Boggy meadows, livestock grazing, and interspecific interactions: influences on the insular distribution of montane Lincoln's Sparrows (*Melospiza lincolnii alticola*)

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BOGGY MEADOWS, LIVESTOCK GRAZING, AND INTERSPECIFIC INTERACTIONS: INFLUENCES ON THE INSULAR DISTRIBUTION OF MONTANE LINCOLN'S SPARROWS (MELOSPIZA LINCOLNII ALTICOLA)

Carla Cicero

ABSTRACT.—I surveyed 34 meadows in California and Oregon to count Lincoln's Sparrows (Melospiza lincolnii alticola) and to identify habitat features that might influence their local, insular occurrence. Lincoln's Sparrows were found at 72% of the sites surveyed. Counts of singing males were low and uncorrelated with meadow size. Lincoln's Sparrows were most common in wet meadows with little damage by grazing. Singing males were concentrated in flooded or boggy areas near meadow edges, where pines (Pinus sp.) provided elevated perches for singing and vigilance. Patches of willows (Salix sp.) were often present nearby. Numbers of male Lincoln's Sparrows were strongly and negatively correlated with abundance of sympatric Song Sparrows (M. melodia). Lincoln's Sparrows breeding in montane meadows are potentially vulnerable to local extirpation because of their insular distribution, low population density, and fluctuating habitat conditions. Heavy damage from livestock grazing drastically increases the probability of local extirpation.

Key words: Melospiza lincolnii, Lincoln's Sparrow, montane meadow, insular populations, habitat association, livestock grazing, conservation biology, Melospiza melodia, Song Sparrow.


Because of their mobility, birds respond quickly to habitat change and thus are model organisms for illustrating the effect of habitat on the distribution and abundance of insular as well as continental populations (Cody 1981, Wiens 1989). Numerous researchers have examined total avifaunal distribution and abundance on montane islands (e.g., Johnson 1975, Kratter 1992, Lentz 1993), in natural habitat patches (e.g., aspen; Flack 1976), or in disturbed forest fragments (e.g., Forman et al. 1976). However, detailed studies of specific taxa occupying natural insular habitats such as meadows are scarce.

The montane form of Lincoln's Sparrow (Melospiza lincolnii alticola; Miller and McCabe 1935, American Ornithologists' Union 1957) is well suited to such a study. This taxon breeds insularly in particular kinds of meadows from Oregon to California and from Idaho to New Mexico. Such sites are separated from other suitable islands of habitat by unoccupied coniferous forest. Two other subspecies (M. I. lincolnit and M. I. gracilis) occur more broadly in brushy bogs from central Alaska through Canada to the northern contiguous United States. Despite the widespread distribution of Lincoln's Sparrows, the species has been poorly studied compared with either of its congeners, the Song Sparrow (M. melodia) or Swamp Sparrow (M. georgiana). Information on the distribution and natural history of M. I. alticola is especially lacking. In this study I provide baseline data on occurrence, abundance, habitat association, and other factors potentially related to their local distribution in western montane meadows. Secondarily, I evaluate the potential impact livestock grazing has on this taxon.

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Range ecologists have shown unequivocally that grazing occurs unevenly across montane vegetation types and that meadows and other riparian areas receive disproportionately heavy use relative to their total acreage (Cook 1966, Roath and Krueger 1982a, 1982b, Gillen et al. 1984, Platts and Nelson 1985). Numerous studies have assessed the impact of such use on riparian habitats and associated wildlife (e.g., Leege et al. 1981, Kauffman et al. 1983, Kauffman and Krueger 1984, Taylor 1986, Ohmart 1994). Montane Lincoln’s Sparrows are potentially vulnerable to disturbance by heavy grazing because of their tendency to nest on or near swampy ground in wet meadows (Grinnell and Miller 1944, Austin 1968). Consequently, changes in their local occurrence or abundance may reveal degradation of meadows by livestock.

**STUDY AREAS AND METHODS**

I surveyed meadows for Lincoln’s Sparrows from mid-May to early July 1987–1989. A total of 34 meadows belonging to 29 systems were visited, including 1 in northern Oregon and 28 in California from the southern Cascade Mountains (Lassen County) through the Sierra Nevada to the San Bernardino Mountains (Fig. 1). Elevations ranged from 1365 to 2470 m, with lodgepole pine (*Pinus contorta*) forest dominating the surrounding vegetation. Size, land ownership, and type and intensity of livestock grazing varied among meadows. Although several

![Fig. 1. Breeding distribution of Lincoln’s Sparrows in California. The general locations of 28 meadow systems surveyed in California are indicated; an additional meadow in Oregon is not shown. Closed circles denote meadows where Lincoln’s Sparrows were present; open circles, meadows where Lincoln’s Sparrows were absent. Closed squares show other known breeding localities based on specimens deposited in the Museum of Vertebrate Zoology, Berkeley, California; published records (Grinnell and Miller 1944, Lentz 1993); records obtained during a survey of meadows for Willow Flycatchers (Empidonax traillii) M. A. Flett and J. Harris unpublished data).](image-url)
groups of meadows were clustered geographically, differences in habitat characteristics, elevation, and/or grazing regime occurred between even the most proximal sites. Consequently, each meadow was treated as an independent sample point. Twenty-five sites consisted of single meadows without any connection to other sites. Another meadow (Beasore Meadow [site 22]) was divided by a fence into 2 parts with strikingly different grazing regimes; because the 2 sides also contrasted dramatically in abundance of Lincoln's Sparrows, they were separated for purposes of analysis and discussion. Three meadow systems (Lacey [8], Haypress Creek [9], and Sagehen Creek [12]) contained multiple meadows within 1 drainage or basin that were separated from each other by a distance of at least 0.8 km. Because these were visited only during the breeding season, when males were singing and thus territorial, presumably there was no movement of Lincoln's Sparrows between meadows. This was confirmed by multiple visits to the same meadow system (e.g., Haypress Creek) during a single breeding season, when individual singing males could be identified repeatedly by their location in each meadow.

To ensure breeding status, counts were limited to singing males. Lincoln's Sparrows sing vigorously from elevated perches during the breeding season, particularly near watercourses or along the meadow edge, and thus are easily detectable. Numbers of singing males were counted by traversing each meadow and recording their presence and location. Because my goal was to survey a broad range of sites in order to evaluate the kinds of meadows inhabited by montane Lincoln's Sparrows, length and repeated visits to individual meadows were not possible. However, the size and discrete, linear configuration of most meadows enabled complete surveys of all singing males during 1 or, at most 2, consecutive mornings (2-5 h/morning). Thus, standard census techniques appropriate for expansive areas of non-insular habitat were unnecessary.

Complete counts of singing males were obtained at 26 (76%) of the 34 meadows. Partial surveys were conducted at the remaining 8 sites because of their large size and/or because fencing restricted access. Nonetheless, these estimates still provide valuable information regarding the occurrence of Lincoln's Sparrows. Six of the 8 sites were visibly impacted by grazing. Surveys took longer in large meadows or at sites with high numbers of Lincoln's Sparrows. Because the amount of time spent at each site varied, count values were standardized by dividing the number of singing males observed per visit by the length of the survey. As with all count methods, some silent males may have been overlooked. Thus, these counts represent minimal estimates of total abundance.

The geographic scope of this study precluded surveying all meadows simultaneously. To verify the reliability of counts conducted at different times, I surveyed 17 meadows (50%) twice or more during the same or subsequent seasons. Counts of singing males in the same meadow at different stages of the breeding cycle were identical. Because annual climatic differences might also influence counts taken in different years, I obtained data on mean temperature and precipitation during May and June 1987-1989 (National Oceanic and Atmospheric Administration 1987, 1988, 1989) from weather stations located near 3 main clusters of meadows: (1) northern Sierra Nevada—Sagehen Creek, Nevada County, California, 1932 m; (2) central southern Sierra Nevada—Huntington Lake, Fresno County, California, 2140 m; (3) San Bernardino Mountains—Big Bear Lake, San Bernardino County, California, 2070 m. I analyzed these data by analysis-of-variance using Statview for the Macintosh (Abacus Concepts 1988). With the exception of mean June temperature, which was slightly different among years ($P = 0.0387$), there was no annual effect on temperature or precipitation ($P > 0.05$). I counted similar numbers of Lincoln's Sparrows at the same meadow in different years.

In a daily field journal, I recorded numbers of other singing birds at each meadow and provided detailed descriptions and sketches of the meadows. I also took notes on the characteristics of meadows with and without Lincoln's Sparrows, and on the location of singing males relative to the meadow edge and to habitat features such as extent of flooding, presence or absence of willows ($Salix$ sp.), presence or absence of corn lily ($Veratrum$ sp.), and presence or absence of pines ($Pinus$ sp.). The first 3 habitat variables (flooding, willows, corn lily) are presumably important for breeding (Grinnell and Miller 1944, Austin 1968, Speirs and Speirs 1968). Although published accounts do not provide information on the use of edges
and/or pines, observations of singing males suggest that these features might be equally important. Because of the broad geographic sampling and concomitant variability in meadow type, data on the herbaceous composition of each meadow were beyond the scope of this study. Differences in habitat features associated with individual males (n = 75) were tested statistically using a nonparametric binomial test, with the normal approximation for N > 35 (see Siegel and Castellan 1988:38-44).

A complex classification system has been developed for meadows in the Sierra Nevada, incorporating similarities in physiographic, hydrologic, edaphic, vegetative, and floristic characteristics (Ratliff 1985). However, only "in a few situations have enough sites been studied to adequately define the [classification] series" (Ratliff 1985:9). Because of the close association between breeding Lincoln's Sparrows and boggy or flooded ground, I used a simpler approach to rate meadows on a scale of 1 to 5 according to wetness (Table 1). Scores assigned to meadows reflect the wetness characteristics observed during the period of study. Higher or lower ratings may be more appropriate at other times depending on seasonal and annual variability in hydrologic regimes.

Quantitative information on livestock use in each meadow was difficult to obtain because of variability in land-ownership patterns and because stocking rates, determined for entire grazing allotments, do not accurately reflect the concentration of livestock on meadows and other riparian areas. Consequently, damage to meadows caused by livestock grazing (see Fig. 2) was assessed subjectively and also rated on a scale of 1 to 5, taking into account the amount of bare ground exposed, extent of gullying and/or streambank erosion, presence of old or recent livestock droppings, and network of livestock trails (Table 1). As with wetness, scores were assigned based on overall damage observed during the period of study. Although gradient and/or soil type also may contribute to differences in erosion seen between meadows, impacts from grazing clearly had a major effect.

Evaluation of the effects of grazing on plant species composition and diversity was beyond the scope of this study. Both wetness and grazing damage may vary with changes in grazing practices.

Areas of meadows were estimated from USGS 7.5-minute topographical maps using a point-grid system modified for a scale of 1:24,000; these data were supplemented by U.S. Forest Service data where available. For large meadows where counts are incomplete, both the total area and the area surveyed were estimated.

### Results

#### Distribution and Abundance of Lincoln's Sparrows

I found Lincoln's Sparrows in 26 (76.5%) of the 34 sites surveyed (Table 2). Absolute numbers of breeding males varied from 1 to 16, which translates to standardized counts of 0.2–4 males/h. Counts were low in most meadows:

<table>
<thead>
<tr>
<th>Score</th>
<th>Characterization</th>
</tr>
</thead>
<tbody>
<tr>
<td>WETNESS</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Meadow very dry: no standing water or boggy ground; single, well-defined stream channel</td>
</tr>
<tr>
<td>2</td>
<td>Less than 25% of meadow wet: few areas of standing water or boggy ground</td>
</tr>
<tr>
<td>3</td>
<td>25–50% of meadow wet: some flooded or boggy areas, other areas dry</td>
</tr>
<tr>
<td>4</td>
<td>50–75% of meadow wet: many areas of standing water or boggy ground; some rivulets of running water</td>
</tr>
<tr>
<td>5</td>
<td>75–100% of meadow wet: most or all of meadow covered with standing water and/or rivulets of running water</td>
</tr>
</tbody>
</table>

| GRAZING |
|-------|------------------|
| 1 | Meadow essentially pristine: no bare ground exposed; grassy, undercut streambanks; no evidence of gullying and/or bank erosion; few to no signs of livestock |
| 2 | Slight grazing damage: <25% of meadow with bare ground exposed; slight gullying and/or streambank erosion; low density of livestock droppings and trails |
| 3 | Moderate grazing damage: 25–50% of meadow with bare ground exposed; gullying and/or streambank erosion clearly evident; low to moderate density of livestock droppings and trails |
| 4 | Heavy grazing damage: 50–75% of meadow with bare ground exposed; pronounced gullying and/or streambank erosion; moderate to high density of livestock droppings and trails |
| 5 | Meadow severely damaged: >75% of meadow with bare ground exposed; extreme gullying and/or streambank erosion; very high density of livestock droppings and trails |
Table 2. Characteristics of meadows surveyed for M. l. alticola in California (1–28) and Oregon (29). See Figure 1 for locations in California.

<table>
<thead>
<tr>
<th>Meadow</th>
<th>Total area surveyed (ha)</th>
<th>Area surveyed (ha)</th>
<th>Number of surveys</th>
<th>Time per survey (h)</th>
<th>Number of singing males</th>
<th>Number of singing males per survey hour</th>
<th>Wetness score</th>
<th>Grazing damage score</th>
<th>Type of grazing</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Battle Creek Meadows, 1460 m (P)</td>
<td>511</td>
<td>447</td>
<td>1</td>
<td>10</td>
<td>0</td>
<td>0.0</td>
<td>3</td>
<td>4</td>
<td>Cattle</td>
</tr>
<tr>
<td>2. Grass Lake, 1960 m (NF)</td>
<td>5</td>
<td>5</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1.5</td>
<td>5</td>
<td>1</td>
<td>Not grazed</td>
</tr>
<tr>
<td>3. Church Meadows, 2040 m (P)</td>
<td>6</td>
<td>6</td>
<td>2</td>
<td>5</td>
<td>11</td>
<td>2.2</td>
<td>2</td>
<td>2</td>
<td>Cattle</td>
</tr>
<tr>
<td>4. French Meadows, 2055 m (P)</td>
<td>16</td>
<td>18</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>2.0</td>
<td>2</td>
<td>3</td>
<td>Cattle</td>
</tr>
<tr>
<td>5. Lincoln Valley, 2250 m (P)</td>
<td>26</td>
<td>28</td>
<td>3</td>
<td>4</td>
<td>16</td>
<td>4.0</td>
<td>4</td>
<td>1</td>
<td>Cattle</td>
</tr>
<tr>
<td>6. Cottonwood Creek, 1770 m (NF)</td>
<td>52</td>
<td>52</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>0.0</td>
<td>4</td>
<td>2</td>
<td>Sheep</td>
</tr>
<tr>
<td>7. Perazzo Meadows, 2010 m (P)</td>
<td>369</td>
<td>59</td>
<td>1</td>
<td>5</td>
<td>0</td>
<td>0.0</td>
<td>3</td>
<td>4</td>
<td>Cattle</td>
</tr>
<tr>
<td>8A. Lacey Valley, 2070 m (P)</td>
<td>164</td>
<td>120</td>
<td>5</td>
<td>1</td>
<td>3</td>
<td>1.5</td>
<td>3</td>
<td>4</td>
<td>Sheep</td>
</tr>
<tr>
<td>8B. Little Lacey Valley, 2005 m (NF)</td>
<td>42</td>
<td>42</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1.5</td>
<td>3</td>
<td>4</td>
<td>Not grazed</td>
</tr>
<tr>
<td>9A. Upper Haypress Creek, 2105 m (NF)</td>
<td>20</td>
<td>20</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>2.0</td>
<td>4</td>
<td>2</td>
<td>Not grazed</td>
</tr>
<tr>
<td>9B. Middle Haypress Creek, 2110 m (NF)</td>
<td>8</td>
<td>8</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>1.5</td>
<td>3</td>
<td>1</td>
<td>Not grazed</td>
</tr>
<tr>
<td>9C. Lower Haypress Creek, 2035 m (NF)</td>
<td>26</td>
<td>26</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>0.7</td>
<td>2</td>
<td>2</td>
<td>Not grazed</td>
</tr>
<tr>
<td>10. Coppins Meadow, 2070 m (P)</td>
<td>164</td>
<td>60</td>
<td>2</td>
<td>8</td>
<td>8</td>
<td>2.0</td>
<td>3</td>
<td>3</td>
<td>Cattle</td>
</tr>
<tr>
<td>11. W of Coppins Meadow, 2070 m (P)</td>
<td>9</td>
<td>9</td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>2.0</td>
<td>4</td>
<td>1</td>
<td>Cattle</td>
</tr>
<tr>
<td>12A. Upper Sagehen Creek, 2050 m (NF)</td>
<td>14</td>
<td>14</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>0.7</td>
<td>2</td>
<td>2</td>
<td>Sheep</td>
</tr>
<tr>
<td>12B. Lower Sagehen Creek, 2010 m (NF)</td>
<td>54</td>
<td>54</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>0.3</td>
<td>4</td>
<td>1</td>
<td>Not grazed</td>
</tr>
<tr>
<td>13. Austin Meadow, 2070 m (NF)</td>
<td>6</td>
<td>6</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>0.7</td>
<td>2</td>
<td>3</td>
<td>Cattle</td>
</tr>
<tr>
<td>14. Leek Spring Valley, 2255 m (P)</td>
<td>56</td>
<td>49</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>2.0</td>
<td>3</td>
<td>2</td>
<td>Cattle</td>
</tr>
<tr>
<td>15. Pleasant Valley, 1850 m (NF)</td>
<td>207</td>
<td>51</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0.0</td>
<td>1</td>
<td>4</td>
<td>Cattle</td>
</tr>
<tr>
<td>16. Swauger Canyon, 2390 m (NF)</td>
<td>23</td>
<td>23</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0.0</td>
<td>4</td>
<td>1</td>
<td>Sheep</td>
</tr>
</tbody>
</table>

<2 males/h were recorded in 16 (61.5%) of the 26 meadows, 2–3 males/h in 8 meadows, and 3–4 males/h in only 2 meadows. Numbers of singing males were highest at Church Meadows (3) and Lincoln Valley (5) in the northern Sierra Nevada, Bluff Lake (27) and Metcalf Creek (28) in the San Bernardino Mountains, and Hood River Meadows (29) in northern Oregon. Counts were not correlated with meadow size ($r = 0.240, P > 0.05$).

Distribution and abundance were clearly associated with scores for wetness and/or extent of grazing damage (Fig. 3). Lincoln’s Sparrows were most common in moderately wet to very wet, i.e., flooded, meadows with low levels of grazing damage. Except for Little Lacey Valley (8B) and Upper Beasore Meadow (22A), the species was absent from all meadows with heavy grazing pressure (score ≥ 4). The presence of Lincoln’s Sparrows at these 2 sites is accounted for by the method of analysis, in which scores were assigned based on overall appearance of the meadow. Thus, all 3 males at Little Lacey Valley were concentrated in the lower, wetter portion of the meadow, where impacts from grazing were slight; none was observed in the more heavily damaged, upper reaches. Likewise, the single male in Upper Beasore Meadow occurred at the lower edge of the site, which was in good condition relative to the meadow as a whole. As expected, Lincoln’s Sparrows were absent from the single site that lacked standing water and showed signs of heavy grazing (Pleasant Valley [15]).
Despite this general tendency, the distribution of Lincoln's Sparrows showed a more complex pattern. For example, I failed to find the species in several meadows with fairly high scores for wetness and low scores for grazing damage (Cottonwood Creek [6], Swauger Canyon [16], White Wolf [17]). Although abundance was highest in the wettest, most pristine meadows (e.g., Lincoln Valley [5], Metcalf Creek [28], Hood River Meadows [29]), other equally wet sites had notably fewer males (e.g., Upper Haypress Creek [9A], west of Coppins Meadow [11], Lower Sagehen Creek [12B], Hogdon Meadow [19], Markwood Meadow [24], Dinkey Meadow [25]). Meadows with lower wetness scores also supported relatively high numbers of Lincoln's Sparrows as long as grazing damage was fairly low (e.g., Church Meadows [3], Coppins Meadow [10], Bluff Lake [27]).

Habitat Features Associated with Individual Male Lincoln's Sparrows

Singing males were strongly associated with particular habitat features (Fig. 4). The most important attribute was the presence of nearby surface water. Only 3% of the males were observed in areas of dry ground, while 93% were seen in either boggy (54.2%) or flooded (38.9%) sites (a difference significant at \( P < 0.001 \)). Numerous locations had networks of small, narrow channels with running water that coursed through tussocks of sedges, grasses, or other herbaceous plants. The presence of willows, corn lily, and pines (especially *P. contorta*) also appeared to be important attributes of Lincoln's Sparrow habitat. Approximately 84% of all males occurred near clumps of willows (\( P < 0.001 \)), and 59% were in areas with at least scattered

**Table 2. Continued.**

<table>
<thead>
<tr>
<th>Meadowa</th>
<th>Total area (ha)</th>
<th>Area surveyed (ha)</th>
<th>Number of surveysb</th>
<th>Number of singing males per survey hour</th>
<th>Wetness scorec</th>
<th>Grazing damage scorec</th>
<th>Type of grazingd</th>
</tr>
</thead>
<tbody>
<tr>
<td>17. White Wolf, 2360 m (NF)</td>
<td>6</td>
<td>6</td>
<td>1</td>
<td>0.0</td>
<td>3</td>
<td>1</td>
<td>Not grazed</td>
</tr>
<tr>
<td>18. Ackerson Meadow, 1400 m (NF)</td>
<td>139</td>
<td>61</td>
<td>1</td>
<td>0</td>
<td>0.0</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>19. Hogdon Meadow, 1400 m (NF)</td>
<td>30</td>
<td>30</td>
<td>1</td>
<td>0</td>
<td>0.0</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>20. Crane Flat, 1890 m (NF)</td>
<td>22</td>
<td>22</td>
<td>1</td>
<td>0.7</td>
<td>3</td>
<td>1</td>
<td>Not grazed</td>
</tr>
<tr>
<td>21. Persicope Flat, 2470 m (NF)</td>
<td>6</td>
<td>6</td>
<td>1</td>
<td>0.0</td>
<td>2</td>
<td>1</td>
<td>Not grazed</td>
</tr>
<tr>
<td>22A. Upper Besore Meadow, 2025 m (F)</td>
<td>16</td>
<td>16</td>
<td>2</td>
<td>0.3</td>
<td>2</td>
<td>5</td>
<td>Cattle</td>
</tr>
<tr>
<td>22B. Lower Besore Meadow, 2057 m (F)</td>
<td>15</td>
<td>15</td>
<td>2</td>
<td>1.7</td>
<td>3</td>
<td>2</td>
<td>Not grazed10</td>
</tr>
<tr>
<td>23. Poison Meadow, 1740 m (NF)</td>
<td>10</td>
<td>10</td>
<td>2</td>
<td>1.0</td>
<td>3</td>
<td>2</td>
<td>Cattle</td>
</tr>
<tr>
<td>24. Markwood Meadow, 1500 m (NF)</td>
<td>45</td>
<td>45</td>
<td>1</td>
<td>1.5</td>
<td>4</td>
<td>2</td>
<td>Cattle</td>
</tr>
<tr>
<td>22. Dinkey Meadow, 1680 m (F)</td>
<td>37</td>
<td>37</td>
<td>2</td>
<td>0.8</td>
<td>3</td>
<td>3</td>
<td>Cattle</td>
</tr>
<tr>
<td>26. Long Meadow, 2100 m (F)</td>
<td>15</td>
<td>15</td>
<td>2</td>
<td>2.0</td>
<td>3</td>
<td>1</td>
<td>Not grazed</td>
</tr>
<tr>
<td>27. Bluff Lake, 2215 m (F)</td>
<td>7</td>
<td>7</td>
<td>2</td>
<td>2.7</td>
<td>3</td>
<td>1</td>
<td>Not grazed</td>
</tr>
<tr>
<td>28. Metcalf Creek, 2225 m (F)</td>
<td>7</td>
<td>7</td>
<td>2</td>
<td>11</td>
<td>2.8</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>29. Hood River Meadows, 1365 m (NF)</td>
<td>12</td>
<td>12</td>
<td>1</td>
<td>3.7</td>
<td>5</td>
<td>1</td>
<td>Not grazed</td>
</tr>
</tbody>
</table>

aMultiple meadows within a single system are designated alphabetically. Letters in parentheses indicate dominant ownership (P = private; NF = national forest; NP = Yosemite National Park). Specific localities and dates of surveys are available from the author.
bSurveys were conducted on 1-2 consecutive days. This was sufficient to count every singing male in all of the areas surveyed (see Methods).
cSee Table 1.
dDetermined from fieldwork and U.S. Forest Service data.

1Not estimated because numerous small, patchy openings occur along the canyon bottom.

Despite this general tendency, the distribution of Lincoln's Sparrows showed a more complex pattern. For example, I failed to find the species in several meadows with fairly high scores for wetness and low scores for grazing damage (Cottonwood Creek [6], Swauger Canyon [16], White Wolf [17]). Although abundance was highest in the wettest, most pristine meadows (e.g., Lincoln Valley [5], Metcalf Creek [28], Hood River Meadows [29]), other equally wet sites had notably fewer males (e.g., Upper Haypress Creek [9A], west of Coppins Meadow [11], Lower Sagehen Creek [12B], Hogdon Meadow [19], Markwood Meadow [24], Dinkey Meadow [25]). Meadows with lower wetness scores also supported relatively high numbers of Lincoln's Sparrows as long as grazing damage was fairly low (e.g., Church Meadows [3], Coppins Meadow [10], Bluff Lake [27]).

Habitat Features Associated with Individual Male Lincoln's Sparrows

Singing males were strongly associated with particular habitat features (Fig. 4). The most important attribute was the presence of nearby surface water. Only 3% of the males were observed in areas of dry ground, while 93% were seen in either boggy (54.2%) or flooded (38.9%) sites (a difference significant at \( P < 0.001 \)). Numerous locations had networks of small, narrow channels with running water that coursed through tussocks of sedges, grasses, or other herbaceous plants. The presence of willows, corn lily, and pines (especially *P. contorta*) also appeared to be important attributes of Lincoln's Sparrow habitat. Approximately 84% of all males occurred near clumps of willows (\( P < 0.001 \)), and 59% were in areas with at least scattered
Fig. 2. Views of the lower (top) and upper (bottom) portions of Beasore Meadow, Madera County, California (site 22). Photos illustrate 2 extremes in the condition of meadows surveyed in this study. Lower Beasore Meadow, which was not grazed, had an uneroded creekbank, swampy ground, rich herbaceous cover, and scattered patches of willow (Salix sp.). Upper Beasore Meadow showed severe soil erosion, compaction, and dessication due to cattle grazing, with 3-7 m gullying. Lincoln's Sparrows were fairly common in Lower Beasore Meadow but essentially absent from Upper Beasore Meadow. Song Sparrows were abundant in the willows in Upper Beasore Meadow.
patches of lily (although this proportion was nonsignificant, $P = 0.0823$). However, unlike Song Sparrows, which were observed only in areas with willow, Lincoln’s Sparrows were not limited to willow patches. The concentration of male Lincoln’s Sparrows was greatest near the edges of meadows (67% of males, $P < 0.01$), where they were often seen perched or singing in pines (68% of males, $P < 0.01$). Although most Lincoln’s Sparrows were observed within meadows, singing males or pairs were occasionally seen in small, nearby openings in surrounding forest as long as suitable habitat was present.

Data from egg sets at the Western Foundation of Vertebrate Zoology (WFVZ) also revealed the importance of wet ground and clumps of herbaceous vegetation or shrubs for breeding. Of 65 records from California, 56 contained information on moisture characteristics at the nest site, and 54 (96%) of these indicated damp to very wet conditions. Over 90% of the nests were placed on the ground or slightly aboveground, where they were well concealed by tufts of grass and/or other plants. Approximately 35% of the nests in the WFVZ records were situated under a patch of willows.

### Negative Association Between Distribution and Abundance of Lincoln’s Sparrows and Song Sparrows

Counts of singing male Lincoln’s Sparrows and Song Sparrows showed a strong negative correlation ($r = 0.701$, $P < 0.01$; Fig. 5). Although some meadows had approximately equal numbers of the 2 congers (e.g., Dinkey Meadow, Little Lacey Valley, Lower Beasore Meadow), most sites appeared to be dominated by one or the other species. Song Sparrows were common at several meadows where Lincoln’s Sparrows were either absent (Battle Creek Meadows, Cottonwood Creek, Ferazzu Meadows, Pleasant Valley, Swaiger Canyon, and Ackerson Meadow) or rare (Lacey Valley, Sagehen Creek, Upper Beasore Meadow). These sites included dry, heavily grazed meadows as well as wet, fairly pristine areas that otherwise looked suitable. Likewise, Song Sparrows were absent or rare from several meadows with relatively large numbers of Lincoln’s Sparrows (e.g., Lincoln Valley, Coppins Meadow, Metcalf Creek, Hood River Meadows), as well as from

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**Fig. 3.** Three-dimensional graph illustrating the relative abundance (vertical axis; counts per hour) of singing male Lincoln’s Sparrows in 29 meadows systems scored according to wetness and grazing damage (see Table 1). Meadows are numbered as in Table 2. Circles indicate sites with Lincoln’s Sparrows; squares, sites where Lincoln’s Sparrows were absent.

**Fig. 4.** Proportion of singing male Lincoln’s Sparrows associated with different habitat attributes. Ecotonal males were those singing along the edge between the meadow and adjacent coniferous forest. All pairwise comparisons, except for the presence/absence of corn lily, were significant at $P < 0.01$.

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Fig. 5. Negative correlation between number of singing male Lincoln's Sparrows and Song Sparrows.

Of the 34 meadows surveyed, Lincoln's Sparrows occurred only in sites with certain habitat features. Data on the specific locations of singing males, combined with descriptions of nest sites from WFVZ egg data slips, indicate that combinations of the following attributes are important for breeding: boggy or flooded ground; thick groundcover of herbaceous vegetation, often with raised tussocks of live or dead grasses or sedges; patches of corn lily; willow thickets or other low shrubs; and some conifers. Raised clumps of herbaceous vegetation are probably critical for breeding under such wet conditions, as suggested by the nest site descriptions. Likewise, dense herbaceous plant material, in conjunction with willows and corn lily, may provide important concealment. The association between male Lincoln's Sparrows and pines undoubtedly reflects the importance of elevated perches for singing and vigilance.

Although Lincoln's Sparrows were present in the majority of wet meadows studied, their absence at certain sites that otherwise looked suitable deserves discussion. One example is White Wolf (17) in Yosemite National Park, where Beedy and Granholm (1985:190) reported the species in summer but did not present any dates of nesting. Although Grinnell and Storer (1924:471) noted that Lincoln's Sparrows arrive in the Yosemite region by mid-May, this date may apply to lower elevation meadows in Yosemite Valley. White Wolf is one of the highest (2380 m) meadows surveyed in this study, and it is possible that the timing of my visit in early June preceded the arrival of this species for breeding. However, examination of museum records (MVZ, WFVZ) showed that Lincoln's Sparrows already have nests with eggs by early to mid-June at sites of similar or higher elevation elsewhere. Furthermore, I observed Lincoln's Sparrows singing in mid-May at other high-elevation meadows such as Bluff Lake and Metcalf Creek, when temperatures were cold and snow was still present on the ground. Although these 2 meadows were visited in a different year than White Wolf, the lack of a significant annual difference in climate during the period of study suggests that timing alone cannot account for the disparity. Additional surveys are needed to determine the population status of Lincoln's Sparrows breeding at White Wolf.

Another wet meadow where I failed to find Lincoln's Sparrows was Swauger Canyon (16), northeast of Yosemite National Park in the

**Discussion and Conclusions**

Of the 34 meadows surveyed, Lincoln's Sparrows occurred only in sites with certain habitat features. Data on the specific locations
Sweetwater Mountains. According to Johnson (1975), the species has never been found to nest in that range despite extensive fieldwork there by parties from the Museum of Vertebrate Zoology. More puzzling was the absence of Lincoln’s Sparrows along Cottonwood Creek (6) and Lower Sagehen Creek (12B) in the northern Sierra Nevada, especially since the species breeds regularly at other comparable meadows in the same region. (Subsequent visits to these 2 sites have confirmed the results of earlier counts.) Both meadows had large areas that were flooded by beaver (Castor canadensis) activity during the period of study. Unlike Lower Sagehen Creek, however, the meadow along Cottonwood Creek is grazed by sheep during the summer, with the season of use occurring from mid-June through September (S. F. Bishop personal communication). Although damage caused by sheep (e.g., trampling of herbaceous vegetation, browsing of willows) may be sufficient to disrupt breeding of Lincoln’s Sparrows along Cottonwood Creek, it does not explain their rarity along Lower Sagehen Creek.

In contrast to Lincoln’s Sparrows, Song Sparrows were among the most common birds seen at both of these meadows, with abundance higher than at most other sites surveyed. Differences in habitat choice and tolerance for disturbance may account, at least partially, for the unexpected negative association between the 2 species at these and other meadows surveyed. For example, Song Sparrows were abundant at several dry, severely grazed sites that were unsuitable for Lincoln’s Sparrows. Likewise, heavily flooded areas such as Hood River Meadows may be shunned by Song Sparrows (only 1 singing male was observed). Of greater interest than these extremes, however, are the patterns observed at intermediate sites, which were often dominated by one or the other species. In fact, Lincoln’s Sparrows were common at a number of wet meadows that appeared similar in habitat to both Cottonwood Creek and Lower Sagehen Creek and where Song Sparrows were surprisingly scarce. One hypothesis is interspecific competition, acting in concert with differences in habitat use and/or tolerance for disturbance caused by grazing. Speirs and Speirs (1968:1440) noted that Song Sparrows often utilized the same perches and were able to “compete strongly and very successfully” against Lincoln’s Sparrows. I observed interspecific interactions on at least 5 occasions and, in all cases, Song Sparrows instigated the chase, displacing male Lincoln’s Sparrows singing from elevated posts. Although there is no evidence that Lincoln’s Sparrows and Song Sparrows are interspecifically territorial, additional behavioral and ecological studies are needed to understand the underlying factor(s) responsible for the negative association observed between these 2 congeners on both a local and regional scale. Removal experiments, in which Song Sparrows are excluded from boggy meadows within the range of Lincoln’s Sparrows, would especially shed light on the role of interspecific competition, if any, in controlling Lincoln’s Sparrow distribution and/or abundance.

Spatial or temporal fluctuations in the distribution and abundance of certain bird species may indicate short-term or long-term trends in climate, resource availability, and habitat quality. Such effects are probably most pronounced in populations occupying ecological islands, which may be in nonequilibrium dynamics (Johnson 1975, 1995). Species with narrow habitat requirements are especially useful as indicators of trends because of their greater vulnerability to natural or human-induced changes. Of the 4 species of sparrows occupying meadows in the Sierra Nevada–Cascade mountains (Savannah Sparrow [Passerculus sandwichensis], Song Sparrow, Lincoln’s Sparrow, and White-crowned Sparrow [Zonotrichia leucophrys]), Lincoln’s Sparrows may be most susceptible to local extirpation because of their generally low population size and their restriction to wet or flooded areas. Although different lines of evidence suggest that mountain meadows may be as temporally stable as the surrounding environment (Benedict 1982), moisture characteristics of meadows are highly variable depending on annual precipitation. Short-term fluctuations in precipitation may affect habitat quality directly through snowmelt and groundwater recharge (Wood 1975) and/or indirectly through availability of food (e.g., insect) resources (Cody 1981, Johnson 1995). In addition, beaver activity may profoundly influence the extent of flooding in meadows.

Livestock grazing can alter natural hydrologic regimes by increasing runoff and exacerbating erosion and gullying, thereby lowering the groundwater table (e.g., Upper Beasore Meadow, Fig. 2B; also see Rauzi and Hanson 1966, Lusby 1970, Platts 1981, Kaufman et al. 1983, Ratliff 1985). Consequently, grazing may
elaborate potential nesting habitat for Lincoln’s Sparrows. In addition, hydrologic and vegetative changes associated with grazing can alter the distribution and abundance of more tolerant species such as Song Sparrows, which may compete with Lincoln’s Sparrows for territories and other resources. These indirect effects of livestock grazing, combined with direct impacts such as reduction of cover and trampling of nests, undoubtedly have resulted in the extirpation of Lincoln’s Sparrows from some meadows. Because populations of this species are already vulnerable to natural fluctuations in moisture, any further changes caused by grazing may exacerbate their probability of local extirpation.

Careful range management practices can significantly reduce the impacts of grazing on plant and animal communities in riparian or meadow ecosystems (Leege et al. 1981, Gillen et al. 1985, Taylor 1986, Schulz and Leininger 1990, Popolizio et al. 1994, Bich et al. 1995). Although range condition will vary with landownership patterns (Loring and Workman 1987), strict control of grazing intensity and season of use will result in higher abundances of breeding birds, primarily through increased shrub volume and height (Taylor 1986). Long-term exclusion of livestock on meadows, combined with erosion-control measures, will especially benefit Lincoln’s Sparrows and other similar species because of the combined vegetative and hydrologic effects. Baseline data on abundance and distribution, such as those provided in this study, are essential for monitoring population trends resulting from disturbance or restoration of sensitive, ephemeral meadow systems.

ACKNOWLEDGMENTS

Numerous people from the U.S. Forest Service and National Park Service assisted with general information on meadows within their jurisdiction. Marianne Flett and John Harris kindly provided unpublished data on avian species composition of meadows surveyed in 1986 for Willow Flycatchers (Empidonax traillii), including presence or absence of Lincoln’s Sparrows. Lloyd Kiff supplied photocopies of data slips for egg sets housed at the Western Foundation of Vertebrate Zoology. Karen Klitz sketched the Lincoln’s Sparrow in Figure 1. I am grateful to Ned K. Johnson, Ross Lein, Martin Morton, Robert Ohmart, James Rising, and an anonymous reviewer for reading drafts of this manuscript and offering many useful suggestions. Fieldwork was supported partially by 2 Frank M. Chapman grants from the American Museum of Natural History.

LITERATURE CITED


Received 16 September 1996
Accepted 24 February 1997