Habitat and Avifaunal Recovery from Livestock Grazing in a Riparian Meadow System of the Northwestern Great Basin

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Abstract: *Riparian habitats are centers of biological diversity in arid and semiarid portions of western North America, but despite widespread loss and degradation of these habitats there is little quantitative information concerning restoration of native riparian biota. We examined the recovery of a riparian meadow system in the context of long-term versus short-term release from livestock grazing. We compared the structure and dynamics of plant and avian communities on 1.5-ha plots inside a long-term (>30 years) livestock exclosure ("exclosure plots"), with adjacent plots outside the exclosure ("open plots") for 4 years following removal of livestock from open plots. Throughout the study, sedge cover, forb cover, and foliage height diversity of herbs were greater on exclosure plots; bare ground, litter cover, shrub cover, and shrub foliage height diversity were greater on open plots. Forb, rush, and cryptogamic cover increased on open plots but not on exclosure plots. Grass cover increased, whereas litter and bare ground decreased on all plots in conjunction with increased availability of moisture. Sedge cover did not change. Avian species richness and relative abundances were greater on exclosure plots; species composition differed markedly between exclosure and open plots (Jaccard Coefficient = 0.23–0.46), with exclosure plots dominated by wetland and riparian birds and open plots dominated by upland species. The appearance of key species of wet-meadow birds on open plots in the third and fourth years following livestock removal signaled the beginning of restoration of the riparian avifauna. We interpret the recovery of riparian vegetation and avifaunal composition inside the exclosure as a consequence of livestock removal, which led to a rise in the water table and an expansion of the hyporheic zone laterally from the stream channel. The lack of change in sedge and shrub cover on open plots suggests that restoration to a sedge-dominated meadow will not happen quickly.*

Hábitat y Recuperación de la Avifauna de Actividades de Pastoreo en un Sistema de Pradera Riparia en el Noroeste de Great Basin

Resumen: *Los hábitats riparios son centros de diversidad ecológica en porciones áridas y semiáridas del Oeste de Norte América, sin embargo, a pesar de la ampia pérdida y degradación de estos hábitats, existe muy poca información cuantitativa referente al restablecimiento de la biota riparia nativa. Examinamos la recuperación de un sistema de pradera riperia en el contexto de su liberación de actividades de pastoreo a largo plazo contra uno a corto plazo. Comparamos la estructura y dinámica de comunidades de plantas y aves en lotes de 1.5 ha. dentro de una zona exluyente de ganado por largo plazo (30 años) "lotes excluyentes" con lotes adyacentes fuera de la zona de exclusión "lotes abiertos" durante cuatro años después de que el ganado fuera removido de los lotes abiertos. A lo largo del estudio, la cobertura de ciperáceas, cobertura de hierbas forrajeras (diferentes a pasto) y la diversidad de la altura del follage de las hierbas fue mayor en los lotes excluyentes; suelo descubierto, cobertura de hojarasca, cobertura arbustiva y diversidad de la altura de arbustos fue mayor en los lotes abiertos. La cobertura de hierbas diferentes al pasto, juncáceas y criptógamas*

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incrementó en los lotes abiertos, pero no en los lotes excluyentes. La cobertura de pasto incrementó, mientras que la hojaraca y suelo descubierto disminuyó en todos los lotes en conjunctión con el incremento en la disponibilidad de humedad. La cobertura de ciperáceas no cambió. La riqueza y abundancia relativa de especies de aves fue mayor en lotes excluyentes; la composición de especies difirió marcadamente entre lotes excluyentes y abiertos (coeficiente Jaccard = 0.23–0.46), con lotes excluyentes dominados por especies de tierras altas. La aparición de especies clave de aves de praderas húmedas en el tercero y cuarto año posteriores a la remoción de ganado señala el inicio de la restauración y avifauna riparina. Nosotros interpretamos la recuperación de la composición de vegetación y avifauna riparina dentro de las zonas de exclusión como una consecuencia de la remoción del ganado, lo cual conduce a un incremento en el manto acuífero y una expansión de la zona hiporréica lateral al canal del arroyo. La carencia de cambios en la cobertura de ciperáceas y arbustos en lotes abiertos sugiere que la restauración de una pradera dominada por ciperáceas no sucederá rápidamente.

> The current that with gentle murmur glides . . . being stopped, impatiently doth rage; but when . . . not hindered He makes sweet music . . . Giving a gentle kiss to every sedge.
>
> —William Shakespeare

Introduction

Riparian habitats constitute less than 1% of total area in arid and semiarid portions of the western United States, but they are the key to ecosystem integrity and function in these landscapes. The critical and disproportionate value of these habitats was recognized only recently and resulted in a flurry of conferences and symposia (Johnson & Jones 1977; Johnson & McCormick 1979; Warner & Hendrix 1984; Johnson et al. 1985).

Western riparian zones are focal points of maximum conflict among competing uses for livestock grazing, timber harvest, recreation, and water diversion for agriculture and domestic consumption (Thomas et al. 1979; Johnson et al. 1985). Among these factors, the most widespread and pervasive adverse influence continues to be exerted by livestock (Chaney et al. 1990; Fleischner 1994; Ohmart 1994). Since 1950 there has been a pronounced shift from sheep to cattle on western public lands that likely has improved upland habitat conditions since earlier in the century, but any ostensible improvement has been achieved at the cost of an unprecedented impact on moist habitats, which now have reached their nadir of ecological function and economic utility west of the Rocky Mountains (Chaney et al. 1990; U.S. Department of Interior 1994).

The recovery and restoration of these riparian habitats is a high priority for land-management and conservation agencies (U.S. General Accounting Office 1988). Despite years of attention from range scientists and land managers, quantitative research at temporal scales appropriate to address the question of riparian habitat restoration is sorely lacking. Riparian recovery often has been narrowly viewed as restoration of vegetation structure—(not necessarily restoration of native species composition)—with attention seldom given to restoration of riparian faunal communities (Morrison 1995). Although it appears that exclusion of livestock often can lead to recovery of riparian vegetation (U.S. General Accounting Office 1988; Platts 1991; Elmore & Kauffman 1994), there is little indication of whether native faunal communities can be reassembled in conjunction with restoration of vegetation composition or structure (Platts 1991; Kreuper 1993; Ohmart 1994).

Riparian ecosystems harbor the most species-rich avifaunas found in the arid and semiarid portions of the western United States (Knopf et al. 1988; Dobkin 1994; Saab et al. 1995). In the Great Basin, as elsewhere throughout the Intermountain West, riparian habitats support diverse avian communities (Dobkin & Wilcox 1986; Dobkin et al. 1995; Dobkin 1998) and are crucial centers of biodiversity (Brussard et al. 1997). The loss of riparian habitats has been suggested as the most important cause of population decline among landbird species in western North America (DeSante & George 1994).

The conservation importance of rangeland riparian habitats prompted us to undertake a long-term study of riparian habitat and avifaunal recovery from chronic livestock impacts in the northwestern Great Basin. We examined a wide variety of riparian ecosystems across a broad spectrum of habitat conditions in eastern Oregon and northwestern Nevada. As part of this study, we compared a large riparian meadow from which livestock had been excluded for many years with adjacent portions of the watershed that continued to be subjected to regionally typical cattle grazing until our study commenced, at which time livestock were removed completely. The purpose of our research was to gain a better understanding of vegetation dynamics in riparian meadow systems in the absence of livestock, to relate these dynamics to avian species composition and relative abundances, and to examine the temporal pattern of avian community change in association with recovery of the riparian plant community. We report results from the initial 4 years of study following the complete removal of livestock.

Methods

Study Area

This study was conducted in the northwestern Great Basin on the 115,000-ha Hart Mountain National Antelope Refuge (HMNAR; 42°25′N, 119°40′W), a fault block escarpment in southeastern Oregon. The region is characterized by cold winters, hot summers, and average precipitation of 30 cm per year (U.S. Fish and Wildlife Service [USFWS] 1994). Higher elevations of the escarpment are drained by perennial creeks derived from springs and melted snow. As elsewhere in the Great Basin, riparian habitats are extremely limited within these landscapes and occur as narrow (typically less than 100 m in width) ribbons of riparian vegetation surrounded by sagebrush steppe. Stream reaches at middle and lower elevations should support riparian meadows, but much of this habitat has been lost to encroachment by upland shrubs. Meadows comprised less than 2% (1900 ha) of total area, but only 156 ha consisted of high-quality meadow habitat (USFWS 1994).

Season-long (generally May to October, but earlier and later in the absence of snow) livestock grazing began in the 1870s and continued after the refuge was established in 1936. Grazing by domestic sheep ended on the refuge in 1960, and the number of cattle was reduced gradually from 1960 to 1990, when livestock grazing was eliminated entirely. In 1958, 45 ha along Guano Creek (1770 m elevation) was fenced as a demonstration project to exclude livestock. Refuge records characterized the Guano Creek study area as having had "a long history of livestock overuse" (Pyle & Brown, unpublished USFWS report, 1991; Fig. 1). In the autumn of 1958 the exclosure area was rototilled, disked, fertilized, and planted with five varieties of dryland alfalfa (*Medicago*) and five varieties of grass. Although there is no record of grass species composition, it is highly unlikely that any native species were planted due to the predominant practice during that era of utilizing exotic grass species for revegetation on public lands and to the lack of commercial sources of native graminoid seeds. No subsequent management intervention occurred other than continued exclusion of livestock. In May 1991 we established three 1.5-ha (100 × 150 m) plots within the exclosure and matched these with three downstream plots outside the exclosure. The long axis of each plot was centered on the stream corridor, and adjacent plots were separated by at least 100 m. Systematic soil sampling indicated that all plots consisted of wetland soils (fine-loamy aquic Haplargids and cumilic Haplaquolls)

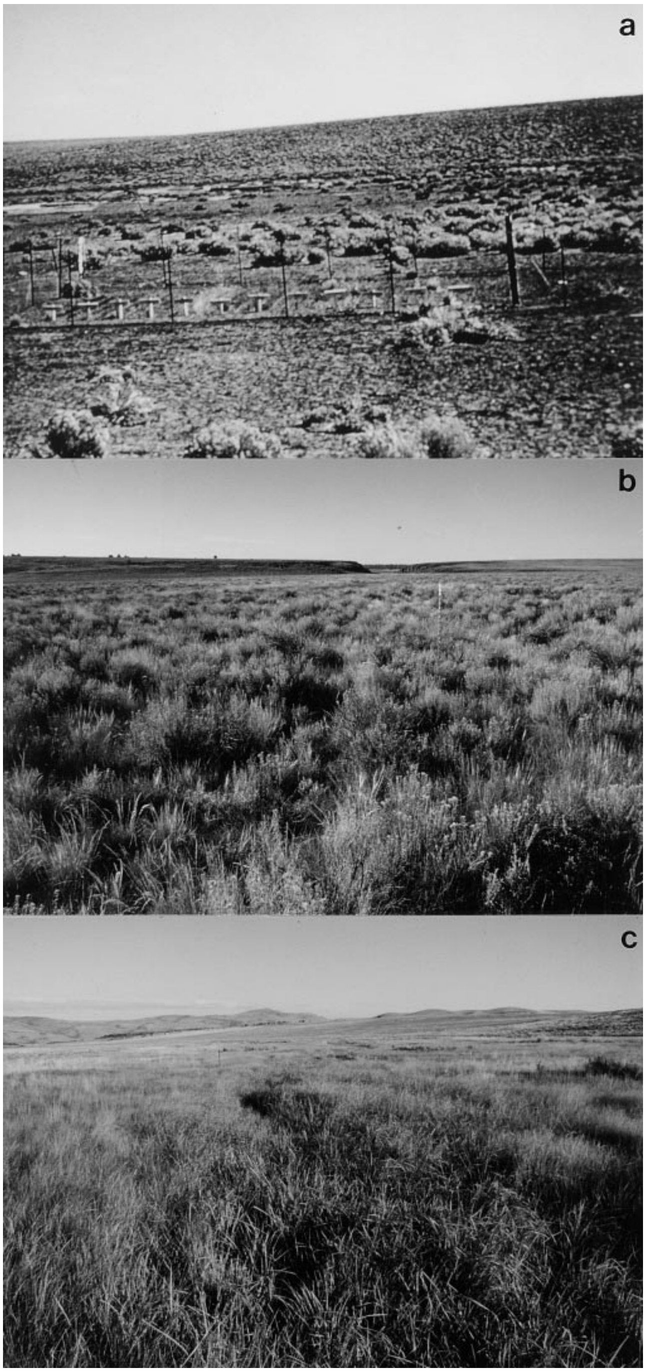

Figure 1. Riparian meadow study area on Hart Mountain National Antelope Refuge in southeastern Oregon: central portion of exclosure area (note stream channel in background) just prior to construction of exclosure fence in 1958 (photo courtesy of USFWS; fencing around small test plot in foreground was removed at time of exclosure) (a); downstream view in central portion of outside-exclosure plot in October 1993, 3 years after livestock removal (stream channel visible to right of metal post in upper right) (b); upstream view in central portion of exclosure plot in October 1993 (stream channel visible in center of photo) (c).

capable of supporting lush dry and wet meadow vegetation (Pyle & Brown, unpublished USFWS report, 1991).

Temperature and precipitation data were recorded by a weather station located at 1700 m on HMNAR. Traditional summaries of annual precipitation (January through December) encompass portions of two annual cycles for plants and thus fail to index actual available moisture for each annual cycle. To circumvent this problem, we combined total monthly precipitation from October through June annually to more closely approximate cumulative moisture for the plant community during each annual cycle (Fig. 2).

Vegetation Sampling

Vegetation sampling of all plots was conducted at the height of the growing season within phenologically equivalent 5-day periods in July of 1992 and 1994. In each plot 12, 100-m vegetation transects were established at 12-m intervals centered on the riparian corridor and running perpendicularly to the stream axis. The distance of the first vegetation transect from the end of the plot was determined by random number generation. Each vegetation transect was divided into 10 subplots, each of which was 10 m in length. Ground-cover percentages (forb, grass, sedge, rush, nonvascular plant [cryptogams], litter, rock, bare ground, and water) were measured inside quadrats 20 × 50 cm (0.10 m^2) placed at the center of each subplot on 6 vegetation transects selected randomly from the 12 transects in each plot.

Shrub cover and foliage height diversity (fhd) were recorded on the six selected vegetation transects in each plot. Shrub cover was measured as the length of the transect line per subplot that was intercepted by live shrubs below 1.5 m (including within-shrub gaps of less than 10 cm). Foliage height diversity was recorded at the center of each subplot with a 2-m rod marked in decimeter (dm) increments and was defined as the number of decimeters intercepted by vegetation within two height classes: <0.5 m and 0.5–2.0 m.

Avian Relative Abundances and Community Composition

We sampled birds in the plots from May through July during the 1991–1994 breeding seasons using modified fixed-width line transects (Emlen 1971, 1977). Six times each year, in three pairs of consecutive morning samples (each pair of samples was separated by 3 weeks), we walked a 150-m transect in each plot for 15 minutes and recorded all birds seen or heard. In 1994 each plot was sampled only twice (a single pair of consecutive-morning samples), and consequently these data are not

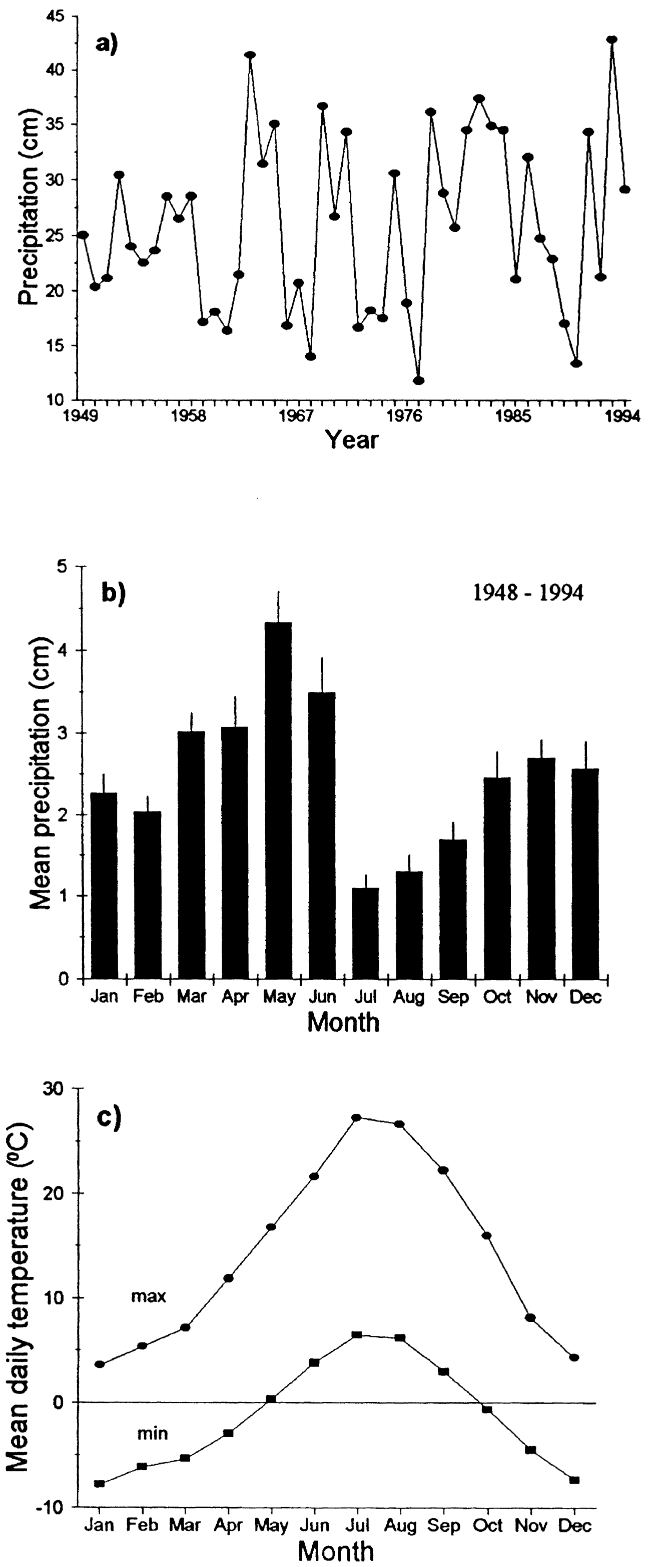

Figure 2. Total cumulative precipitation for each October through June from 1948–1949 through 1993–1994 (a), mean (±1 SE) monthly precipitation (b), and mean daily maximum and minimum temperatures for each month (c) recorded by a National Oceanic and Atmospheric Administration weather station located at approximately 1700 m on Hart Mountain National Antelope Refuge in southeastern Oregon.

included in the following analyses except where specifically indicated.

Statistical analyses of avian relative abundances were based on the maximum estimated number of breeding pairs recorded within each plot in each breeding season. For each plot, we calculated the maximum number for each pair of samples as follows: maximum number of individual males + number of females in excess of maximum number of males + one half of the maximum number of adults of unknown sex. For the breeding season as a whole, our estimated number of breeding pairs per plot for each species was the highest number obtained by the preceding formula from among the three pairs of samples. This metric was developed (Dobkin et al. 1995) to compensate for the high proportion of unknown-sex detections in monochromatic, comparatively nonvocal species relative to dichromatic or highly vocal species with low proportions of unknown-sex detections. Our estimate is of *potential* breeding numbers; clearly, not all detected birds successfully attracted mates and bred, and not all species were characterized by breeding "pairs."

Qualitative and quantitative indices of community-level similarity were calculated for the 1991–1993 breeding seasons to facilitate comparison between avian communities inside and outside the exclosure:

(1) The Jaccard Coefficient, a simple binary measure of species presence and absence, was calculated as

$$C_j = j/(a + b - j),$$

where j is the number of species found in both sites, a is the number of species inside the exclosure, and b is the number of species outside the exclosure (Magurran 1988; Krebs 1989). The index ranges from 0 if the two sites have no species in common to 1 if both sets of species are identical.

(2) The complement of the Morisita-Horn index, a robust measure based on species composition and relative abundance (Magurran 1988), was calculated as

$$C_{mh} = 1 - [2(an_i\ bn_i)/(da + db)aN\ bN],$$

where aN equals the total relative abundances inside the exclosure, an_i is the relative abundance of the ith species inside the exclosure, and da is an_i^2/aN^2. We used the complement of the Morisita-Horn index so that it would scale from 0 to 1 corresponding to the Jaccard index.

Data Analysis

Data were analyzed with the SPSS statistical package (Norusis 1993). Assumptions of normality and homoscedasticity were tested with normal probability plots and $F_{\max}$ tests. Square root, logarithmic, or angular transformations were used where necessary to satisfy the assumptions of parametric analyses, and nonparametric statistics were used whenever transformation of the data failed to produce distributions that did not violate parametric assumptions.

To assess habitat recovery, a measure of vegetation expansion and retreat (percent cover) was deemed to best represent changes in habitat condition. We wanted to know the overall direction and relative magnitude of change for each component within and between exclosure and open plots, rather than simply whether differences existed in average cover for each parameter. Because transformation of some parameters still failed to meet assumptions underlying parametric tests, and to facilitate interpretation of the results, we analyzed these data nonparametrically with Mann-Whitney *U*-tests for comparisons between exclosure and open plots within years, and we used Wilcoxon matched-pairs signed-ranks for comparisons within exclosure and open plots across years (Zar 1984).

Results

Climatic Variation

Mean cumulative moisture for October to June periods from 1949 to 1994 was 26 cm per year (86% of mean calendar-year precipitation). Vegetation sampling occurred in years that were much drier than preceding years (Fig. 2a). Precipitation was below average in 1992, which was preceded by above-average precipitation in 1991 following four successive years of drought (Fig. 2a). Precipitation from October 1992 through June 1993 was the highest ever recorded; although 1994 was drier, it was still above average (Fig. 2a). Precipitation fell mainly as snow in early winter and in spring.

Spring months (March through June) exhibited the highest monthly mean values (Fig. 2b), and accounted for nearly half (44%) of mean calendar-year precipitation and slightly more than half (54%) of June-October precipitation. July through September were the distinctly driest months (Fig. 2b). June through September were the only months with mean daily minimum temperatures above freezing, and the only months with mean daily maximum temperatures that exceeded 20°C (Fig. 2c).

Habitat Characteristics

Riparian plots inside the exclosure were characterized qualitatively as dense, sedge-dominated meadows—(primarily Nebraska sedge (*Carex nebrascensis*) and short-beaked sedge (*C. simulata*; taxonomy follows Hitchcock & Cronquist 1973)—with dry-meadow grasses and scattered shrubs in the uppermost portions of the riparian zone (Fig. 1). In contrast, riparian plots outside the exclosure were sparsely vegetated, had little sedge cover, and supported a high density of shrubs (Fig. 1). Herbaceous riparian vegetation on open plots was restricted to a narrow band adjacent to the stream channel.

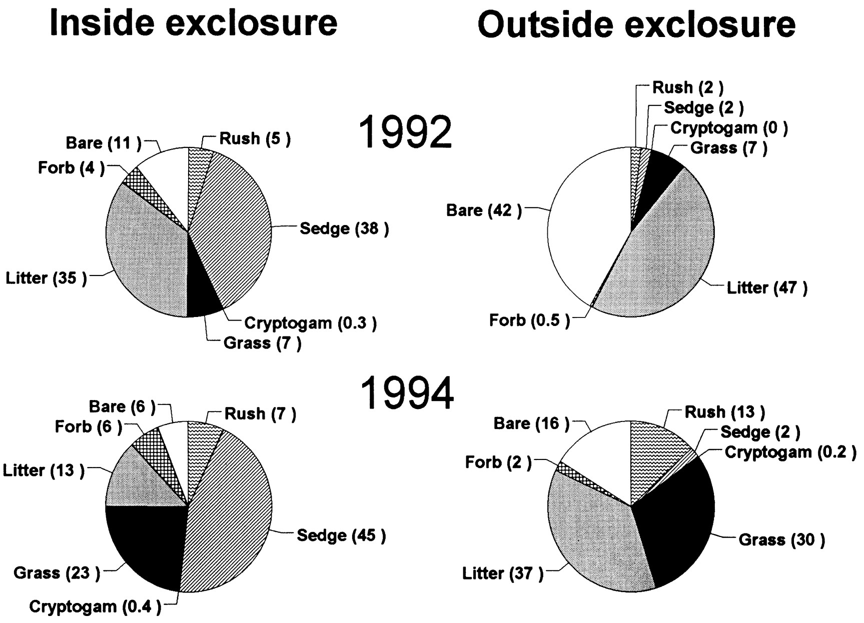

Figure 3. Mean percentages of relative ground cover for riparian meadow habitat on 1.5-ha plots inside and outside a 45-ha, long-term livestock exclosure on Hart Mountain National Antelope Refuge in southeastern Oregon in 1992 and 1994.

Exotic species of grasses that likely were remnants of the initial seeding in the exclosure plots occurred in small, scattered patches (reed canarygrass [*Phalaris arundinacea*] and quack grass [*Agropyron repens*]), except smooth brome *(Bromus inermis)*, which formed locally prominent stands in drier portions of the exclosure. Alfalfa was not detected on any of the plots. Predominant native grasses were Nevada bluegrass (*Poa nevadensis*), Cusick's bluegrass (*P. cusickii*), *Agrostis* spp., and mat muhly (*Muhlenbergia richardsonis*). On open plots, grass cover consisted mostly of squirreltail (*Sitanion hystrix*), an upland species.

Relative cover differed markedly between exclosure and open plots in both years of sampling (Fig. 3, Table 1). On plots inside the exclosure, 73% of total cover consisted of sedges and litter in 1992; sedges and grasses accounted for 68% of total cover in 1994 (Fig. 3). In contrast, bare ground and litter accounted for 89% of total cover on plots outside the exclosure in 1992, but litter and grasses totaled 67% of cover in 1994 (Fig. 3).

Table 1. Shrub cover (cm/transect) on 1.5-ha plots[a] inside and outside a long-term livestock exclosure on Hart Mountain National Antelope Refuge in southeastern Oregon.[b]

	Shrub cover	
	1992	*1994*
Location and species	$\bar{x} \pm SE$ (%)	$\bar{x} \pm SE$ (%)
Inside the exclosure		
Artemisia cana	41 ± 16.6 (<1)	48 ± 25.9 (<1)
Artemisia tridentata	0	0
Chrysothamnus spp.	0	<1
Outside the exclosure		
Artemisia cana	1087 ± 107.9 (11)	1066 ± 134.1 (11)
Artemisia tridentata	145 ± 28.4 (1)	182 ± 47.2 (2)
Chrysothamnus spp.	638 ± 57.0 (6)	518 ± 49.2 (5)

[a] *$n = 3$ plots inside and 3 plots outside the exclosure; 6, 100-m vegetation transects per plot.*
[b] *No significant differences occurred between years within plots ($p > 0.10$, Wilcoxon matched-pairs signed-ranks tests).*

Sedges and forbs constituted significantly greater percentages of cover on exclosure plots than on open plots in both years ($p < 0.001$), whereas bare ground ($p < 0.001$) and litter ($p < 0.05$ in 1992, $p < 0.001$ in 1994) were significantly more extensive on open plots than on exclosure plots. Grasses and cryptogamic cover did not differ between exclosure and open plots within years ($p > 0.05$). Rush cover (*Juncus balticus*) did not differ between exclosure and open plots in 1992 but was greater on open plots in 1994 ($p < 0.05$). Rock and water each accounted for less than 1% of cover.

Significant changes occurred across years on plots outside the exclosure as well as on plots inside the exclosure: grass cover increased ($p < 0.001$), whereas litter ($p < 0.001$ on exclosure plots, $p < 0.05$ on open plots) and bare ground ($p < 0.05$ on exclosure plots, $p < 0.001$ on open plots) decreased. Forbs, rushes, and cryptogamic cover increased on plots outside the exclosure ($p < 0.001$ for forbs and rushes, $p < 0.05$ for cryptogams) but did not change significantly on plots inside the exclosure. Sedge cover did not change across years.

Shrub cover differed dramatically between exclosure and open plots (Table 1). Silver sagebrush (*Artemisia cana*) was virtually the only shrub present on exclosure plots and provided less than 1% cover. In contrast, *A. cana*, big sagebrush (*A. tridentata*), and rabbitbrush (*Chrysothamnus* spp.) collectively averaged 18% cover on plots outside the exclosure (Table 1). No significant changes in shrub cover ($p > 0.10$, Wilcoxon matched-pairs signed-ranks tests) occurred from 1992 to 1994.

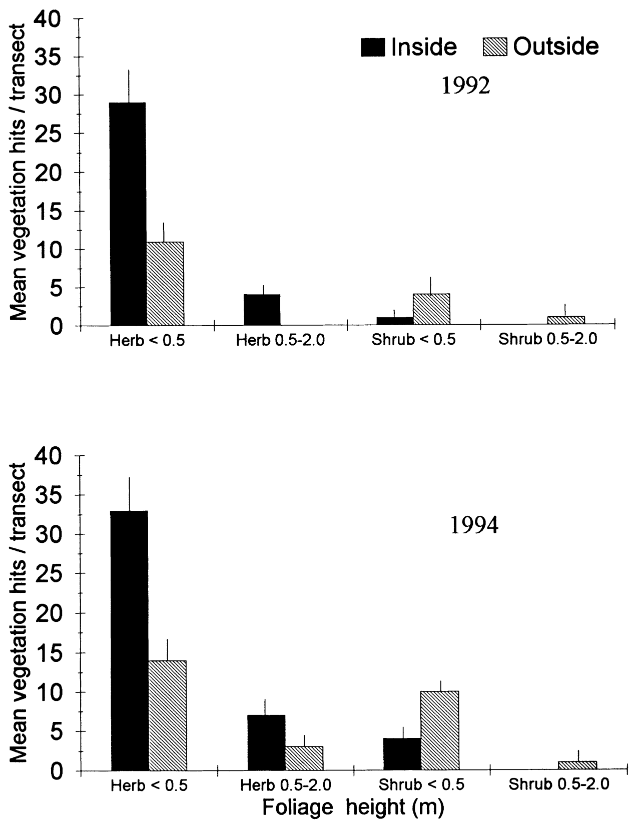

Figure 4. Foliage height diversity measured separately for herbaceous plants and for shrubs in riparian meadow habitat on 1.5-ha plots inside and outside a 45-ha, long-term livestock exclosure on Hart Mountain National Antelope Refuge in southeastern Oregon in 1992 and 1994.

Vertical structural complexity of plot vegetation paralleled patterns of horizontal complexity (Fig. 4). Herbaceous foliage height diversity (fhd) below 0.5 m and from 0.5 to 2.0 m was far greater on exclosure plots than on open plots in both years ($p < 0.001$). There was, in fact, no measurable herbaceous layer above 0.5 m on open plots in 1992 (Fig. 4). In contrast, shrub fhd below 0.5 m was far greater on open plots than on exclosure plots ($p < 0.001$). There were no shrubs greater than 0.5 m in height on exclosure plots.

Relatively small but significant changes occurred in fhd across years within plots (Fig. 4). Herb fhd increased at both heights on all plots ($p < 0.05$, except $p < 0.001$ for the taller layer on exclosure plots). Shrub fhd below 0.5 m did not change significantly on exclosure plots but did increase on plots outside the exclosure ($p < 0.01$). No change occurred in fhd for the taller shrub layer.

Avian Species Composition and Abundances

From 1991 to 1994 we detected 34 bird species during the breeding season in the six plots (see Appendix for nomenclature). Ten species typically associated with wetland and riparian habitats were found only on exclosure plots: Northern Pintail, Northern Shoveler, Northern Harrier, Sandhill Crane, Killdeer, American Avocet, Common Snipe, Short-eared Owl, Song Sparrow, and Yellow-headed Blackbird. Five species typically associated with upland habitats were detected only on plots outside the exclosure: Red-tailed Hawk, American Kestrel, Prairie Falcon, Horned Lark, and Vesper Sparrow. No upland species were found only on exclosure plots, and only one wetland species (a single American Wigeon seen in 1993) was found only on open plots. The nest-parasitic Brown-headed Cowbird did not occur on exclosure plots, although it ocurred widely on Hart Mountain and was abundant in other riparian habitats (Dobkin et al., unpublished data).

Avian species richness (Fig. 5) was greater on exclosure plots than on open plots in all 3 years (repeated measures analysis of variance (ANOVA), $p = 0.007$; Table 2). Species richness was higher in 1993 than in 1992 on exclosure plots, and higher in 1993 than in either 1991 or 1992 on plots outside the exclosure.

Similarly, avian relative abundance (Fig. 5) was consistently greater on exclosure plots than on open plots (repeated measures ANOVA, $p = 0.003$; Table 2) and was depressed in 1992 relative to all other years on plots inside and outside the exclosure.

Differences in avian species composition between exclosure and open plots were substantial at the beginning of our study ($C_j = 0.35$; Fig. 6), grew more pronounced in the 1992 drought ($C_j = 0.23$), but lessened in 1993 ($C_j = 0.46$). The Morisita-Horn index varied little across the 3 years (Fig. 6). The large differences in species composition between exclosure and open plots did not simply reflect disparities in the occurrence of relatively rare species. Considering only species with relative abundances of three or higher on exclosure plots, species-rankings by their abundances differed significantly between exclosure and open plots in each year except the 1992 drought year, when abundances were much reduced (Wilcoxon matched-pairs signed-ranks tests: $T_{1991} = 12.5, p = 0.05$; $T_{1993} = 2.5, p < 0.01$; $T_{1992} = 10.5, p > 0.10$).

Discussion

Vegetation Recovery and Dynamics

Herds of large, native herbivores have been absent from the Intermountain West since at least the end of the Pleistocene, 10,000–12,000 years ago (Mack & Thompson 1982). The ubiquitous presence of domestic livestock throughout these landscapes during the past 135 years has disrupted riparian ecosystems and altered both floral and faunal community composition (Platts 1991; Dobkin 1994; Fleischner 1994; Saab et al. 1995). Our

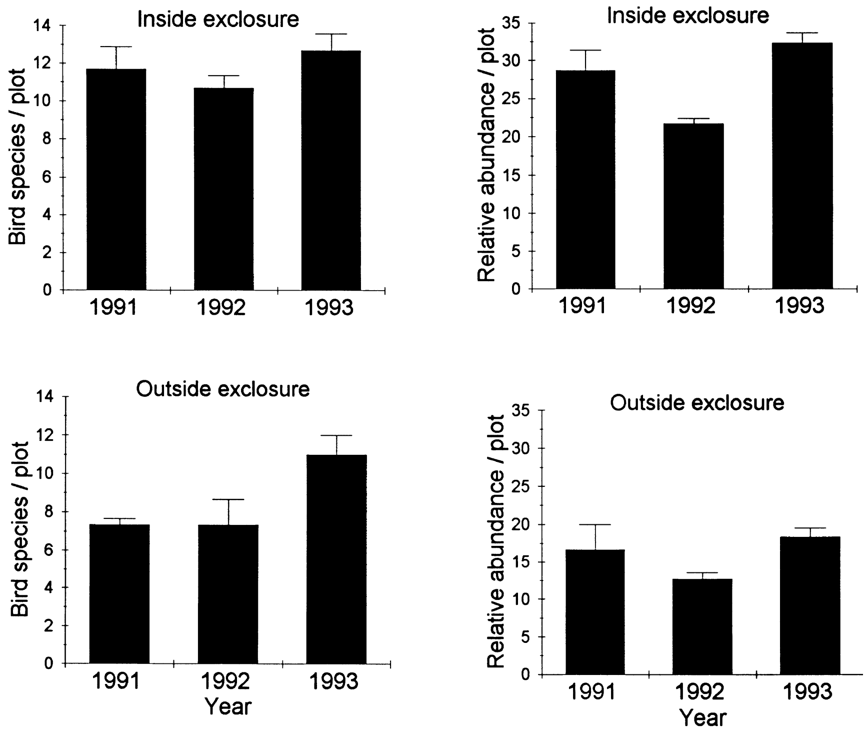

Figure 5. Avian species richness and avian relative abundance (±1 SE) from 1991 to 1993 in riparian meadow habitat on 1.5-ha plots inside and outside a 45-ha, long-term livestock exclosure on Hart Mountain National Antelope Refuge in southeastern Oregon.

study quantitatively illustrates the legacy of livestock's role in the conversion of a riparian meadow system into an essentially upland vegetation association.

Although there is a large body of literature concerning the response of plants to different systems of livestock grazing, there is relatively little understanding of the natural ecological relationships and dynamics of plant communities in the Intermountain West in the absence of livestock (e.g., Vavra et al. 1994). Our study appears to be the first quantitative examination of riparian meadow recovery in the Intermountain West to follow the temporal dynamics of the plant community beginning with the complete removal of livestock.

Our results indicate that recovery of vegetation in these riparian meadow systems does not follow a simple, unidirectional trajectory of succession. Structure and relative composition of these plant communities are not static as climatic variation clearly superimposes a dynamic responsiveness driven largely by interannual variation in precipitation. Even in the long-term exclosure plots, we documented dramatic changes in some plant groups, such as the expansion of grass cover from 1992 to 1994 (which largely replaced litter cover and bare ground) in association with a pattern of drought followed by extraordinarily wet conditions.

Most studies of wetland recovery and restoration have dealt with tidal systems or freshwater marshlands (e.g., National Research Council 1992; Delphey & Dinsmore 1993). Even this extensive literature, however, provides little understanding of the dynamics of wetland restoration or recovery because there is (1) a lack of long-term data that describe the patterns, trends, and variability in natural wetland responses to disturbance (Simenstad & Thom 1996) and (2) an absence of reference wetlands

Table 2. Repeated-measures analysis of variance examining the effect of location^a and year on avian species richness and relative abundance for breeding-season birds on 1.5-ha plots^b at Hart Mountain National Antelope Refuge in southeastern Oregon, 1991–1993.

	Species richness				*Relative abundance*			
Source of variation	*df*	*MS*	F	p	*df*	*MS*	F	p
Location	1	72.0	25.9	0.007	1	612.5	45.6	0.003
Error	4	2.8			4	13.4		
Year	2	14.9	4.9	0.040	2	104.1	10.1	0.006
Year × location	2	2.7	0.9	0.451	2	9.5	0.9	0.435
Error	8	3.0			8	10.3		

[a] *Inside versus outside a long-term livestock exclosure.*

[b] $n = 3$ *plots inside and 3 plots outside the 45-ha exclosure.*

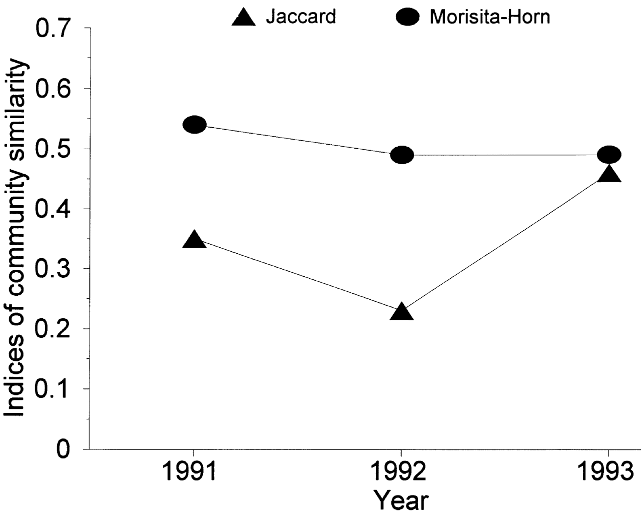

Figure 6. Indices of avian community similarity for the 1991–1993 breeding seasons in riparian meadow habitat on 1.5-ha plots inside and outside a 45-ha, long-term livestock exclosure on Hart Mountain National Antelope Refuge in southeastern Oregon. The Jaccard Coefficient and the complement of the Morisita-Horn index both scale from 0 (no similarity) to 1 (complete or very high similarity).

that can provide long-term baselines for assessment of functional and structural characteristics of mature, relatively undisturbed systems (Brinson & Rheinhardt 1996; Race & Fonseca 1996).

We are unaware of any quantitative studies in comparable wet-meadow habitats that could shed light on the temporal pattern of succession. Crop production followed by abandonment to temperate meadow succession is somewhat analogous to the disking and seeding that initiated the exclosure's succession to a riparian meadow system. Studies of such old-field succession present a general pattern of initial rapid transformation followed by decreased rates in successional change through time (Shugart & Hett 1973) and convergence in pattern after approximately 10 years, despite differences in initial (seeded) species composition and in whether or not fields were plowed or unplowed (e.g., Myster & Pickett 1994).

We cannot differentiate between the roles of seed dispersal and rhizomatous propagation in the expansion (colonization?) of the riparian meadow community because there are no records of the initial species composition inside the exclosure. *Carex* species persist primarily by vegetative growth and are characterized by very low annual seed production (van der Valk & Davis 1979). It seems likely that sedges either were extirpated completely or were reduced to tiny remnant patches at the time of exclosure. Whether or not any of the seeded exotic species played significant roles in facilitating or hindering the subsequent restoration of the riparian meadow community now dominated by sedges is unknown.

Comparisons of exclosed and grazed areas often produce mixed results that can be difficult to interpret (Miller et al. 1994) due to (1) lack of comparability between grazed and ungrazed areas, (2) complete absence of replication, and (3) differences in grazing intensity (number, distribution, and biomass of animals) that defy meaningful quantification. Our study avoids the first and last of these difficulties. Management treatment of the area prior to exclosure removed the ambiguity of differences in grazing intensity and represented perhaps the most extreme starting conditions possible for inaugurating a disturbance-initiated recovery. Furthermore, we contend that the exclosed area was large enough to minimize many of the problems associated with the use of replicate plots within a single exclosure (Bock & Bock 1993). Inclusion of meadow plots from other watersheds in our study would have introduced additional sources of variation (e.g., recent grazing history, plant species composition).

We believe that the successional outcome inside the exclosure is most reasonably interpreted as a consequence of the removal of livestock, which led to a rise in the water table within the exclosure and an expansion of the hyporheic zone laterally from the stream channel. This view is supported by continued waterflow in the stream reach within the exclosure for many weeks beyond the time when water ceased to flow in stream reaches above and below the exclosure during dry years of our study and in recent drought years prior to 1991 (there are no springs along this section of Guano Creek).

Depth of channel entrenchment is likely to be a principal factor governing the temporal trajectory of restoration in these riparian meadow communities. The system we studied was a low-gradient stream with relatively shallow (<1 m) channel entrenchment at the time of exclosure. The absence of change in sedge cover on exclosure plots may indicate that some degree of stasis has been achieved in water-table level. Restoration of the water table to pre-livestock condition outside the exclosure should result in restoration of lush meadow vegetation on open plots (e.g., Stromberg et al. 1996). The increase in cover of rushes on open plots in 1994 is suggestive of increased water retention and sediment capture in the entrenched creek channel. The lack of change in sedge cover on open plots, however, suggests that restoration to a sedge-dominated meadow will not happen quickly, although we do not know whether sedge expansion will be slow and incremental or whether expansion may occur rapidly after the water table rises to some threshold level. Higher-gradient streams with channel entrenchment of several meters are common in the region and are likely to take much longer to recover from degradation than will our plots.

The widespread invasion of exotic plant species in the Intermoutain West poses a suite of often insurmountable challenges to the successful restoration of native plant communities in the region (D'Antonio & Vitousek 1992; Young 1994). In this context the recovery of the riparian meadow plant community inside the exclosure appears quite remarkable.

Avian Communities

Most studies of riparian avifaunas in the region have examined the more species-rich avian communities of woody riparian habitats (Dobkin & Wilcox 1986; Dobkin et al. 1995). Little attention has been paid previously to riparian meadow avifaunas (Dobkin 1994; Saab et al. 1995). We suspect that the lack of attention results largely from the scarcity of native riparian meadows (Dobkin 1995; Brussard et al. 1997) with structural conditions suitable to support a habitat-appropriate avifauna.

For many riparian birds, presence or absence in a particular habitat is highly dependent on the complexity and density of vegetation structure, especially in the shrub and herbaceous layers (Dobkin 1994). The most direct effect of livestock on riparian vegetation is removal of the lower vegetation layers. Not surprisingly, ground-nesting birds appear to be most negatively affected by livestock grazing (Saab et al. 1995). Although we have no direct data regarding the reproductive success of nesting birds in our plots, we speculate that the greater herbaceous cover and foliage height diversity in the exclosure plots should result in greater nesting success. Nest parasitism by cowbirds also is likely to be much lower in these plots because cowbirds were never detected in exclosure plots in spite of being one of the most abundant and widespread species across all riparian habitats at Hart Mountain (Dobkin et al., unpublished data).

Recovered meadow plots had more diverse and abundant avian communities than the open plots. The avifaunas of exclosure and open plots contrasted strongly in species composition and in the relative abundances of most shared species. Exclosure avifaunas consisted primarily of wetland and riparian species, whereas open-plot avifaunas were composed essentially of grassland and upland-shrub species. Both species richness and relative abundance were greater in wet years than in dry years and thus varied as vegetation changed in response to climatic variation. The most dramatic example was provided by Wilson's Phalaropes, which were abundant in 1993 and 1991 but nearly absent in the dry year of 1992 (Appendix). Waterfowl and Western Meadowlarks followed similar patterns.

No pre-livestock baseline data describe the avifaunal composition of riparian meadows in the Great Basin, and long-term studies of avifaunas in restored riparian meadows are nonexistent. Irrigated hay meadows prior to mowing may be the closest analog to native riparian meadows in the region. McAdoo et al. (1987) reported breeding avifaunas of hay meadows dominated by Red-winged Blackbirds, Savannah Sparrows, and Western Meadowlarks, all of which were important in our meadows as well.

Several species associated closely with riparian meadow habitats had stable or increasing numbers on the exclosure plots (Killdeer, Western Meadowlarks, Savannah Sparrows), which contrasted with declining population trends at the regional level (Dobkin 1998). The western populations of all five shorebird species that nested on exclosure plots are among the most at-risk of all North American shorebirds assessed by a habitat-based ranking system (Page & Gill 1994). Some of the key species nesting in the exclosure plots (e.g., Wilson's Phalarope) occur too sparsely to be sampled adequately by regional population monitoring schemes, which further suggests the importance of riparian meadows as relatively rare but critical components of regional biodiversity (Brussard et al. 1997).

Aside from work with salmonid fishes (Platts 1991), few studies have examined the restoration or recovery of riparian faunal communities in degraded riparian zones. Although our results indicate substantial recovery of plant species composition and structure in (exclosure) riparian meadows, we do not know how closely the restoration of avian community composition will track vegetation recovery. It is encouraging that Sora were first detected in open plots in 1993 and that Wilson's Phalarope (as well as Green-winged Teal and Gadwall) were detected in 1994. The appearance of these key wet-meadow species in the open plots is a promising sign of initial restoration of a riparian meadow avifauna. Given the close proximity of potential colonists, the numerical recovery of these species likely will follow in concert with the development of suitable habitat as riparian meadow vegetation replaces upland vegetation.

Future Prospects

The lack of landscape-scale riparian systems that have never been grazed by livestock and the nonexistence of long-term studies of riparian areas from which livestock have been removed present significant impediments to our understanding of riparian ecosystems in the arid and semiarid western United States. Given the ubiquity of past and continuing livestock influences on the plant and animal communities of these landscapes, there is a clear need for knowledge about these systems in a livestock-free context.

Across public lands of the West there exist isolated examples of long-term livestock exclosures that have received little attention subsequent to their establishment. These exclosures offer opportunities to acquire many years of successional plant and animal information in a much-condensed period of time. But the extraordinary scientific potential of these exclosures and the unique opportunity they afford for gaining knowledge directly applicable to improving management of critical and fragile riparian habitats are often not appreciated by land managers. This was made astonishingly clear to us when the exclosure fence in our study was removed inexplicably by refuge management in 1994.

There are significant limitations for most exclosure studies, however, that must be kept in mind: (1) data generally are nonexistent regarding plant and animal community composition at the time of exclosure; (2) virtually all exclosed areas were grazed by livestock prior to exclosure; and (3) most exclosures are too small to encompass landscape-scale processes and biodiversity and thus do not function as intact ecosystems. We strongly concur with Bock et al. (1993) that there is an urgent need to establish a series of large, landscape-scale livestock exclosures across the western United States in order to create clear ecological benchmarks against which the effects of livestock grazing can be measured. Only through such studies will the necessary insight be gained to effectively manage the restoration of these landscapes.

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Appendix

Maximum relative abundance of birds* on 1.5-ha plots inside and outside a long-term livestock exclosure on Hart Mountain National Antelope Refuge in southeastern Oregon.

	Inside exclosure				*Outside exclosure*			
	1991	*1992*	*1993*	*1994*	*1991*	*1992*	*1993*	*1994*
Canada Goose (*Branta canadensis*)	0	1	0	0	0	0	1	0
Green-winged Teal (*Anas crecca*)	1	0	1	2	0	0	0	1
Mallard (*Anas platyrhynchos*)	5	4	2	4	3	0	3	0
Northern Pintail (*Anas acuta*)	4	1	5	1	0	0	0	0
Cinnamon Teal (*Anas cyanoptera*)	3	1	4	1	2	0	4	1
Northern Shoveler (*Anas clypeata*)	0	0	1	0	0	0	0	0
Gadwall (*Anas strepera*)	4	0	1	0	0	0	0	1
American Wigeon (*Anas americana*)	0	0	0	0	0	0	1	0
Northern Harrier (*Circus cyaneus*)	0	1	0	1	0	0	0	0
Red-tailed Hawk (*Buteo jamaicensis*)	0	0	0	0	1	0	0	0
American Kestrel (*Falco sparverius*)	0	0	0	0	0	0	1	0

(continued)

Appendix. Continued

	Inside exclosure				Outside exclosure			
	1991	*1992*	*1993*	*1994*	*1991*	*1992*	*1993*	*1994*
Prairie Falcon (*Falco mexicanus*)	0	0	0	0	0	1	0	0
Sage Grouse (*Centrocercus urophasianus*)	0	2	0	0	1	0	0	0
Sora (*Porzana carolina*)	2	2	2	0	0	0	2	1
Sandhill Crane (*Grus canadensis*)	1	2	0	1	0	0	0	0
Killdeer (*Charadrius vociferus*)	3	2	3	0	0	0	0	0
American Avocet (*Recurvirostra americana*)	0	0	2	0	0	0	0	0
Willet (*Catoptrophorus semipalmatus*)	5	5	5	1	4	3	1	0
Common Snipe (*Gallinago gallinago*)	2	1	1	1	0	0	0	0
Wilson's Phalarope (*Phalaropus tricolor*)	21	3	21	9	0	0	0	1
Short-eared Owl (*Asio flammeus*)	0	1	0	0	0	0	0	0
Horned Lark (*Eremophila alpestris*)	0	0	0	0	0	0	0	1
Cliff Swallow (*Hirundo pyrrhonota*)	7	6	8	2	21	9	3	4
Common Raven (*Corvus corax*)	0	0	0	1	0	0	0	1
Sage Thrasher (*Oreoscoptes montanus*)	0	0	1	0	0	1	4	0
Brewer's Sparrow (*Spizella breweri*)	0	0	1	0	1	3	4	3
Vesper Sparrow (*Pooecetes gramineus*)	0	0	0	0	0	3	5	4
Savannah Sparrow (*Passerculus sandwichensis*)	5	4	7	5	7	9	8	6
Song Sparrow (*Melospiza melodia*)	0	0	1	0	0	0	0	0
Red-winged Blackbird (*Agelaius phoeniceus*)	20	26	21	14	7	4	5	3
Western Meadowlark (*Sturnella neglecta*)	2	3	8	1	2	4	7	3
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	1	0	0	0	0	0	0	0
Brewer's Blackbird (*Euphagus cyanocephalus*)	0	0	2	0	0	1	6	4
Brown-headed Cowbird (*Molothrus ater*)	0	0	0	0	1	0	0	1

[*] *Each plot was sampled six times with three pairs of consecutive-morning samples during each breeding season from 1991 to 1993. In 1994 each plot was sampled only twice (one pair of consecutive-morning samples).*