my findings. My specific questions are:

- What habitats are used by Brewer's Sparrow fledglings?
- Do juveniles and adults show preference towards certain habitats?
- Do these habitats differ from those used for nesting?
- How is habitat use related to juvenile age and dispersal distance? i.e. What types of habitats do they disperse to, and how far away are these habitats from natal sites?
- What is the age of independence from parental care for Brewer's Sparrow fledglings?
- How do answers to these questions affect management goals for Brewer's Sparrows?
METHODS

Study Sites

This study was conducted from May 1 to August 25, 2000 in the South Okanagan and Similkameen valleys at four sites in sagebrush shrub-steppe habitats. The same sites were used in a four-year demographic study (1997-2000) conducted by N. Mahony (unpubl.). The South Okanagan/Similkameen region lies from Penticton, B. C. in the north (49°29'N, 119°35W) to the Canada-US border in the south, and Princeton to the west. It is the northernmost extension of the Great Basin. The four study sites were Kilpoola Lake (KP) (49°02'N, 119°34W), Schneider (SC) (49°01’N, 119°36’W), International Grasslands (IG) (49°01’N, 119°38’W), and White Lake (WL) (49°19’N, 119°38’W). From east to west, Kilpoola Lake, Schneider, and International Grasslands are 2 km to 2.5 km apart with an elevation range of 800m to 950m. White Lake is approximately 35 km north of these three sites and at an elevation of 560m (Fig. 1).

All sites were dominated by big sagebrush (*Artemisia tridentata*) and lie within the Southern Interior Ecoprovince and the Okanagan Range Ecoregion of British Columbia (Demarchi 1991) and in the Ponderosa Pine-Bunchgrass biogeoclimatic zone (Nicholson *et al.* 1991). The valley bottom has a semi-arid steppe climate. Precipitation is low with annual mean values of 327 mm at Osoyoos and 290 mm at Penticion. With increasing elevation (as for the three high sites), the average temperature drops and precipitation increases (Cannings *et al.* 1987). At the beginning of the breeding season in early May, the weather is relatively cool (lows ~5°C and highs below 20°C) and moist with overnight frosts. In June, it becomes considerably warmer (low ~13 °C, high 25-30°C ) and drier. By July, the weather becomes even warmer (low 15-20°C, high 30-35°C).
Kilpoola Lake (0.7km², mean elevation=850m) has a flat big sagebrush-dominated section and a steep east-facing slope of heterogeneous vegetation. On the slope, big sagebrush is interspersed with patches of snowberry (*Symphoricarpos albus*), currant (*Ribes spp.*), taller shrubs including saskatoon (*Amelanchier alnifolia*) and ocean spray (*Holodiscus discolor*), and a few large Douglas-fir trees (*Pseudotsuga menziesii*). Mature trembling aspen (*Populus tremuloides*) stands and open coniferous woodland forms the ridge boundary at the top of the slope. Crested wheatgrass (*Agropyron cristatum*) is the dominant grass at Kilpoola and needle-and-thread grass (*Stipa comata*) is common. Herbaceous plants such as arrow-leaved balsamroot (*Balsamorhiza sagittata*), silky lupine (*Lupinus*...
sericeus), and buckwheat (Eriogonum sp.) are also common. Since 1994, Kilpoola has been
managed by Nature Trust BC. Similar sagebrush habitat occurs on adjacent private land.

**Schneider** (0.9 km²) is 2.5 km west of Kilpoola. It lies on a south-facing slope at a
mean elevation of 900 m and 250 m below the mountain ridge. The grassland is interspersed
by gullies dominated by aspen. In the fall of 1994, an intense wildfire altered both the
grassland and gully habitats. The re-growing sagebrush and aspen are small and have not
attained their pre-fire canopy height. Many areas are dominated by herbaceous vegetation
including arrow-leaved balsamroot, silky lupine, tarragon (Artemisia dracunculus), knapweed
(Centaurea diffusa), and buckwheat. Needle-and thread grass (Stipa comata) is the major
grass species, and on some hilly slopes it is the only vegetation present. Knapweed is
widespread and dominates some areas. Mature aspen stands in the gullies were replaced
after the fire by young aspen stands of 3-6 m tall; fallen dead aspen logs also occurred
among non-sage deciduous shrubs and grasses. Schneider is privately owned and grazed
lightly by horses. Heavily grazed sagebrush shrubsteppe and grassland surround the site
both east and west and beyond the Canada-United States border to the south.

**International Grasslands** (0.7 km²), is approximately 2 km southwest of Schneider
on the same mountain slope but with a southeast aspect. The intervening area and the
upper part of International Grasslands were burned in the 1994 wildfire. The study area,
however, remained unburned and has a high density of big sagebrush. Other common
vegetation includes needle-and thread grass, buckwheat, and brittle prickly-pear cactus
(Opuntia fragilis). The grass and forb components at International Grasslands have less
variety and are less dense and patchy than at Kilpoola or Schnieder. The site is bordered on
the east by deep creek bed surrounded by mature aspen. Approximately 300 m northwest
from the surveyed area is a gully with young aspen and there is a forested ridge to the
northwest. To the south and west lies grazed sagebrush. This site is on Provincial Crown
Land.
The White Lake basin lies 35 km north of the other sites and is the largest piece of intact sagebrush habitat (6 km²) in the South Okanagan region. The study plot (0.8 km²) is dominated by big sagebrush. Plant community structure including sagebrush size and density, grass and forb components, is similar to that at International Grassland, but knapweed is more common and widespread at White Lake. Since 1995, this site has been managed as a “biodiversity ranch” by the Nature Trust of BC with yearly fall grazing or spring grazing every other year.

**Nest Searching and Banding**

N. Mahony and I searched the area for nests by mapping territories of singing males, flushing the incubating females, and following nest-building females with nesting materials from early May to late July. All nests were checked every four days. Nestlings from both first and second broods were banded at 4-5 days of age with two or three color bands and one numbered Canadian Wildlife Service aluminum band. At the 4 sites, 272 individuals were colour-banded as nestlings and 22 individuals were banded as independent juveniles after capture in mist-nets. At each site, about 15 pairs of breeding adults were mist-netted and banded by N. Mahony [unpublished data].

**Surveys of Habitat Use**

At each site, a grid (0.7-0.9 km²) of intersecting transects 50m apart was established in May and early June. From mid-June to mid-July, systematic surveys were conducted along grid lines every four to five days at each site to locate banded fledglings and independent juveniles. Systematic surveys were conducted from: June 22 to July 27 at Kilpoola (8 surveys), June 21 to July 15 at Schneider (8 surveys), June 20 to July 12 at International Grasslands (6 surveys), June 18 to July 13 at White Lake (5 surveys). In mid-
June, fledglings from first broods ranged from 10 to 25 days old. In mid-July, first broods reached 40 to 65 days old and second broods reached 10 to 30 days old.

Shrub-steppe grasslands provide a tractable visual environment where movements of birds can be readily observed and where patches of shrubs and vegetation used by dependent fledglings and independent juveniles can be readily identified. On each sighting, I recorded the following variables: vegetation used for perching or feeding, vegetation within 6 m radius, terrain (direction, slope, gully), location, appearance of juveniles sighted, group size (numbers of adults and juveniles), and their activities. Individuals or groups were observed for 10 minutes or until they departed. Based on the vegetation within 6 m radius, a habitat category was assigned to each sighting (Table 1).

<table>
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<tr>
<th>Habitat Categories</th>
<th>Description</th>
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<tbody>
<tr>
<td>Dead conifer with aspen</td>
<td>Dead conifer and live aspen present.</td>
</tr>
<tr>
<td>Dead conifer</td>
<td>Dead standing conifer present.</td>
</tr>
<tr>
<td>Live conifer</td>
<td>Live conifer present.</td>
</tr>
<tr>
<td>Dense aspen</td>
<td>Aspen present in openings among tall and short shrub and deadfall.</td>
</tr>
<tr>
<td>Open aspen</td>
<td>Tall shrub such as Saskatoon, ocean spray, Douglas maple presents. Small shrub can also occur.</td>
</tr>
<tr>
<td>Tall shrub</td>
<td>Dominated by small shrub such as snowberry, rose, and currant. Sage also present.</td>
</tr>
<tr>
<td>Small shrub and sage</td>
<td>Dominated by small shrub such as snowberry, rose, and currant. Sage also present.</td>
</tr>
<tr>
<td>Small shrub, no sage</td>
<td>Small shrubs such as snowberry, roses, and currant present. No sage.</td>
</tr>
<tr>
<td>Big dense sage</td>
<td>Sage dominated, average height &gt;50cm, cover &gt;40%</td>
</tr>
<tr>
<td>Big sparse sage</td>
<td>Sage dominated, average height &gt;50cm, cover &lt;40%</td>
</tr>
<tr>
<td>Small dense sage</td>
<td>Sage dominated, average height &lt;50cm, cover &gt;40%</td>
</tr>
<tr>
<td>Small sparse sage</td>
<td>Sage dominated, average height &lt;50cm, cover &lt;40%</td>
</tr>
<tr>
<td>Dead sage</td>
<td>Dominated by dead sage.</td>
</tr>
<tr>
<td>Forbs and herbs</td>
<td>Dominated by forbs and herbs such as lupine, balsamroot, tarragon, buckwheat, etc. Grasses can also present.</td>
</tr>
<tr>
<td>Weeds</td>
<td>Dominated by knapweed</td>
</tr>
<tr>
<td>Bunch grass</td>
<td>Bunchgrasses only. No forbs/herbs or shrubs</td>
</tr>
<tr>
<td>Other grass</td>
<td>Introduced grasses such as crested wheatgrass dominant.</td>
</tr>
<tr>
<td>Bare soil</td>
<td>Area with no vegetation</td>
</tr>
</tbody>
</table>

Table 1. Habitat categories above were assigned to each sighting on a systematic survey and to radio telemetry locations to explore habitat use. The same categories were used to determine habitat availability.
Habitat Availability

Habitat availability was estimated for each site using the intersections of the grid (n = 53-90) and the habitat categories scored for habitat use (Table 1). At each intersection, a habitat category was assigned, based on the presence of vegetation within a 6m radius. Terrain was also recorded.

To convert locations from the local grid to Universal Transverse Mercator (UTM) map projections, the UTM coordinates for each intersection of the local grid were determined using a handheld Global Positioning System (GPS) receiver (Model Magellan GPS 2000 XL). The accuracy of GPS unit was determined by repeating the readings at 8 locations across 4 sites over 4 days (n=32); it was accurate to within 4m 70% of the time, and within 8m 95% of the time.

Nesting Habitat

Nest locations were also mapped on the local grid and the UTM coordinates of each nest were recorded with the GPS receiver. Vegetation and terrain information were recorded for habitat use and habitat availability, and a habitat category was assigned for each nest.

Off-Grid Search

When resightings became low towards mid July, off-grid searches for dispersing birds were conducted from mid to late July at all sites except Kilpoola (due to the presence of adjacent private lands). At Schneider, 6 searches were done from July 14 to July 29 along gullies; at International Grasslands, 5 searches were done from July 10 to July 26 along gullies; and at White Lake, 3 searches were done from July 13 to July 24. Off-grid searches were concentrated in habitats where juveniles tended to occur, rather than
systematically across the landscape. Sightings from off-grid searches were not included in analyses of habitat use.

Radio Telemetry

Radio telemetry was employed at Schneider in August 2000 to follow a sample of 12 independent juveniles and 3 adults. From the end of July to mid-August, individuals were caught by mist-nets in a gully surrounded by sagebrush breeding habitat. Mist-netted individuals were color-banded and measurements taken. Back-mounted radio transmitters were used (Holohil Systems Ltd. Model LB-2, 0.47g, ca. 5% of body weight).

Due to the short battery life of the transmitters (10 to 21 days), each transmitter was activated on-site after a bird was captured. The transmitter was activated by soldering two pieces of thin wire together with a hand-held butane soldering iron. Before mounting the transmitter on the bird, successful activation was confirmed by testing for a signal with a handheld receiver (Wildlife Materials TRX-1000).

The transmitter on the bird was attached to the bird between the shoulder blades. One person held onto the bird and spread apart the feathers. A second person applied a thin layer of latex cement Skin Bond (Canada Care Medical) to the skin (area of approximately 0.5 cm$^2$) and the flat side of the transmitter. After 2 minutes of partial drying, the transmitter was placed on the skin and was held for 4 minutes. Radio-tagged birds were released 20 to 30 minutes after capture.

Radio-tagged juveniles were followed immediately after release, relocated and followed on foot daily using the same receiver and a 6-element Yagi antenna until signals were no longer detectable or until the tag fell off. Radios could be detected from up to 1 km on the same side of a mountain ridge. When the radio-tagged birds travelled outside the systematic survey grid, the UTM coordinates of each location were recorded using the GPS unit. The bird was considered to have moved when a location was more than 30 m from the
previous one and if it stayed there for more than 2 minutes. The observer kept at least 20m from the tagged bird at all times. If the radio-tagged individual was located visually, I recorded its activity, the vegetation used, and whether it was alone or with conspecifics. It was then observed continuously until it flew out of sight, until the signal remained in the same location for more than an hour, or until the tagged bird had been followed for 5 hours in a single day. If the radio-tagged individual was not observed visually, its location was determined by triangulation and the vegetation at that point was recorded.

Data Analysis

For each site, two-sample Kolmogorov-Smirnov tests (Siegel and Castellan Jr. 1988) were used to compare distributions of habitat use and availability. As individuals might not have made independent choices, sample size for habitat use were based on number of groups of birds sighted at a location rather than the number of individuals sighted.

Habitat preference for each site was determined by constructing 95% confidence intervals for the proportional use of each habitat type with Bonferroni normal statistics (Neu et al. 1974, White and Garrott, 1990). To determine whether a habitat was avoided or preferred, the confidence interval was checked for overlap with the available proportion of the corresponding habitat. If the lower bound of the interval exceeds the available proportion, then the habitat type is preferred.

All location data were converted to UTM coordinates for analysis and mapping using ArcVew GIS Version 3.1. I created two base maps by digitizing the roads, rivers, and lakes from Canadian Geological Survey 1:50000 map sheets 82 E4 (for Kilpoola, Schneider and International Grasslands) and 82 E5 (for White Lake). Since the UTM coordinates recorded with GPS were based on North American Datum 83 (NAD 83), the digitized base maps were converted from NAD 27 to NAD 83.
RESULTS

Banding and Resightings of Juveniles

During plot-based surveys, 49 of the 272 banded fledglings were resighted at least once and 29 of these were resighted more than once (Table 2). The first fledging date ranged from May 29 to June 1 among the 4 sites, and the last fledging date ranged from July 10 to July 14 (Appendix 1).

<table>
<thead>
<tr>
<th></th>
<th>KP</th>
<th>SC</th>
<th>IG</th>
<th>WL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nestlings</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Banded</td>
<td>113</td>
<td>76</td>
<td>50</td>
<td>33</td>
</tr>
<tr>
<td>Resighted total</td>
<td>17</td>
<td>22</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>Resighted at other sites</td>
<td>2 (SC)</td>
<td>0</td>
<td>3 (SC)</td>
<td>0</td>
</tr>
<tr>
<td>Juveniles</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Banded</td>
<td>0</td>
<td>21</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Resighted total</td>
<td>--</td>
<td>5</td>
<td>1</td>
<td>--</td>
</tr>
<tr>
<td>Resighted at other sites</td>
<td>--</td>
<td>1 (IG)</td>
<td>1 (SC)</td>
<td>--</td>
</tr>
</tbody>
</table>

Table 2. Number of individuals banded as nestlings and juveniles at each site and numbers resighted. The resighted total is the total number of banded nestlings/juveniles resighted, including the ones resighted at other sites.

Age of Independence

Independence from parental care appears to occur between 26 and 30 days of age based on observations of 49 banded fledglings and occasions of parental feeding. Brewer's Sparrow fledglings fledged at day 9 on average, and dependent fledglings behaved cryptically from 9 to 25 days of age, but conspicuously afterwards. Only 13 banded fledglings were seen before day 25 (Fig. 2). They were mostly observed perching quietly inside bushes or foraging with parents who became agitated when I approached. Between day 26 to day 30, fledglings become more mobile, with some fledglings remaining dependent longer than others. After day 25, most fledglings were seen without parents and foraging successfully on their own. Some fledglings, however, were seen to be fed by parents up to
day 30. Therefore, I call day 9 to 25 the *early dependent period*, day 26 to 30 the *transition period*, and >day 30 the *independent period*. Less than 15% of juveniles were resighted before the age of independence and then numbers of resightings increased (Fig. 2).

![Graph showing number of sightings per age category](image)

**Figure 2.** Numbers of juvenile resightings in relation to age, for all sites combined. The number on the x-axis is the upper age limit of each category. Some individuals were resighted more than once.

**Flocking and Fledgling Age**

In the dependent period, fledglings were usually found perching motionlessly with two to four other fledglings on small shrubs and tall shrubs such as Saskatoon bushes. In most cases, these groups were not siblings. By the beginning of July, when the average age of first-brood fledglings was >30 days, independent fledglings were sometimes seen in flocks of 10-20 juveniles and adults, though they were more commonly in groups of 5 or less. There were usually more juveniles than adults in the flocks. In most cases, about half of the juveniles in the flock were Vesper Sparrows (*Poecetes gramineus*), which were more numerous than Brewer's Sparrows at most sites. Chipping Sparrows (*Spizella passerina*) were also found in these multi-species flocks.
Habitat Availability, Use, and Preference

Kilpoola

Of the four sites, Kilpoola and Schneider had the most heterogeneous landscapes and vegetation. At Kilpoola, the habitat types that were most available were small shrubs with sage and big dense sage. Tall shrub patches were the third most common habitat type. Brewer’s Sparrows nested mainly in sage-dominated patches (29 of 53 nests) and in patches of sage with other small shrubs (19 nests). The five other nests were in patches with tall shrubs (2), small sparse sage (1), and dead sage (1) (Fig. 3a). Although less than 20 percent of the habitat available was tall shrub such as Saskatoon and ocean spray, more than 40% of the juvenile (Fig. 3b) and adult (Fig. 3c) resightings were in this habitat. Total habitat use by juveniles and adults differed significantly from the distribution of habitats available (maximum D=0.221, m=156, n=56, p<0.05). Both adults and juveniles preferred tall shrub habitats (z=2.85, n=70 for adults, n=16 for juveniles, k=11, p<0.05). Adults and juveniles had the same pattern of habitat use during post-fledging period (maximum D=0.056, m=70, n=106, p>0.10, Fig. 3d). However, this pattern of use differed significantly from nesting habitat (maximum D=0.358, m=106, n=53, p<0.001; maximum D=0.347, m=70, n=53, p<0.005 respectively, Fig. 3e). At Kilpoola, 91% of nests were found in patches of sage and/or small shrubs, but only 43% of resighted juveniles, and 41% of resighted adults were observed in the habitats used for nesting.

Kilpoola was divided into a flat sage-dominated section and a steep-hillside with mixed vegetation (sage among small shrubs, big shrubs, and a few scattered conifers). Although nesting densities were similar for both sections (22 nests in 0.3km², 29 nests in 0.4km²), 72% of juveniles sightings occurred on the mixed vegetation slope and only 28% on the sage dominated section. Some banded fledglings from the sage dominated section moved to the hill section with more heterogeneous vegetation. Of 18 sightings of banded fledglings on the hill section, 3 fledged from nests in the flat section, while none of the 10
Resightings on the sage-dominated section were from the hill section. Kilpoola (0.7km²) is surrounded by private lands. While an estimated 80% of all fledglings from Kilpoola were banded, more than 70% of all resighted birds were unbanded. Thus, more than 50% of the juveniles sighted on the hill section were from adjacent private lands or from more distant sites.

### Kilpoola

<table>
<thead>
<tr>
<th>Available (n=56)</th>
<th>Nests (n=53)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small shrub with sage</td>
<td>Big dense sage</td>
</tr>
<tr>
<td>Tall shrub</td>
<td>Big sparse sage</td>
</tr>
<tr>
<td>Small shrub no sage</td>
<td>Forbs &amp; herbs</td>
</tr>
<tr>
<td>Live conifer</td>
<td>Others</td>
</tr>
</tbody>
</table>

**Figure 3a.** Habitat available and use for nesting at Kilpoola.
Figure 3b. Habitat availability and habitat use by juveniles at Kilpoola.

Figure 3c. Habitat availability and postbreeding habitat use by adults at Kilpoola.
Figure 3d. Postbreeding juvenile and adult habitat use at Kilpoola.

Figure 3e. Juvenile habitat use and nesting habitat at Kilpoola.

Schneider

Although forbs and herbs were more available than small sparse sage at Schneider, the highest number of nests (13 of 34) were found in small sparse sage and only 7 of 34 nests were found in forbs and herbs (Fig. 4a). The other nests were in areas with other
small shrubs (with or without sage) and in big dense sage that was not affected by the fire in 1994. No nests were found in habitat with weeds or aspen. However, the distributions of nesting habitats and their availability are not significantly different (maximum D=0.114, m=34, n=90, p>0.10).

Both juvenile and adult habitat use differed significantly from availability (maximum D=0.577, m=39, n=90, p<0.005; maximum D=0.374, m=39, n=90, p<0.005 respectively, Fig 4b, 4c). Although the shrub-steppe grassland of forbs and herbs, sage and other shrubs covered about 85% of the survey area and aspen gullies represented only 15% of the available habitat, 69% of juveniles were resighted in aspen-tall shrub habitats. Both juveniles and adults preferred aspen habitats (z=2.87, n=39 for adults, n=52 for juveniles, k=12, p<0.05). Although adults associated more with forbs and herbs, and with sage habitats than juveniles, the distributions of habitat use by adults and juveniles are not significantly different (maximum D=0.246, m=39, n=52, p>0.10, Fig. 4d). During postfledging period, both adult and juvenile habitat use differed markedly from the habitats used for nesting (maximum D=0.351, m=39, n=34, p<0.025; maximum D=0.597, m=52, n=34, p<0.001, Fig. 4e, respectively). Sixty-nine percent of the juveniles were resighted in habitat with aspen or tall shrubs where none of the 34 nests were located, while only 31% of the juveniles were found in nesting habitats.
Figure 4a. Habitat available and use for nesting at Schneider.

Figure 4b. Habitat availability and habitat use by juveniles at Schneider.
**Figure 4c.** Habitat availability and habitat use by postbreeding adults at Schneider.

**Figure 4d.** Juvenile and postbreeding adult habitat use at Schneider.
International Grasslands and White Lake

The smaller sample sizes in surveys at both International Grasslands and White Lake reflect the fact that the breeding populations there were smaller (fewer nests were found, see Table 2) at these sites than at Kilpoola or Schneider and that few Brewer's Sparrows remained at these sites by mid July. Due to the small number of sightings, records of adult and juvenile habitat use were pooled for analysis. For International Grassland, the 24 sightings composed of 21 adults and 17 juveniles. For White Lake, the 47 sightings consists of 37 adults and 50 juveniles. Each sighting consists of more than one individuals.

The habitats at both International Grasslands and White Lake were dominated by big sagebrush. At International Grasslands, sagebrush made up more than 90% of the landscape, with the rest composed of tall shrubs in a few small gullies and small shrubs among sage. The landscape at International Grassland was quite homogeneous. There were no significant differences between: habitat availability and habitat use for nesting (maximum D=0.132, m=53, n=30, p>0.10, Fig. 5a ), between availability and postfledging total habitat use by juveniles and adults (maximum D=0.084, m=53, n=30, p>0.10, Fig. 5b).
or between postfledging habitat use and nesting habitats (maximum D=0.077, m=24, n=30).

No preference of habitat use by adults and juveniles was detected at International Grasslands (z=2.81, n=24, k=10, p>0.05).

Figure 5a. Habitat available and use for nesting at International Grasslands.

Figure 5b. Habitat availability and habitat use by adults and juveniles combined at International Grasslands.
The situation at White Lake was similar to that at International Grassland with a few minor differences (Figure 6a, 6b). Big sagebrush made up 85% of the area surveyed, with the rest covered by big patches of knapweed, other weeds, and bunchgrass. A few Saskatoon shrubs were scattered in the area. Nests were found exclusively in sage habitats, and no significant difference was detected between the availability of habitats and their use for nesting (maximum $D=0.184$, $m=78$, $n=34$, $p>0.10$, Fig. 6a). However, 12% of habitat at White Lake consisted of weed patches, and habitat availability differed significantly from postbreeding habitat use by adults and juveniles combined (maximum $D=0.300$, $m=78$, $n=47$, $p<0.025$, Fig. 6b). The weed patches were not used by Brewer’s Sparrows, and big dense sagebrush was preferred ($z=2.69$, $n=47$, $k=7$, $p<0.05$). There was no significant difference between postbreeding habitat use by adults and juveniles combined and nesting habitat (maximum $D=0.116$, $m=47$, $n=34$, $p>0.10$).

![Figure 6a](image)

**Figure 6a.** Habitat available and use for nesting at White Lake.
Movement Patterns

Seasonal Changes

During the systematic surveys at each site from mid-June to mid-July, juveniles or adults did not change their patterns of local habitat use over time (Figure 7a, 7b). Since less than 10% of juveniles detected by systematic surveys were of early dependent fledglings <25 days old, (Fig. 2), figs. 7a and 7b do not show the habitat shift that occurred from the early dependent period to independent period. However, while many individuals remained at Kilpoola and in the gully habitats of Schneider until mid-July, few individuals remained at International Grasslands and White Lake. During systematic surveys, only a total of 24 sighting events occurred at International Grasslands compared to 176 sighting events at Kilpoola and 91 sighting events at Schneider (results). The average number of birds sighted per survey was: 31 at Kilpoola, 28 at Schneider, 7 at International Grasslands, and 20 at White Lake (Figure 8a, 8b, 8c, 8d). Numbers of sightings were low before the end of June.
because most of the second broods had not yet fledged and most fledglings from first broods were still in the early dependent period <25 days old.

Figure 7a. Total habitat use of adults and juveniles over time from June 21 to July 27.

Figure 7b. Juvenile habitat use over time at Schneider.
Off-Grid Searches

As the number of sightings decreased or remained low towards mid-July, I found some banded juveniles and adults beyond the survey grid (Figure 8b, 8c, 8d). Two-thirds of all resightings of banded individuals occurred beyond the site boundary in gully habitats. Out of 8 resightings of banded fledglings at International Grasslands, 6 were sighted during searches in young-aspen gullies approximately 200m from the grid. However, no banded Brewer's Sparrows and few unbanded ones were sighted along the mature aspen gully at International Grassland. At Schneider, 16 of 27 (60%) resightings of banded fledglings occurred during searches along gullies of young aspen that extend beyond grid, even though total effort for off-grid searches (6 searches) was less than effort for systematic surveys (8 surveys). No banded birds were found during three off-grid searches at White Lake.

Figure 8a. Number of adults and juveniles sighted over 8 systematic surveys at Kilpoola from June 18 to July 28.
Figure 8b. Number of adults and juveniles sighted at Schneider during 8 systematic surveys (in grid) from June 21 to July 15, and 6 out-of-grid searches along gullies from July 14 to July 29.

Figure 8c. Number of adults and juveniles sighted at International Grasslands during 6 systematic surveys from June 20 to July 12 and 5 out-of-grid searches from July 10 to July 26.
Dispersal

Resightings of banded fledglings allowed me to examine the relationship between age of juveniles and their distance from the natal nest. As expected, juveniles moved further from the nest as their ages increased (Fig. 9a, 9b). Moderate positive correlations exist between distance from nest and age of fledglings ($r = 0.44$ for Kilpoola, 0.49 for Schneider, and 0.46 for International Grasslands, Fig. 9a). Average dispersal distance increased steadily with age (Fig. 9b). There were few data for White Lake. Before age 15, fledglings were cryptic and seldom seen; the few that were observed were within 40m of the nest site. From age 15 to 20, distance from nest was typically below 90m, except for one day-18 fledgling which moved more than 200m at Schneider. Fledglings day 20 to 25 were found on average 150m from nest. After independence at age 30, fledglings were often found more than 200m from nests with high variance. Few fledglings moved >300m because most nests were <300m from the site boundary. The seven cases of inter-site dispersal were of
juveniles aged from 43 to 60 days. The few sightings of fledglings over 50 days old reflect the limited duration of the study, and the dispersal of early fledglings beyond the site boundaries.

There was one fascinating case of highly mobile siblings <35 days old. At International Grasslands, 5 of 6 resightings of banded juveniles were of 4 siblings (24 to 34 days old) who all moved more than 500m from their nest (Fig. 9a). These data points were much higher than the average dispersal distance (<200m) at this age. While some fledglings age 24 to 34 were still partly dependent on parental care, this case showed that some were highly mobile. Sibling A was first seen on July 12 at day 24 more than 700m from the nest. Siblings B, C, D were seen together 5 days later (day 29) more than 500m from nest in aspen openings. At day 34, sibling B was sighted again 650m from nest; moreover, it was seen later at Schneider August 11 (day 54) and August 17 (day 60), 1.5km and 1.7km from the nest respectively.

Also, I observed seven cases of inter-site dispersal from Kilpoola and International Grasslands to Schneider (Fig. 9c). Two fledglings banded at Kilpoola were sighted at Schneider, 2.5 km away from their nests 53 to 54 days after hatching. Three banded fledglings from International Grasslands were sighted at Schneider 1.5 to 2 km away from their nests 43 to 60 days after hatching. One fledgling moved from Schneider to International Grassland.
Figure 9a. Dispersal of banded fledglings within survey grids.
Figure 9b. Average dispersal distance of fledglings for each age class, pooling all four sites. The first data point is of age class 11 to 15 days old, and the last one is of 66 to 70 days old. Error bars denote standard errors.

Figure 9c. Inter-site dispersal of fledglings.
Radio Telemetry

Habitat Use and Preference

My results from radio telemetry further support the hypothesis that postfledging juveniles use and disperse to habitats that differ from nesting habitats. Three hundred and seven locations were obtained from 15 radio-tagged birds (12 juveniles and 3 adult females) at Schneider. Radio-tagged birds displayed a similar pattern of habitat use to resighted birds (maximum D=0.139, m=15, n=81, p>0.10). Non-nesting habitats were used most often and use by radio-tagged birds differed significantly from availability (maximum D=0.553, m=15, n=90, p<0.001) (Figs. 10a, 10b). More than 60% of locations occurred in gullies of open and dense aspen, which made up less than 10% of the area at Schneider (Fig. 11). Open and dense aspen habitats were preferred over nesting grassland habitats (z=2.9, n=307, k=13, p<0.05). When juveniles were within aspen gullies, they were often located in semi-open areas with abundant deadfall or in the aspen stands. When they were not within aspen gullies, they were most often in tall shrubs and dead conifer trees. They were located in sagebrush habitat less than 10 percent of the time.

![Graph showing habitat use](image)

**Figure 10a.** Habitat use of juveniles and adults by radio telemetry and systematic surveys at Schneider.
Figure 10b. Habitat availability and use by 15 radio-tagged Brewer’s Sparrows (12 juveniles and 3 adults) at Schneider.
Figure 11. Locations of 15 radio-tagged birds during from July 28 to August 23. Gullies shown are creek beds that are mostly dry in August. Some are wide aspen groves while others have few trees or shrubs. Gullies at Schneider and International Grasslands are aspen groves with width reaching 200m.
Movement Patterns

Radio telemetry allowed me to obtain additional movement data on individuals for up to 2 weeks. In observations of individuals within the same day, most individuals traveled along the gullies rather than across the grassland matrix. When they did leave a gully, they usually flew directly to another gully. Four of five individuals that left Schneider site were found in other gully habitats.

Radio telemetry also revealed that juveniles are highly mobile. Appendix 2 summarizes information on the 15 radio-tagged birds, and Appendices 3a-o present individual maps of their temporal and spatial movement patterns. Eight of twelve radio-tagged juveniles dispersed out of the site over the 1-15 day period they were followed (5 of these cases were determined by following signals and 3 were deduced by loss of signal). Most radio-tagged juveniles retained their radios for only a few days. Thirteen of 15 birds retained their radios for <= 6 days, with an average of <4 days. Of the 7 juveniles that retained their radios for <=4 days, 5 remained within 500m of the place they were caught, and 2 were followed out of the study area without being detected again (Appendix 3f, 3i). One moved to open Douglas-fir habitat with grasses as understory where there was a large flock (>50) of Brewer's and Chipping Sparrows. The other juvenile moved to an open grazed gully with sparse grasses and no shrub cover.

Three dispersal events were witnessed among the radio-tagged juveniles. Two of the three juveniles that retained their radios for 5 to 6 days dispersed from the site (Fig. 12a, 12b). Juvenile B from a known nest was followed closely during the dispersal event. On day 33, it traveled alone up a major aspen gully with a horizontal distance northward of 1.5 km and an elevation gain of 250m. When it reached the top of the ridge (elevation of 1250m), where the habitat was burned Douglas-fir forest, it stopped travelling and joined a flock of more than 20 Brewer's and Vesper sparrows. The understory at the site it moved to consisted of small shrubs including huckleberry (Vaccinium spp.) and western tea-berry
(Gaultheria ovatifolia). Juvenile D dispersed more than 1.5km from Schneider to a sage-rose habitat at International Grasslands <150m from an aspen gully. Juvenile C was followed intermittently over 14 days and it dispersed out of the study area to shrubby aspen habitat more than 1.5km away near Kilpoola in one or two days (Fig. 12c). In all three cases, radio-tagged juveniles moved from the natal site to other non-nesting habitats.

The three radio-tagged adult females also used non-nesting habitats. Two of them retained their radios for 3 and 4 days and one was followed for 11 days until the battery died, and all three remained within Schneider while the transmitters were active. Bird M spent time in both aspen gully and in a nesting grassland area <200m away during the three days it was followed (Appendix 3m). Bird N, a breeding female with two known nests at Schneider, (fledged June 12 and July 15), spent most of its time alone in thick aspen gully, with a movement range <500m in three days (Appendix 3n). Nine out of ten of its locations were <200m from its nests. Bird O moved <600m in 11 days (Appendix 3o). Of its 35 locations, 25 were in the aspen gully and 10 were in a grassland area adjacent to the aspen gully. It was seen both alone and in flocks of 5 to 20 Brewer's and Vesper sparrows.
Radio-tagged Bird B

Figure 12a. Locations and dispersal of radio-tagged bird B. Bird B fledged from a known nest on July 11, 2000 at Schneider and it was spotted during systematic survey on July 31 (29 days after hatching) within 100m from nest. It was radio-tagged on August 2 (day 31) and was followed for the next three days. It spent August 2 and 3 in the major aspen gully 200m from its nest. A dispersal event was observed on August 4 (day 33) when bird B travelled up an elevation of 250m (a horizontal distance of 1.5km) along the aspen gully to the top of the ridge where the habitat was burned subalpine Douglas-fir area.
Figure 12b. Locations and dispersal of radio-tagged juvenile bird D. It was tagged on August 18 and it was found in the same area within 500m the next day, travelling in the direction of International Grasslands. Its signal was undetected on August 20 and picked up again on August 21 at International Grasslands in rose-sage habitats 200m from aspen gully. Its dropped radio was found in the same area 2 days later.
Figure 12c. Locations and dispersal of radio-tagged bird C. Bird C, a juvenile was tagged on August 10. It spent two days in the vicinity of aspen gullies and in grassland slope, with a range <700m. On the second day, it travelled out of Schneider site towards a grazed area with a deep treeless gully. Its signal was picked up 2 days later (and again 10 days later), 1.5km north of the previous locations, near aspen gullies north west of Kilpoola site.
DISCUSSION

While it is common knowledge that Brewer's Sparrows occur mainly in areas of homogeneous sagebrush cover (Knopf et al. 1990, Wiens and Rotenberry 1981), they are known to use other habitats during summer (Rotenberry et al. 1999). My results provide the first quantitative evidence that postbreeding adults and independent fledglings exhibit strong local habitat shifts and inter-site dispersal to non-nesting habitats. In the following sections, I relate my findings to postfledging habitat shifts in other species; then I speculate on the reasons for habitat shifts in Brewer's Sparrow; finally, I discuss the conservation implications of my work.

Habitat Shifts by Postfledging Juveniles

My strongest evidence of habitat shifts comes from the preferences of older dependent and independent young for aspen habitats at Schneider and deciduous shrubby habitats at Kilpoola. At Schneider, few birds were sighted on grassland towards the end of the nesting period, while many birds were sighted near or in the gullies dominated by young aspen. Habitat elements such as deadfall (from mature aspen that fell in the wildfire of 1994), dense young aspen, aspen openings with shrubs were all used by juveniles. J. D. Carlisle et al. (unpubl.) also found in an independent study in Idaho that Brewer's Sparrows rely to a large extent on deciduous habitats during postbreeding and autumn migration periods. Their autumn mist-netting results showed high numbers of capture in both mountain shrub and willow riparian shrub habitats.

Other evidence of habitat shifts comes from the disappearance of juveniles and adults from sites that lacked the tall shrub and aspen habitats found at Kilpoola and Schneider. As did Best (1985), I found that resightings of Brewer's Sparrows on nesting areas were frequent at the beginning of the breeding season, but declined later. At Kilpoola
and Schneider, where habitats other than shrubsteppe/grassland were available locally, Brewer's Sparrows remained active into mid-August. Schneider was the most frequently used site by Brewer's Sparrows in August, possibly due to its distinctive landscape characteristics and the presence of major gullies 20-200m wide dominated by 6-year old aspen regrowth from the 1994 fire. Interestingly, all 5 cases of inter-site dispersal were to young aspen habitats at Schneider. Also, at International Grasslands, five of the six resightings occurred off-grid in a gully with young aspen (also burned in 1994), while few juveniles were detected along an equidistant mature aspen gully. Brewer's Sparrows thus seem to prefer young aspen (3-6m tall) habitats with deadfalls and relatively dense understory over mature aspen habitats. Carlisle et al. (unpubl.) also found significant habitat shifts from breeding to postbreeding period. During the breeding season, they found that Brewer's Sparrows were most common in unburned shrubsteppe followed by burned mountain shrub. During autumn migration periods, they were most common in unburned mountain and both burned and unburned riparian shrub habitats.

Evidence on movements of banded birds is typically biased (Koenig 1996) due to variable visibility in different habitats and to the dispersal of birds beyond survey area. There is therefore potential uncertainty over whether the patterns of habitat use I observed are representative. Fortunately, the independent method of radio telemetry at Schneider provided a check on the findings from systematic surveys. In accordance with surveys of banded birds, radio tagged birds were located in aspen gully habitats more often than in grassland habitats. Radio telemetry also revealed that independent juveniles are highly mobile. In two of the dispersal events, I discovered another habitat which is used by postfledging Brewer's Sparrows—Douglas-fir stands, which tend to occur at higher elevations than sage grasslands in my study area.

Postfledging dispersal to non-nesting habitats is also known in other species. Some Green-tailed Towhees (Pipilo chlorurus) disperse upslope from sagebrush dominated
shrubby vegetation in lower canyon to subalpine meadows (Morton 1991). K. Martin (pers. comm.) has found similar upslope movements in a variety of forest breeding songbirds.

Wood Thrush fledglings disperse from natal territories and settle in different habitats with less canopy covers, fewer mature trees, and denser understory (Power et al. 1995, Vega Rivera et al. 1998). While Yellow-eyed Juncos breed in both forested and open habitats, the juveniles prefer to congregate in open, park-like areas (Sullivan, 1989).

Age-dependency of Habitat Shifts by Juveniles

Independence from parental care in Brewer’s Sparrows appears to occur between 26 and 30 days of age. After day 30, juveniles began to move more than 200m away from nests. Similar to my result, Morton et al. (1991) found that, for White-crowned Sparrows, family subunits were located a mean distance of 200m from their nests three weeks after fledging and when young were becoming independent. After 40 days old, Brewer’s Sparrow juveniles began to disperse more than 1.5km away from their natal areas. Vega Rivera (1998) found that in Wood Thrushes, independence was achieved around day 32 when juveniles dispersed up to 1.5km from natal sites to first dispersal sites.

Habitat Shifts by Postbreeding Adults

Adult Brewer’s Sparrows also moved away from nesting habitats to other habitats during postbreeding period. At International Grasslands and White Lake where the dominant vegetation was homogeneous sagebrush, breeding activity decreased sharply in late June, because few females attempted second broods and most adults left the site as soon as fledglings from first broods became independent. Only 5 of 15 breeding females at White Lake, and 6 of 12 breeding females at International Grasslands attempted second broods, while 12 of 15 at Kilpoola and 10 of 13 at Schneider did so (N. Mahony, pers. comm.). By early July, the nesting areas were very quiet. The decreased activity of
Brewer's Sparrow at International Grasslands and White Lake suggests that both juveniles and adults left these areas for other habitats soon after nesting. It is even possible that some of these adults attempted second broods at the sites they moved to. Evidence from Kilpoola and Schneider suggests that these habitats include non-sage small shrub, tall shrub and aspen. Brewer's Sparrows from International Grasslands or White Lake would not have to travel far to find these habitats. Only 200m from International Grasslands boundary lies a gully with young aspen (grove width of 20-100m). However, bird activity in this gully declined a month earlier than in the more extensive gully system in Schneider 1.5km away. Brewer's Sparrows at White Lake would have to travel at least 1-2km to find similar habitats.

Except for anecdotal reports, the postbreeding period has received little attention in Nearctic-Neotropical migrants. However, Carlisle et al. (unpubl.) studied postbreeding habitat use and stopover biology of Brewer's Sparrows in Idaho and found similar habitat shifts by adult Brewer's Sparrows. Also, Vega Rivera (1999) found that 19 of 30 radio-tagged Wood Thrush adults moved from nesting sites to areas 0.5 to 7km away for molting. These molting sites had significantly higher densities of deciduous saplings and understory.

**Why do Brewer's Sparrows shift habitat after fledging or breeding?**

Several hypotheses may explain postfledging movements by adults and juveniles. I now consider the following five hypotheses for Brewer's Sparrows: food acquisition (Hutto 1985, Vickery et al. 1995, Wunderle 1995) response to heat stress, predator avoidance (Anders et al. 1998, Norrdahl and Korpimäki 1998), habitat imprinting for orientation (Baker 1993), and identification for potential breeding areas (Gluck 1984, Pärt 1990, Morton 1997).

One reason to shift habitat is to improve foraging success. Small insects are the main food items for Brewer's Sparrows, although seeds are also taken (Rotenberry et al. 1999). Like most Neotropical migrants, adult and juvenile Brewer's Sparrows need to fuel a full or partial pre-basic molt before migration. While most adults complete their molt on
breeding ground, juveniles interrupt their molt during migration and resume on wintering grounds (Willoughby 1991). Besides molting, they also need to accumulate sufficient fat reserves to commence migration. In one study, Brewer's Sparrows captured during autumn generally carried small to moderate fat stores (Carlisle et al. unpubl.). They were also observed foraging in deciduous habitats. It is possible that insects are more abundant in shrubby aspen habitat than in dry shrub-steppe grasslands. Aspen gullies are probably more moist than sagebrush grassland especially during June and July. Morton (1991) suggested that moisture may play a role in the early dispersal of juvenile Green-tailed Towhees, as food resources are more abundant in wetter areas. He found that postfledging movements upslope from xeric natal sites in sagebrush to wetter subalpine meadows were greatest in drought years.

I believe that thermal cover contributes to habitat shifts in Brewer's Sparrows. Daily high temperatures in my study sites reach 30°C by late June, and 35°C in July and August. Like other passerines, Brewer's Sparrows respond to heat stress by lowering their activities as temperature increases towards mid-day. Even during the nesting season, birds on the grassland area became very quiet by noon. During the postfledging period, while activity decreased in the grassland shrubsteppe towards noon, activity remained moderate along the aspen gullies. Aspen gullies provide more shade and cover, such that birds could travel and forage without over-heating.

Predator avoidance may also explain habitat shifts, as Brewer's Sparrows may be better concealed from avian predators in aspen foliage and deadfall. To survive the molt period, both juveniles and adults need to avoid predators. Trees also provide perches for avian predators, and concentrations of fledglings may provide rich foraging sites for specialists predators like Accipiter hawks. Despite this possibility, the concealment benefit provided by deciduous shrub habitat overshadows the possible predation risk (Krams 1996). Krams argued that the more dominant Crested Tits (Parus cristatus) were better protected
against predation risk from Sparrowhawks (*Accipiter nisus*) than the subordinate Willow Tits (*Parus montanus*), as Crested Tits foraged lower in the saplings where flying predators are unable to attack due to the dense branch structure. My impression is that gullies with dense aspen, understory and deadfalls are important habitat components that enhance concealment. During radio telemetry, I noticed that tagged juveniles were less likely to be spotted by eye if they were in aspen-shrub habitat than if they were in sagebrush grassland habitat. Moreover, radio-tagged juveniles often stay relatively immobile in aspen areas with deadfall for more than half an hour. Similar to my results, Vega Rivera (1999) found that for Wood Thrush, molting sites have greater densities of understory vegetation, deciduous saplings, and fallen trees.

Other factors may also influence the movements of Brewer’s Sparrows. These include learning the local landscape for juveniles (Baker 1993) and prospecting for future breeding areas for both juveniles and adults (Adams and Brewer 1981, Gluck 1984, Pärt 1990). Postfledging movements could be part of a developmental process where juveniles become familiar with the arrangement of local landmarks in order to establish a directionally oriented “map” for fall and spring migrations (Morton *et al.* 1991). Dispersing Brewer’s Sparrow juveniles must pass through non-nesting habitats as well as nesting habitats in which they could breed the following year. In my study, 7 juveniles were found in other nesting sites 1.5 to 2km away form their natal area. Dispersal to potential breeding areas is further supported by a four-year demographic study by N. Mahony (pers. comm.) on the same sites. Mahony found a few cases of natal dispersal where juveniles banded at one site were found as breeding adults in another site the following year. There were also cases of breeding dispersal of adults.

All five hypotheses are plausible and are likely to operate in conjunction. Further study would be needed to assess their relative importance.
Conservation Implications

The South Okanagan and Lower Similkameen is a unique region with a high diversity of habitats including grasslands, riparian and wetlands, forest and rugged terrain. This region is the only place in B.C. and Canada where many species of plants and animals can be found. In particular, this area has one-third of all provincially red-listed species. It is also home to 23 species of plants and animals currently listed as nationally threatened, endangered, or vulnerable. More than half of these species occur in shrubsteppe habitat which has been dramatically altered by human settlement and agriculture over the past few decades.

To identify and protect endangered species and their habitats, the South Okanagan Conservation Strategy (SOCS) was developed in 1989 through a collaboration of several agencies (Hlady, 1992). These included Nature Trust of B.C., B.C. Ministry of Environment, Canadian Wildlife Service, Royal British Columbia Museum, and University of British Columbia. An initial five-year program (1990-1995) was designed to prioritize management activities for the conservation of natural habitat. In 2000, a prospectus was created to invite the participation of more organizations and individuals (Environment Canada), and to date, 26 conservation organizations, government agencies, and education institutions have joined (www.soscp.org). The program's strategies are to expand community involvement, promote ecologically sustainable land-use, enhance stewardship on private and public land, and negotiate acquisition of key habitats, focusing on the species at risk found in the area. One of its achievements was the South Okanagan Lower Similkameen Habitat Atlas for Wildlife at Risk (MOELP, 1998). This atlas focuses on 32 species considered “at risk” in the region, including the Brewer’s Sparrow, and provides maps and information to show where these species can live and breed.

The habitats identified for Brewer’s Sparrow in the atlas generally agree with the habitats used by Brewer’s Sparrows in my study. The atlas states that Brewer’s Sparrows
“require extensive tracts of open brush lands including sagebrush, plains, alpine meadows, valleys with low shrubbery” and that they “forage in sagebrush habitat, although wetlands and mesic ravines may also be important insect foraging areas during the nesting season” (MOELP, 1998). Although my results do not add to information of the types of habitats used, they provide important quantitative information on how the different habitat types are used by Brewer’s Sparrows during the postfledging period. We can now make a preliminary assessment of the relative importance of each habitat during the breeding season. Although the atlas recognizes that non-sage habitats are used by Brewer’s Sparrows, the management considerations in the atlas concentrate exclusively on the protection of sagebrush areas. I found that Brewer’s Sparrows use ravines with aspen and shrubbery more often than sagebrush during postfledging period. Management plans should therefore consider conserving all the habitats used and preferred by Brewer’s Sparrows during summer. These include sagebrush, gullies dominated by young aspen, ravines and areas of tall shrubs.

Several issues need to be considered when identifying the habitats needed to conserve a migratory species. First, before setting management goals, a detailed understanding the life histories of migratory birds is a basic requirement (Sherry and Holmes, 1993). Information from all stages of the life cycle allows us to determine which factors limit the populations. With the new knowledge of the postfledging period of Brewer’s Sparrow from Carlisle et al.’s and my study, we can better assess the habitats needed over the entire summer season. Second, we need to identify if particular combinations of habitats are needed. For instance, even though juveniles and adults use non-nesting habitats more often than sagebrush habitats during postfledging period, sagebrush or grassland matrix is still an important landscape component for Brewer’s Sparrows. I do not think that as many Brewer’s Sparrows would be found at Schneider if the aspen gullies were surrounded by other wood habitats rather than by grassland. I suggest that the grassland-aspen interface
provides an important edge habitat for Brewer's Sparrows and may do so for other species of conservation interest.

Besides being Neotropical migrants, the Brewer's Sparrow is also one of the many species of North American grassland birds that has been declining for at least the last 30 years (BBS, Sauer et al. 1997). One program that aims to reverse these declining trends is the Conservation Reserve Program (CRP). CRP is a grassland bird conservation effort in United States that sets aside farmland in permanent grass and forb cover for a period of at least 10 years. The success and challenges faced by the CRP demonstrated the importance of pinpointing the species-specific reasons for grassland bird declines (Vickery and Herkert 2001). Since its inception in 1986, several species of grassland birds have benefited from the establishment of CRP habitat, including LeConte's Sparrows (Ammodramus leconteii) and Henslow's Sparrows (A. henslowii). However, populations of several other species such as Grasshopper Sparrow (A. savannarum), Eastern Meadowlark (Sturnella magna), and Western Meadowlark (S. neglecta) have continued to decline. These continual declines suggest that factors that limit these grassland populations have not been ameliorated by the land that is being set aside (Vickery and Herkert, 2001). This may also be the case for Brewer's Sparrows.

Finally, I ask if we have provided enough habitat to conserve Brewer's Sparrow in B. C. In the South Okanagan-Similkameen region, only 3% of Brewer's Sparrow habitat is conservation land, 38% is Provincial Crown Land, 23% is Indian Reserve, and 36% is private land (MOELP 1998). Brewer's Sparrow is more sensitive to rangeland degradation than other shrubsteppe species (Bradford et al. 1998), and grazing occurs in much of its habitats. Brewer's Sparrow remains fairly widespread in the region; wherever there are extensive tracts of sagebrush, breeding Brewer's Sparrows are common (Cannings et al. 1987). The first estimates of the breeding population (Harvey 1992) were 800-1000 birds. More recent estimates are of 2000-2600 birds (S. Paczek and N. Mahony, pers. comm.). The latter
number is being used to set up habitat goals for Brewer's Sparrows. We need to ask if we have provided all the habitats that this population needs. White Lake is the largest piece of intact sagebrush habitat in South Okanagan, but does it provide a benefit to Brewer's Sparrows that is proportional to the size of the area? Although White Lake provides a good breeding habitat for Brewer's Sparrows, it does not support a uniformly high density. In some years it even appears to act as a population sink (N. Mahony, pers. comm.). Also, in my study, Brewer's Sparrows dispersed from White Lake soon after breeding. While the size of protected habitat is important, the quality of habitat and perhaps its distance from other key habitats, may be crucial. For instance, Brewer's Sparrows are distributed in clumps across landscape. Perhaps the location of these "hot spots" depends on the local availability of postfledging habitats with tall shrubs or young aspen.

My findings that both adults and juveniles shift to non-nesting habitats in July and August suggest that protection of the nesting sagebrush habitats of Brewer's Sparrows alone is not adequate to manage the species. Since shrubby aspen gullies are used for rearing before migration for up to four months, protection of such habitats adjacent to all principal breeding habitats could be more beneficial than protection of large pieces of sagebrush habitat alone. Other grassland-shrubsteppe species such as the red-listed Sage Thrasher (Oreoscoptes montanus), Grasshopper Sparrow (Ammodramus savannarum), and Lark Sparrow (Chondestes grammacus) may also use and prefer non-nesting habitats after breeding and fledging. Due to the larger body sizes of Sage Thrasher and Lark Sparrow than Brewer's Sparrow, radio telemetry would be a good tool for exploring the habitat use of these species. Both could carry bigger transmitters with greater detection distances and longer battery lives. For the rarer Grasshopper Sparrow, a study similar to the one presented here could provide useful information on possible habitat shifts. The dispersed breeding distribution of the Grasshopper Sparrow, however, would make such a study harder than it is for the semi-colonial Brewer's Sparrow. To protect the summer breeding
ground of these grassland birds, it may be vital to include a range of habitat types used by the species throughout the entire season.
REFERENCES


55
PERSONAL COMMUNICATIONS

Nancy Mahony
Kathy Martin
Susan Paczek
Appendix 1. Accumulative distribution of fledge dates

![Graph showing accumulative distribution of fledge dates.]

Appendix 2. Summary of 15 radio-tagged Brewer's Sparrows at Schneider

<table>
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<th>Bird</th>
<th>Juvenile/ adult</th>
<th>Known nest</th>
<th>Days followed</th>
<th>Fate</th>
<th>Movement range</th>
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* Bird K's tag fell shortly after attachment within the same day. However it was visually spotted 15 days later less than 200m away (See appendix 3k).

** Dispersed out of Schneider survey grid
Appendix 3a-o. Individual account of the movements of 15 radio-tagged Brewer's Sparrows. For each radio-tagged individual, their locations were first presented on the top map of the same scale for comparisons among individuals. Depending on the distance travelled, locations were then presented on a second diagram in a scale that allows finer examination. The markings for x- and y-axis are 500m apart for all the excel graphs, though the scales are different. Consecutive locations within a day are connected and locations from different days have different symbols. Radio-tagged individuals that have known nests were also included in the second diagram.
Appendix 3a. Locations of radio-tagged bird A. Bird A fledged from a known nest at Schneider site on July 17, 2000. It was followed from day 34 to day 36 after hatching, and was found in a major aspen gully 200m west of its natal site.
Appendix 3b. Locations of radio-tagged bird B. Bird B fledged from a known nest on July 11, 2000 at Schneider and it was spotted during systematic survey on July 31 (29 days after hatching) within 100m from nest. It was radio-tagged on August 2 (day 31) and was followed for the next three days. It spent August 2 and 3 in the major aspen gully 200m from its nest. A dispersal event was observed on August 4 (day 33) when bird B travelled up an elevation of 250m (a horizontal distance of 1.5km) along the aspen gully to the top of the ridge where the habitat was burned subalpine Douglas-fir area.
Appendix 3c. Locations of radio-tagged bird C. Bird C, a juvenile was tagged on August 10. It spent two days in the vicinity of aspen gullies and in grassland slope, with a range <700m. On the second day, it travelled out of Schneider site towards a grazed area with a deep treeless gully. Its signal was picked up 2 days later (and again 10 days later), 1.5km north of the previous locations, near aspen gullies north west of Kilpoola site.
Appendix 3d. Locations of radio-tagged bird D. Bird D, a juvenile was tagged on August 18 and it was found in the same area within 500m the next day, travelling in the direction of International Grasslands. Its signal was undetected on August 20 and picked up again on August 21 at International Grasslands in rose-sage habitats 200m from aspen gully. Its dropped radio was found in the same area 2 days later.
Appendix 3e. Locations of radio-tagged bird E. Bird E, a juvenile was radio-tagged on July 31, 2000. It was followed for 20 minutes before signal was lost. It was visually sighted the next day at the same area, around aspen gully (<100m). Radio failed to transmit.
Appendix 3f. Locations of radio-tagged bird F. Bird F, a juvenile was radio-tagged on August 10 and followed for three days. On the first day, Bird F travelled from one aspen gully to another which was 200m apart, spanned by grassland. On the second day, the signal was picked up out of site Schneider near a very large grassy gully with few aspen. This area was heavily grazed. On the third day, Bird F was followed from big grassy gully back to the two aspen gullies within Schneider site where it was located on the first day. The movement range was <1km within three days.
Appendix 3g. Locations of radio-tagged Bird G. Bird G, a juvenile was radio-tagged on July 28 and was followed for 3 hours before signal was lost. It travelled up and down the major aspen gully. Its signal was not detectable for subsequent days.
Appendix 3h. Locations of radio-tagged Bird H. Bird H, a juvenile was radio-tagged on July 30. It was found in and around the major aspen gully on the first day with a movement range <300m in 2 hours. It was found in the same area the next day and it moved upslope from the gully towards a grassland plateau. Both days it was found with 5-7 other Brewer’s Sparrows. Its signal was not detected for subsequent days.
Appendix 3i. Locations of radio-tagged Bird I. Bird I, a juvenile, was radio-tagged on August 1 and followed for 5.5 hours. It spent the first two hours in the main aspen gully. It then flew across the grassland area towards another aspen gully. It continued flying northeast out of site Schneider passing grazed south-facing slope to a plateau area with Douglas-fir stands and some deciduous shrubs. More than 50 Chipping and Brewer's Sparrows were in this area, where Bird I remained for the next three hours.
Appendix 3j. Locations of radio-tagged Bird J. Bird J, a juvenile was radio-tagged on August 15. It flew from upslope from the aspen gully to a south-facing grassland slope with a flock of <10 Brewer's and Vesper sparrows. On the second day, it was found in the flat grassland area 50m west of the main aspen gully with a flock of <20 Brewer's and Vesper sparrows. A fallen radio transmitter was found on the third day on an east facing slope.
Appendix 3k. Locations of radio-tagged Bird K. Bird K, a juvenile was tagged on August 2, but the fallen transmitter was found shortly after among deciduous bushes in the aspen gully. Bird K was visually spotted 15 days later with a group of Brewer’s Sparrows on grassland matrix near the major aspen gully.
Appendix 31. Locations of radio-tagged Bird L. Bird L was tagged on July 31. On the first day, it travelled along and beside the major aspen gully, <400m in 3 hours. On the second day, it was found upslope from the gully on grassland matrix. On the third day, its transmitter was found.
Appendix 3m. Locations of radio-tagged Bird M. Bird M, an adult female was radio-tagged on August 17 and was found in aspen gully. On the second day, it moved from aspen gully to flat grassland area, <200m from the gully, where its transmitter was picked up on the third day.
Appendix 3n. Locations of radio-tagged Bird N. Bird N, radio-tagged on August 11, was a breeding female with two known nests at Schneider, fledged June 12 and July 15. It spent most of its time alone in thick aspen gully, with a movement range <500m in three days. Nine out of ten of its locations were <200m from its nests.
Appendix 3o. Locations of radio-tagged Bird O. Bird O, an adult female was followed from August 3 to August 13 until the battery of the transmitter died. It moved <600m in 11 days. Out of its 35 locations, 25 of them were in the aspen gully and 10 of them are in grassland area adjacent to the aspen gully. It was seen both alone and in flocks of 5 to 20 Brewer's and Vesper sparrows.