

SPATIAL USE AND HABITAT SELECTION OF GOLDEN EAGLES IN SOUTHWESTERN IDAHO

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ABSTRACT.—We measured spatial use and habitat selection of radio-tagged Golden Eagles (*Aquila chrysaetos*) at eight to nine territories each year from 1992 to 1994 in the Snake River Birds of Prey National Conservation Area. Use of space did not vary between years or sexes, but did vary among seasons (home ranges and travel distances were larger during the nonbreeding than during the breeding season) and among individuals. Home ranges were large, ranging from 190 to 8,330 ha during the breeding season and from 1,370 to 170,000 ha outside of the breeding season, but activity was concentrated in small core areas of 30 to 1,535 ha and 485 to 6,380 ha during the breeding and nonbreeding seasons, respectively. Eagles selected shrub habitats and avoided disturbed areas, grasslands, and agriculture. This resulted in selection for habitat likely to contain their principal prey, black-tailed jackrabbits (*Lepus californicus*). Individuals with home ranges in extensive shrubland ($n = 3$) did not select for shrubs in the placement of their core areas or foraging points, but individuals in highly fragmented or dispersed shrublands ($n = 5$) concentrated their activities and foraged preferentially in jackrabbit habitats (i.e. areas with abundant and large shrub patches). As home ranges expanded outside of the breeding season, individuals selected jackrabbit habitats within their range. Shrubland fragmentation should be minimized so that remaining shrub patches are large enough to support jackrabbits. Received 1 May 1996, accepted 6 May 1997.

IN SOUTHWESTERN IDAHO, the demography and behavior of Golden Eagles (*Aquila chrysaetos*) are closely associated with variation in the abundance of black-tailed jackrabbits (*Lepus californicus*). Jackrabbit populations fluctuate, peaking at 7-to-12 year intervals (Johnson and Peek 1984). More eagles lay eggs and produce more offspring when jackrabbits are abundant than when jackrabbit populations crash (Steenhof et al. 1997), and eagles use alternative prey when jackrabbits decline (Steenhof and Kochert 1988). The importance of jackrabbits to eagles suggests that eagles should locate territories and concentrate foraging activities in habitats most likely to contain jackrabbits. We tested this hypothesis by relating spatial-use patterns of eagles to habitats associated with black-tailed jackrabbits. We then could indirectly describe habitat use by eagles relative to their main prey and quantify habitat characteristics meaningful to land managers.

Although descriptions of average behavior may be most easily understood by biologists and translated into management policy, they do not capture variation among individual animals. If such variation is substantial and ignored by focusing on population averages, conservation strategies and biological descriptions will be inaccurate and rarely effective. Describing individual variation, attempting to understand it, and using this to provide context-specific management recommendations would be preferable. Furthermore, many animals select and use resources at various scales (Allen and Starr 1982, O'Neill et al. 1988, Wiens 1989).

Here, we explore individual variation in Golden Eagle diet, spatial use, and habitat selection and show that, although certain habitat types are consistently preferred, the scale at which individuals exhibit selection for them is variable and dependent on landscape attributes and possibly individual experience. This is likely to be common in long-lived, permanent residents that maintain year-round, all-purpose territories, such as Golden Eagles (Beecham and Kochert 1975, Dunstan et al. 1978,

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TABLE 1. Golden Eagle territories where behavior, productivity, and home-range characteristics were studied, Snake River Birds of Prey National Conservation Area, 1991 to 1994.

Number of eagles		Individuals used in home-range estimation			Years locations were used in home-range estimation			
Captured	Instru- mented	Sex	Age	Capture date	1991	1992	1993	1994
Black Butte								
2	1	M	Ad	12 Nov 91		X	X	X
Beercase								
2	2	M	Ad	18 Jan 92		X	X	X
Wildhorse								
2	2	F	Ad	14 Oct 91		X	X	X
		M	Ad	16 Dec 92			X	X
PP&L 119								
5	4	M	Ad	19 Feb 91	X	X	X	
		F	Ad	23 Oct 92		X	X	X
		M	Subad	11 Mar 94				X
Pole 369^a								
0	0	F	Subad	17 Dec 91			X	
Grand View Sand Cliff								
2	2	F	Subad	17 Dec 91	X			
		M	Ad	24 Oct 92		X	X	X
Ogden								
1	1	M	Ad	14 Dec 92		X	X	X
Beecham								
1	1	M	Ad	22 Nov 91	X	X	X	X
Cabin								
12	2	F	Ad	06 Dec 91	X	X	X	X
		M	Ad	12 Apr 94				X

^a Individual moved from Grand View Sand Cliff to Pole 369.

Collopy and Edwards 1989), because learning and experience may shape behavior (Mayr 1974).

METHODS

Site selection and trapping.—We studied Golden Eagles on 9 of 20 historically occupied territories (defended areas including nesting and foraging sites) along a 140-km stretch of the Snake River canyon (from Walter's Ferry to C. J. Strike Reservoir) within the Snake River Birds of Prey National Conservation Area (NCA). Approximately 75% of historically occupied territories were actually occupied during our study. We selected our subsample of territories to provide a representative sample of currently occupied landscapes in the NCA (none was inactive for more than 5 years from 1970 to 1991, four had >50% of the area within a 2.66-km radius circle centered at traditionally used nests burned by wildfires during the previous 10 years, and four had <30% of this area burned). One territory was added in 1993 when a ra-

dio-tagged female left her territory and joined an untagged eagle at a new site.

From 1991 to 1994, we captured 27 individuals in target territories (Table 1). Sex was determined by observations of copulation and measurements of body mass and footpad length (Edwards and Kochert 1986). Thirteen birds were instrumented with 65-g, solar-assisted transmitters secured by a 10-g harness of 19-mm wide Teflon webbing and a leather sternum patch; two were instrumented with 15-g tail-mounted transmitters. Transmitters may have reduced productivity in one year of study but did not influence behavior and spatial use (Marzluff et al. 1997). More than one individual was captured and radio-tagged in some territories because of transmitter failure or removal, eagle dispersal, and deliberate attempts to catch both breeders.

We monitored the behavior and productivity of radio-tagged Golden Eagles at eight territories during 1992, nine during 1993, and eight during 1994 (Table 1). Both the male and female were tagged in one of the eight territories in 1992, in two of the nine terri-

tories in 1993, and in three of the eight territories in 1994. To avoid concerns over pseudoreplication, we used the territory, not the individual on the territory within a year, as the experimental unit unless otherwise noted.

We captured eagles with radio-triggered bow nets (1991 and 1994), noosed lures (1991), and padded leghold traps (1991, 1992, 1993, 1994; Bloom 1987). We observed traps from 1 to 2 km away and broadcast noises from two-way radios buried near traps to reduce the frequency of catching nontarget species.

Location estimates and behavior.—Instrumented eagles were selected randomly and followed for 6-h observation periods, three to four days per month. Eagles in each territory were followed approximately weekly to balance observation effort across territories. We located eagles for visual observation, then continuously recorded time and activity data, particularly noting where hunting forays occurred and characterizing habitats in those areas. Locations were plotted (± 100 m) in the field on 1:24,000 scale topographic maps assisted by aerial photographs. Locations were obtained for all perched birds, all extreme points used by birds each day, and most points where birds soared. Perched locations included roost sites as well as hunting and resting sites. We also estimated the location of all copulations, undulating flights, and hunting attempts. Travel routes among perches or soaring areas were recorded, but estimates of point locations along these routes were not made. We used all observations on both members of the pair to determine the location of hunting attempts and prey captures. Hunting forays were any flights that included an attempt to capture prey (i.e. a steep dive or chase of potential prey).

Breeding status and habitat.—We considered eagles to have laid eggs if one member of the pair was seen in an incubating posture, or if eggs were seen. In 1992 and 1993, nestlings at sites tended by radio-tagged parents were banded and marked with uniquely numbered patagial tags to aid in observations within territories during the winter and to identify these birds within their parents' territories.

In a concurrent study, Knick et al. (1997) determined areal coverage of habitats from Landsat thematic mapper satellite imagery classified into big sagebrush (*Artemisia tridentata*)/green rabbitbrush (*Chrysothamnus viscidiflorus*), winterfat (*Ceratoides lanata*), salt-desert shrub (*Atriplex confertifolia*, *A. canescens*, *Sarcobatus vermiculatus*), grassland (*Poa secunda*, *Bromus tectorum*, *Sitanion hystrix*), cliff, and water. They also delineated all areas used for agriculture since 1979 (including fallow fields) from a composite of the 1979 Snake River Birds of Prey vegetation map (USDI 1979), 1993 Bureau of Reclamation agriculture maps, and the classified satellite imagery. Resolution of the habitat map was 50 m (resampled from 30-m pixels in the satellite image). Knick et al. (1997) used >5% ground cover of shrubs

to separate shrub and grassland classes. Accuracy of the classification in separating shrub and grassland areas was 80%; accuracy in separating individual habitat classes was 64% (Knick et al. 1997).

Knick and Dyer (1997) developed an index of black-tailed jackrabbit habitats from a multivariate analysis that included number of agriculture cells, a habitat diversity index, number of shrub cells, shrub patch characteristics, and an index of landscape patchiness. The habitat index, scaled into 10% intervals, represented the probability of similarity of the habitat at each 50-m gridded cell in a Geographical Information System map to the mean habitat vector associated with jackrabbits. We used habitat associations of jackrabbits during low population phases and spring/early summer seasons. These were the conditions during the majority of our eagle observations, but jackrabbit population phases and season have little effect on jackrabbit habitat associations (Knick and Dyer 1997). We emphasize that the map of the jackrabbit habitat index did not predict the actual presence of jackrabbits, but rather the similarity of a given cell to habitats used by jackrabbits.

Analyses.—We used all unique locations visited by eagles during an observation session in home-range analyses rather than using a time interval to select "independent" locations. Use of unique locations reduced dependency by removing repeatedly visited locations within a sampling day, but it did not reduce the estimation of the maximum area used by an eagle. However, because many locations within a range were visited repeatedly each day and these tended to be near the center of the range, the exclusion of repeat locations resulted in an expansion of core areas. Because different radio-tagged individuals breeding within a given territory showed similar ranging habits, we used all unique locations from both eagles to define the home range associated with a territory. The nest site constituted a single observation for home-range analyses, even though it was visited multiple times.

We separated our locations into two seasons, breeding and nonbreeding. We defined breeding as the time from when eagles were first observed building nests or incubating until the end of the postfledging dependency period or the breeding attempt failed; nonbreeding included all times not within the breeding period. Therefore, seasons were of different duration for each individual territory.

We analyzed all four years of data using a two-factor repeated-measures ANOVA, with travel distances by year and season as the repeated measures. In this analysis we used only the five territories that were observed every year and where transmitter failure did not limit observations. Mean seasonal travel distances did not differ among years ($P = 0.95$); therefore, we pooled data across years and used data from eight territories to examine seasonal and ter-

ritorial differences in travel distance using a two-factor (season and territory) ANOVA.

We used Ranges V software (Kenward and Hodder 1995) to calculate a variety of home-range estimates for comparative purposes, but we used only selected methods for analysis of habitat use and seasonal differences in home-range size. We used concave polygons with edge length restricted to half the minimum range diagonal to represent eagle home ranges. Concave polygons were most appropriate for estimation of habitat available to foraging eagles within their home ranges because they minimized territory overlap, included all known locations of eagles, and did not rely upon statistical distributions of locations. Harmonic-mean and convex-polygon methods were less satisfying because their reliance on the statistical distribution of locations resulted in extrapolation beyond locations we knew eagles visited, and, as a consequence, included extensive overlap between adjacent territories that we did not observe in the field.

We investigated habitat selection at three scales. First, we determined if eagles selected or avoided certain habitats in establishing a home range by comparing habitat used in concave polygon home ranges with habitat available within the study area. We defined available habitat as that area on either side of the Snake River canyon within the maximum travel distances observed for radio-tagged birds. Buffer areas, derived from maximum travel distances, were determined separately for the breeding and non-breeding seasons. Second, we determined if eagles selected or avoided certain habitats within their home range by comparing the habitat used within core areas defined by hierarchical, incremental cluster analysis with a "nearest neighbor" joining rule (Kenward 1987) with habitat available within each individual's concave home range. We examined habitat in clusters that included 90 and 95% of locations separately. Most territories showed little change in the rate of area increase for cluster polygons that included from 20 to 90% of the locations but typically increased sharply thereafter, both in area within ranges and size variation between ranges, which indicated that the remaining 5 to 10% of locations were outliers. Third, we determined if foraging habitat was selected from within high-use areas by comparing the habitat within 100 m of locations where we saw eagles attempt to capture prey with the habitat available within core areas.

We determined the importance of habitat use with selection ratios (proportion of habitat class used/proportion of habitat type available) for each habitat type (Manly et al. 1993). We normalized selection ratios by using their natural logarithm. We viewed the individual territory as our sampling unit and calculated average selection ratios for our sample of territories. We calculated a 95% confidence interval around each ratio average after a Bonferroni adjust-

ment for multiple comparisons. Selection ratios that did not include 0 in their confidence interval were evidence of significant ($\alpha = 0.05$) avoidance (ratio < 0) or selection (ratio > 0). We used compositional analysis (Aebischer et al. 1993) to test for individual differences in selection or avoidance of habitats.

RESULTS

SPATIAL-USE PATTERNS

Travel distance.—Distance traveled from the nest varied among individuals and between seasons. Eagles traveled farther from their nests outside of the breeding season ($\bar{x} = 3,036.1 \pm \text{SE of } 241.6 \text{ m}$, $n = 248$) than during the breeding season ($\bar{x} = 1,046.8 \pm 366.6 \text{ m}$, $n = 121$; repeated-measures ANOVA, $F = 9.1$, $df = 1$ and 4 , $P = 0.04$). Annual variation in distance traveled was not significant (multivariate $F = 0.05$, $df = 2$ and 3 , $P = 0.95$). However, individuals differed in travel distance between seasons (interaction of individual and season in two-way ANOVA without repeated measures, $F = 2.29$, $df = 7$ and 353 , $P = 0.03$). Males ($\bar{x} = 1,963.7 \pm 251.0 \text{ m}$, $n = 253$) and females ($\bar{x} = 2,094.2 \pm 401.0 \text{ m}$, $n = 116$) traveled similar distances ($F = 0.08$, $df = 1$ and 365 , $P = 0.78$).

An individual's travel distance from the nest was related to behavior (Fig. 1). Most of the extreme travel distances were hunting forays or undulating flights. A few individuals did most of their hunting ($n = 2$) and undulating ($n = 2$) near the nest.

Home range.—Similar patterns of travel also were reflected in individually and seasonally variable home ranges. Home-range estimators in Table 2 are for comparative purposes; we limited our discussion to concave polygons, which best described the total area used by eagles, and to clusters that removed extreme travels and defined high use (i.e. "core") areas.

Eagle breeding ranges encompassed 190 to 8,330 ha and expanded to 1,370 to 170,000 ha outside of the breeding season (Table 2). The average size of ranges was $2,280 \pm \text{SD of } 2,625 \text{ ha}$ ($n = 8$) during the breeding season and $30,484 \pm 59,909 \text{ ha}$ ($n = 8$) during the non-breeding season. The large standard deviations resulted from extreme variation among individuals.

Home-range boundaries have remained fairly consistent for many years. Three of the territories we studied (a, b, i) also were studied

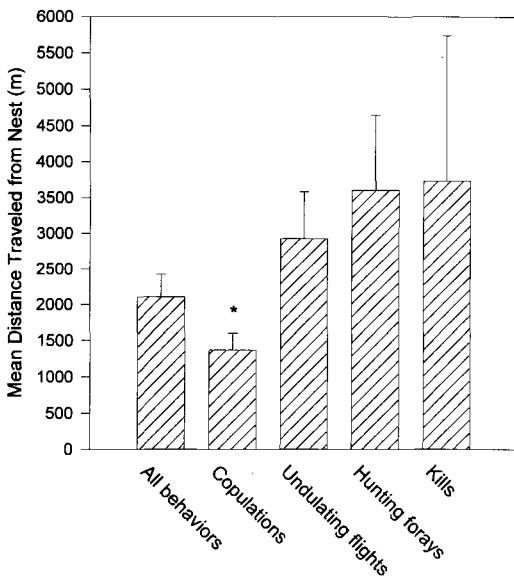


FIG. 1. Distances traveled by adult Golden Eagles where copulations, undulating flights, hunting forays, and kills were observed. Travel distance was calculated for each individual ($n = 9$) and averaged (\pm SE) across individuals. Significantly (*, $P < 0.05$) extreme average travel distances are indicated when the 95% confidence interval around the travel distance for a particular activity does not include the average travel distance to all locations.

with radiotelemetry in the 1970s (Dunstan et al. 1978). Home-range sizes in the 1970s and 1990s were similar (two ranges were larger and one was smaller in the 1970s than in the 1990s; \bar{x} absolute difference in convex polygons = 1,256 \pm SE of 413 ha), and ranges in the 1990s overlapped those from the 1970s by an average of 57.6 \pm SE of 15.8%.

Breeding ranges of neighboring pairs overlapped only slightly ($\bar{x} = 3.7 \pm 1.7\%$, $n = 10$; Fig. 2A), suggesting territorial behavior. Interactions between neighbors were rarely observed because of the mutually exclusive territories. Expanded ranges outside of the breeding season overlapped neighboring ranges more than during the breeding season ($\bar{x} = 22.1 \pm 9.4\%$, $n = 10$; Fig. 2B) and included foraging areas frequented by wintering and nonbreeding eagles.

Nonresidents were captured in three territories (a, d, i) outside of the breeding season. Ten were captured in one territory (i), and only two offspring of residents were among those captured (one in territory d and one in i). Ag-

gression between residents and nonresidents was extremely rare within and outside of the breeding season.

Eagles concentrated their activity within several frequently used cores. Cores defined by clusters of similar use indicated that 95% of the eagle locations were within $14.4 \pm 3.1\%$ of their breeding ranges and $25.3 \pm 5.8\%$ of their nonbreeding ranges (Fig. 2A, B). Ninety percent of the locations were within $6.9 \pm 1.7\%$ of breeding ranges and $12.6 \pm 3.2\%$ of nonbreeding ranges.

PREY

Black-tailed jackrabbits, Townsend's ground squirrels (*Spermophilus townsendii*), and Rock Doves (*Columba livia*) were the most commonly observed prey taken by eagles during our years of study (Fig. 3). Prey taken within and outside of the breeding season differed, with ground squirrels dominating the breeding season and jackrabbits dominating the nonbreeding season (comparing numbers of jackrabbits, ground squirrels, Rock Doves, and other prey for 1992 to 1994; Fisher's exact test, $P = 0.02$). Use of jackrabbits peaked in 1992 and then declined. Rock Doves, reptiles, yellow-bellied marmots (*Marmota flaviventris*), and Nuttall's cottontails (*Sylvilagus nuttallii*) were taken more frequently as jackrabbit use declined.

Jackrabbits varied in importance among individual eagle pairs (pooled data from 1992 to 1994; Fisher's exact test, $P < 0.001$ for six pairs with $n \geq 6$ captures). One pair (b) took predominantly (8 of 10 captures) jackrabbits. However, the other pairs took jackrabbits much less frequently (jackrabbits comprised $\leq 7\%$ of the prey taken by pairs a, f, g, and h). Rock Doves, waterfowl, and marmots comprised the remainder of the prey taken.

HABITAT SELECTION

Vegetation.—Eagle territories occurred along a gradient of shrubsteppe habitats from big sagebrush, winterfat, and green rabbitbrush to salt-desert shrubs. Additionally, wildfires burned significant portions of some territories prior to our study, resulting in varying amounts of grassland among territories (Fig. 2A, B).

Selection of habitat classes.—The variation in

TABLE 2. Estimated areas (ha) of home ranges (concave and convex polygon, harmonic mean) and core areas (cluster analysis) of Golden Eagle territories (letters denote territories in Figures 2 and 5). Data combined across years and birds but analyzed separately for nonbreeding (N) and breeding (B) seasons.

Season	<i>n</i>	Concave 100%	Convex 100%	Harmonic 100%	Harmonic 95%	Core 95%	Core 90%
Black Butte (a)							
N	489	1,376	1,610	2,373	847	485	102
B	312	1,071	1,175	2,670	827	289	161
Beercase (b)							
N	298	11,261	18,541	61,792	10,110	2,581	938
B	325	8,331	9,759	22,929	5,536	1,535	565
Wildhorse (c)							
N	261	36,925	36,925	109,280	29,073	2,729	2,115
B	96	663	875	1,314	1,021	127	74
PP&L 119 (d)							
N	250	6,076	6,762	16,621	6,110	1,535	755
B	112	1,032	2,290	13,686	4,206	254	120
Pole 369 (e)							
N	22 ^a	318	450	559	254	159	136
B	94	506	985	2,331	446	53	35
Grand View (f)							
N	297	176,010	207,069	614,675	86,810	6,387	2,035
B	116	194	336	877	94	30	5
Ogden (g)							
N	233	4,443	4,697	9,135	3,352	1,125	738
B	121	2,576	4,304	15,046	3,251	658	366
Beecham (h)							
N	453	3,721	4,625	16,582	2,001	487	194
B	277	3,055	3,471	29,818	323	86	31
Cabin (i)							
N	167	4,061	4,332	9,721	3,698	1,314	494
B	95	1,321	3,793	11,155	1,311	337	127

^a Range sizes suspect owing to small sample size.

vegetation among territories was evident when we compared habitat classes found within breeding and nonbreeding ranges with available habitats within 4.5 km (the average maximum travel distance during the breeding season) or 9.5 km (the average maximum travel distance during the nonbreeding season) of the canyon rim. Most eagle home ranges had more sagebrush/rabbitbrush, more cliff/rock outcrop, less grassland, and less agriculture than expected from availability (see Table 3). Variation in selectivity among eagles was large (Table 3), and the resulting habitat composition of home ranges varied significantly among individuals (compositional analysis; breeding season, $\lambda = 0.16$, $\chi^2 = 16.5$, $df = 5$, $P < 0.01$; nonbreeding season, $\lambda = 0.20$, $\chi^2 = 14.4$, $df = 5$, $P < 0.05$). Most variation was due to varying amounts of sagebrush/rabbitbrush, salt-desert

shrubs, grassland, and rock outcrop in home ranges. Individuals were more consistent in including less winterfat, agriculture, and water than expected based on availability in their ranges, especially during the breeding season (Table 3).

Eagle selection for shrubland and avoidance of grassland and agriculture was accentuated when we compared habitats in core areas with those available within each individual's home range (see Table 3). Avoidance of agriculture was significant and consistent among individuals during both seasons, especially within 90% core areas. Most individuals avoided grassland and selected shrubland, but individual variation precluded overall significance (Table 3).

Use and availability of habitats.—Selection coefficients are proportions and can mistakenly

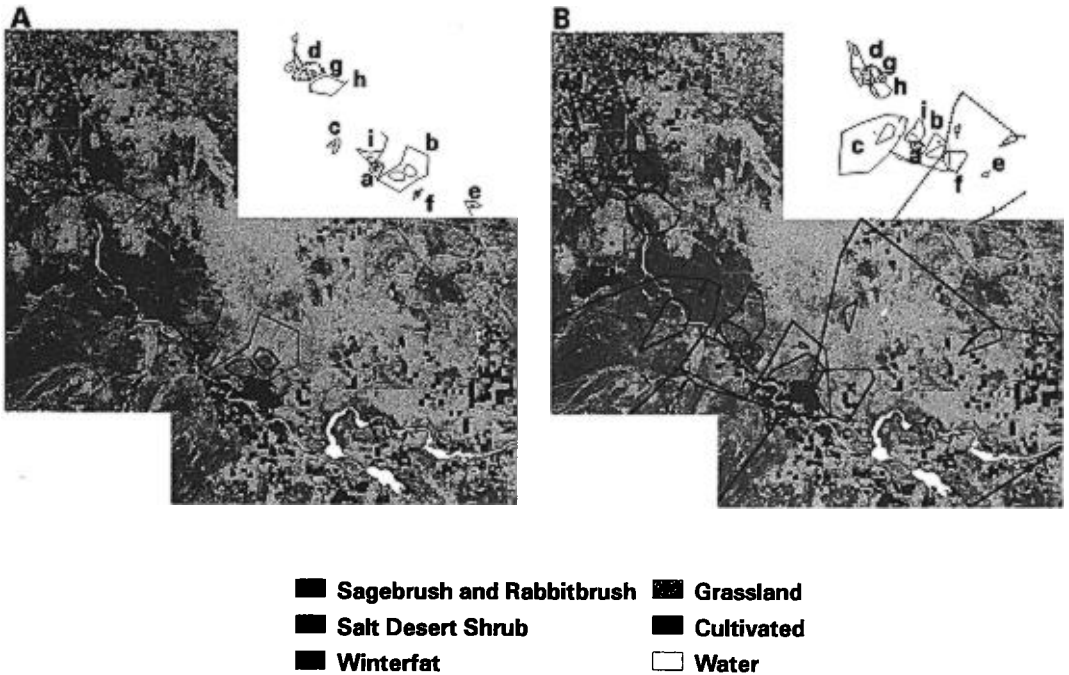


FIG. 2. Home range (solid lines, concave polygons) and core area (polygons within home ranges, 95% use area, cluster analysis) of eagles during (A) and outside of (B) the breeding season. Habitat of the study area is shown in the background to illustrate variation in shrub, grassland, and agriculture among territories. Small letters denote territory identification.

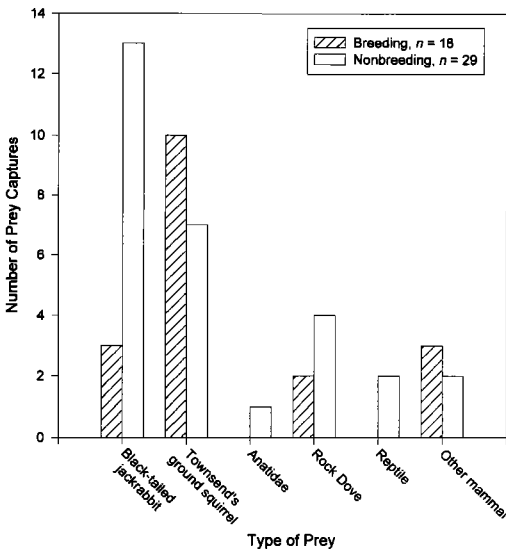


FIG. 3. Prey items captured by Golden Eagles, 1991 to 1994.

indicate strong selection or avoidance of very rare habitats because small absolute differences in use and availability are proportionately much larger than are similar absolute differences between common habitats. This potential problem contributed to the general avoidance of winterfat and water, and selection for cliff habitats (Table 3). The availability and use of these three habitats were very low (Fig. 4A, B, C).

Avoidance of agriculture was unlikely to be an artifact of habitat rarity (Fig. 4). Agriculture was avoided by all but one eagle, even though it represented as much as 24% of the available habitat. The individual that selected a core area with a relatively large amount of agriculture during the breeding season (Individual d) appeared to select agriculture because its territory had a substantial amount (18%) of agriculture available. Selection for agriculture in the nonbreeding season (Fig. 4A, B) and around foraging points (Fig. 4C) was suspect because the availability of agriculture used to compute those selection coefficients was very small.

TABLE 3. Average selectivity ($\bar{x} \pm SE$) by nine Golden Eagles for habitat types at three scales. The mean selection coefficient ($\ln[\text{habitat use}/\text{habitat availability}]$) indicates general avoidance (negative values) or preference (positive values) for each habitat class. The number of eagles selecting each class (use > availability) is shown to indicate consistency of habitat selection among individuals.

Habitat class	Nonbreeding season		Breeding season	
	Selection coefficient	No. eagles	Selection coefficient	No. eagles
Home range				
Sagebrush/rabbitbrush	-0.03 \pm 0.23	6	0.12 \pm 0.21	7
Salt-desert shrub	-0.49 \pm 0.42	4	0.05 \pm 0.53	3
Winterfat	-0.84 \pm 0.55	4	-1.92 \pm 0.82	2
Grassland/disturbed	-0.13 \pm 0.09	3	-0.14 \pm 0.13	3
Agriculture	-1.84 \pm 0.96	3	-2.27 \pm 0.94	3
Cliff	0.75 \pm 0.48	5	0.29 \pm 0.62	6
Water	-0.49 \pm 0.42	3	-1.73 \pm 0.85	2
95% Core area				
Sagebrush/rabbitbrush	0.13 \pm 0.12	6	0.22 \pm 0.16	7
Salt-desert shrub	0.24 \pm 0.14	7	0.24 \pm 0.32	5
Winterfat	-0.66 \pm 0.31	2	-1.07 \pm 0.51	2
Grassland/disturbed	-0.03 \pm 0.09	5	-0.10 \pm 0.09	2
Agriculture	-0.40 \pm 0.21	1	-2.43 \pm 0.80*	1
Cliff	0.55 \pm 0.29	7	0.72 \pm 0.21*	7
Water	-0.85 \pm 0.80	6	-0.68 \pm 0.91	3
90% Core area				
Sagebrush/rabbitbrush	0.26 \pm 0.12	7	0.17 \pm 0.22	7
Salt-desert shrub	0.20 \pm 0.28	6	0.54 \pm 0.40	5
Winterfat	-1.34 \pm 0.51*	3	-1.69 \pm 0.77	2
Grassland/disturbed	-0.13 \pm 0.08	2	-0.20 \pm 0.20	3
Agriculture	-3.16 \pm 1.01*	0	-3.11 \pm 0.85*	0
Cliff	0.86 \pm 0.45	7	0.26 \pm 0.70	7
Water	-1.72 \pm 0.99	3	-1.93 \pm 1.16	3

*, $P < 0.05$ (avoidance or preference different from availability).

Our evidence that sagebrush/rabbitbrush and salt-desert shrub habitats were selected was strengthened because these habitats were common yet included in home ranges, core areas, and around foraging points at frequencies that exceeded general availability. Sagebrush/rabbitbrush appeared to be more important than salt-desert shrub because it comprised a larger percentage of used habitats at all levels of comparison (Fig. 4).

Individual variability in selectivity for sagebrush/rabbitbrush tended to be correlated with the availability of those shrubs within a home range. Individuals tended to be more selective for sagebrush/rabbitbrush when it was relatively rare within their home range (depending upon season and level of comparison, r values ranged from -0.68 to -0.39, $n = 9$ in each case), but this relationship was only significant during the breeding season when selectivity within the 95% core area was compared with availability in the home range ($P = 0.04$, all other P -values < 0.29).

Avoidance of grassland by most individuals at all levels of comparison, especially during the breeding season, was not due to the rarity of grassland. Grassland was the most common habitat type regardless of season or level of comparison (Fig. 4). Even though it was used less than expected based on availability, grassland remained a dominant feature of eagle home ranges, core areas, and foraging locations, regardless of season. Individual variability in avoidance of grassland was not correlated with the abundance of grassland within home ranges. In most seasons and levels of comparison, eagles with the largest amount of grassland in their home range avoided it, but these relationships were weak (all r -values < 0.50, P -values > 0.17).

Selection for jackrabbit habitat.—Jackrabbit habitats varied significantly among territories (compositional analysis; breeding season, $\lambda = 1.29 \times 10^{-16}$, $\chi^2 = 329.3$, $df = 9$, $P < 0.001$; nonbreeding season, $\lambda = 2.57 \times 10^{-14}$, $\chi^2 = 281.6$, $df = 9$, $P < 0.001$). Five territories (a, b, f, h, i)

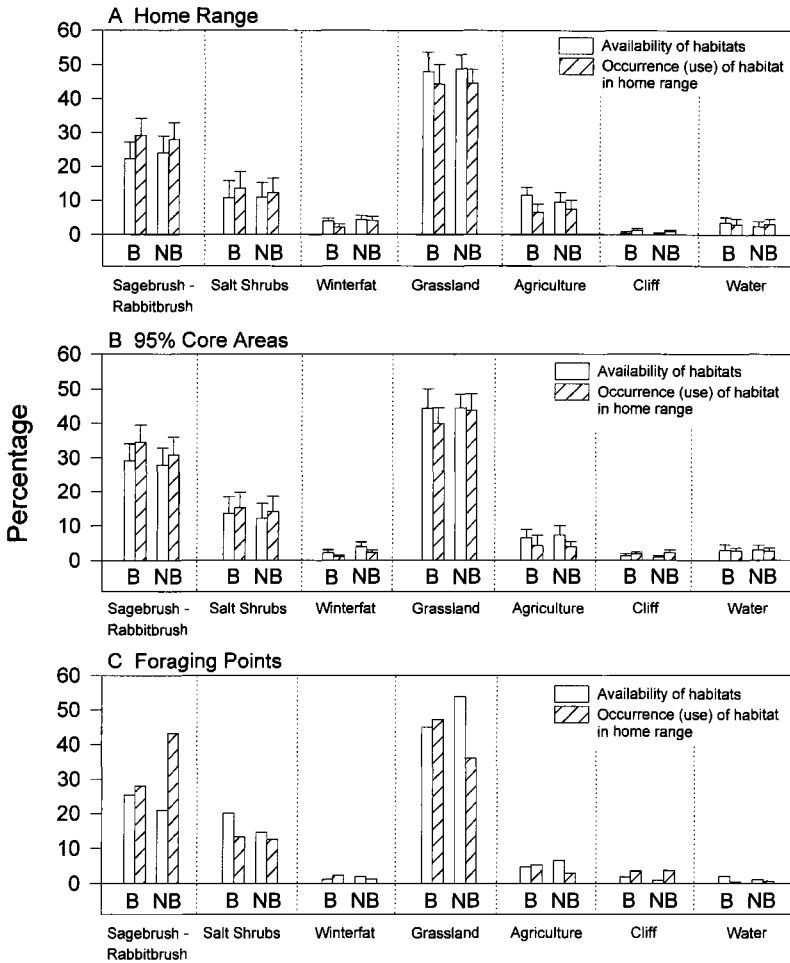


FIG. 4. Availability and use of habitat classes during the breeding and nonbreeding season. Use and availability is plotted for all nine territories in comparisons of home ranges with the study area (A) and of core area with home range (B). Data were insufficient to analyze habitat around foraging points separately for individuals, so all individuals were pooled (C). Values are $\bar{x} \pm SE$.

contained lower indexes of jackrabbit habitat, three territories (c, d, g) contained higher indexes, and one territory (e) contained intermediate indexes compared with availability in the study area (Fig. 5A, B).

Overall, eagles in the nine territories studied did not select or avoid habitats based on the probability of supporting jackrabbits (Table 4). However, some individuals were more selective than others. Five pairs (a, b, c, f, i) centered their 95% core areas within the best jackrabbit habitat available within their home range during the breeding season (Fig. 5A). All five pairs had territories containing less sagebrush/rabbitbrush than expected based on availability (\bar{x}

selection coefficient = $-0.23 \pm SE$ of 0.29) and less absolute occurrence of sagebrush/rabbitbrush ($\bar{x} = 20.8 \pm 5.95\%$) than the other four pairs (\bar{x} selection coefficient = 0.56 ± 0.12 ; Mann-Whitney $U = 19, P = 0.03$; \bar{x} abundance = $39.6 \pm 4.08\%$; $U = 19, P = 0.03$). Territories of pairs that selected for jackrabbit habitat had lower jackrabbit habitat indexes (\bar{x} index = 0.34 ± 0.07) than territories of other eagles ($\bar{x} = 0.48 \pm 0.06$), but this difference was not significant ($U = 14, P = 0.33$).

In contrast to the breeding season, few eagles selected for jackrabbit habitats within core areas outside of the breeding season. Only one pair (i) had a 95% core area that included the best jack-

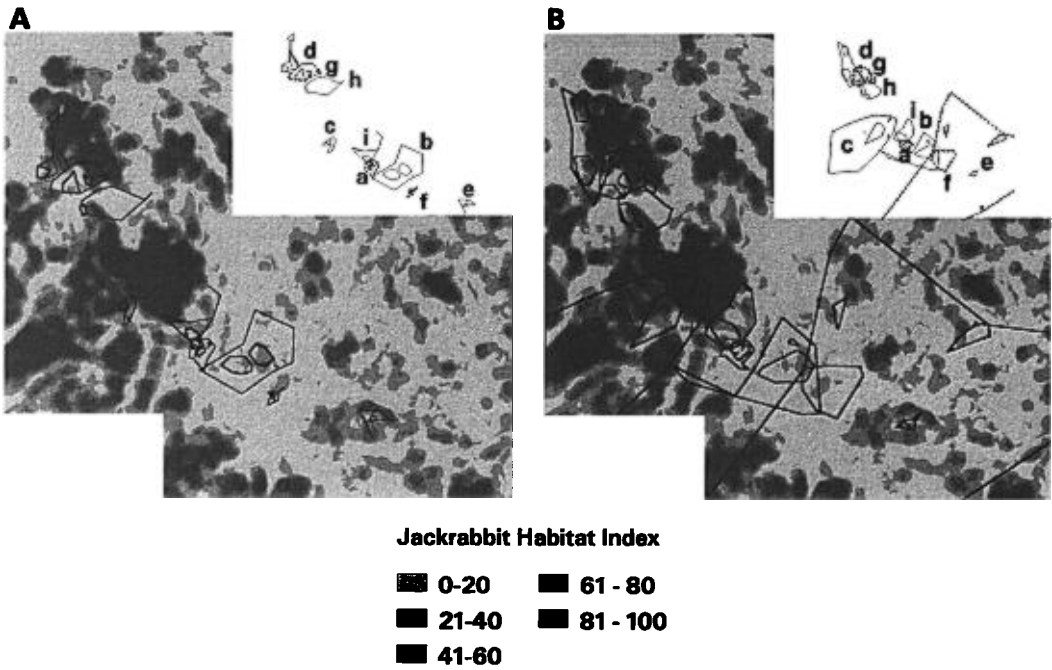


FIG. 5. Occurrence of black-tailed jackrabbit habitat in Golden Eagle home ranges (solid lines, concave polygons) and core areas (polygons within home ranges, 95% use area, cluster analysis) during (A) and outside of (B) the breeding season. Shading indicates the similarity of habitat at a given location to habitat used by jackrabbits. Progressively darker shading indicates habitats of progressively higher quality for jackrabbits. Small letters denote territory identification.

TABLE 4. Average selectivity ($\bar{x} \pm SE$) by nine Golden Eagles for black-tailed jackrabbit habitat types at three scales. The mean selection coefficient ($\ln[\text{habitat use}/\text{habitat availability}]$) indicates general avoidance (negative values) or preference (positive values) for each habitat class. The number of eagles selecting each class (use > availability) is shown to indicate consistency of habitat selection among individuals.

Jackrabbit index class	Nonbreeding season		Breeding season	
	Selection coefficient	No. eagles	Selection coefficient	No. eagles
	Home range			
Highest 30%	-2.50 ± 1.15	3	-2.43 ± 1.23	3
Middle 40%	-0.03 ± 0.18	5	-0.64 ± 0.64	3
Lowest 30%	-0.16 ± 0.23	5	-0.23 ± 0.29	5
	95% Core area			
Highest 30%	-0.98 ± 0.65	1	-1.59 ± 1.00	2
Middle 40%	-0.02 ± 0.24	4	0.03 ± 0.28	5
Lowest 30%	0.01 ± 0.17	6	-0.61 ± 0.86	4
	90% Core area			
Highest 30%	-1.15 ± 0.64	1	-2.23 ± 1.23	2
Middle 40%	-0.58 ± 0.82	6	-2.00 ± 1.19	2
Lowest 30%	-0.01 ± 0.13	4	-0.48 ± 0.86	7

rabbit habitat available in its home range, and one other (b) had a 90% core that included some of its best jackrabbit habitat (Fig. 5B).

Foraging locations.—Selection of foraging locations within core areas differed between the breeding and nonbreeding season (Fig. 6). During the breeding season, individuals used winterfat shrublands, cliffs, and agriculture more frequently than expected; sagebrush/rabbitbrush was used in proportion to availability. As a result, eagles did not select foraging points in jackrabbit habitat within core areas during the breeding season. In contrast, during the nonbreeding season foraging points were primarily in sagebrush/rabbitbrush and along cliffs. Eagles also foraged within the best jackrabbit habitat inside their core areas during the nonbreeding season.

INTERRELATIONSHIPS OF HABITAT QUALITY, RANGE SIZE, AND EAGLE PRODUCTIVITY

Home-range size was not significantly related to eagle productivity. Breeding-range size tended to increase as the total number of young fledged from 1992 to 1994 increased ($r = 0.56$, $n = 9$, $P = 0.12$). Size of the nonbreeding range and size of core areas, regardless of season, were less closely correlated with productivity (all $P_s > 0.25$).

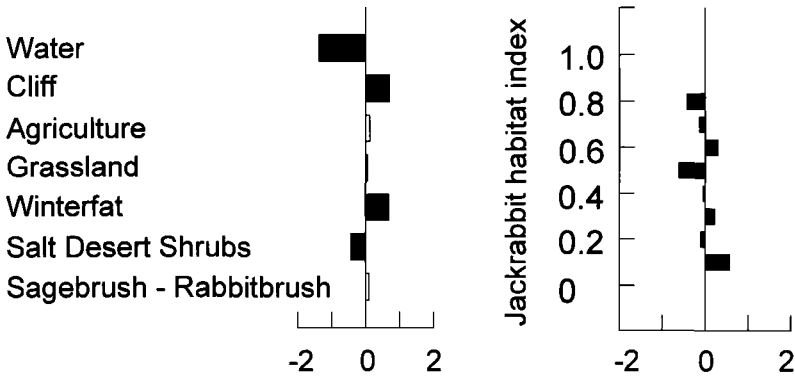
Two distinct groups of territories were evident during the breeding season. Pairs a, b, f, h, and i had a scarcity of shrubland associated with jackrabbits in their territories (Figs. 2, 5). In contrast, pairs c, d, and g had an abundance of shrubland associated with jackrabbits (Figs. 2, 5). Variation in habitat quality was not significantly related to differences in home-range size during the breeding season (high-quality territories, $\bar{x} = 1,423 \pm 586$ ha, $n = 3$; low-quality territories, $\bar{x} = 2,794 \pm 1,460$ ha, $n = 5$; $U = 5$, $P = 0.46$) or during the nonbreeding season (high-quality territories, $\bar{x} = 15,814 \pm 10,566$ ha, $n = 3$; low-quality territories, $\bar{x} = 39,286 \pm 34,221$ ha, $n = 5$; $U = 10$, $P = 0.46$). Territories in poor jackrabbit habitats had similar productivity compared with those in good jackrabbit habitats (total number of young fledged from 1992 to 1994; high-quality territories, $\bar{x} = 0.67 \pm 0.67$, $n = 3$; low-quality territories, $\bar{x} = 2.4 \pm 0.81$, $n = 5$; $U = 3$, $P = 0.17$).

DISCUSSION

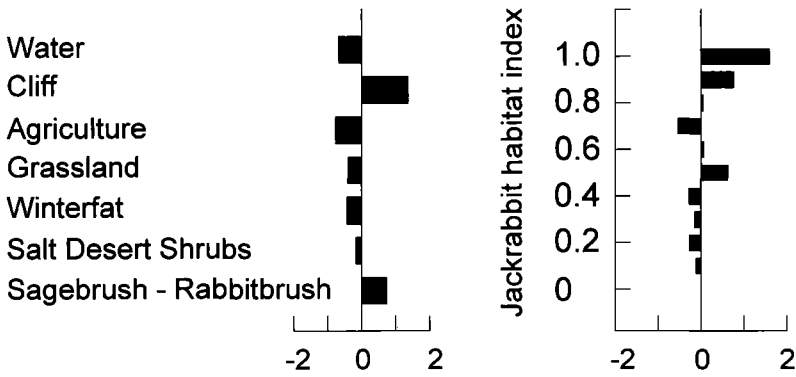
Golden Eagles in our study varied considerably in patterns of spatial use. Size of the home range, size of the core area, and travel distances for various activities varied by two orders of magnitude among individuals. Habitat composition, potential prey abundance, and individual preferences developed by long-lived, permanent residents likely account for much of this variation. Eagles do not simply maximize home-range size, nor should they, because their breeding success was only weakly correlated with range size. Rather, eagles adjusted their ranging and foraging behavior to take advantage of the types and configuration of prey habitat found in the vicinity of their nest. Where high-quality jackrabbit habitat was abundant, pairs foraged evenly throughout the shrublands and had relatively small home ranges (e.g. pairs c, d, g; Figs. 2, 5). However, pairs in territories with little sagebrush/rabbitbrush (where jackrabbits were expected to be scarce) showed two patterns of space use that may reflect individual experiences: they either ranged over large areas and concentrated their use in the better habitats for jackrabbits (pairs b, f; Figs. 2, 5), or they restricted their activities to a small area of cliff and riparian habitat around their nests (pair a; Figs. 2, 5). Pairs that maintained small territories took fewer jackrabbits and more alternate prey, notably Rock Doves, waterfowl, and marmots found in the cliff and riparian habitats. Thus, quality of habitat is more important than quantity, but "quality" habitat comes under a variety of guises depending upon habitat availability and eagle prey selection (riparian habitat [Pair a], agricultural lands [Pair d], or shrublands [other pairs]).

Consistencies in habitat selection became more apparent as we refined our assessment of selection from the scale of the territory, to the scale of the core area, to the foraging point. This may indicate the scale at which eagles actually select habitats, or it may reflect the progressive reduction in use of excursive travels in our analysis. At progressively finer scales, where excursions are not included in the analysis, the majority of eagles selected shrubland and avoided grassland and agriculture. Sagebrush/rabbitbrush was the most important shrub type. Thus, habitat selection by resident

Breeding Season



Nonbreeding Season



Selection Coefficient

FIG. 6. Selection of foraging habitat within core areas by Golden Eagles. Selection coefficients (ln [percent habitat used / percent habitat available]) compare habitat within 100 m of foraging points with habitat available in 95% core areas during and outside of the breeding season. Selection is plotted separately for habitat classes and habitat quality for jackrabbits (0 is worst habitat, 1 is best habitat for jackrabbits). Vertical histograms show the relative preference (selection coefficient > 0) and avoidance (selection coefficient < 0) of each habitat or jackrabbit habitat-index category.

eagles was similar to selection previously documented for wintering vagrants (Craig et al. 1986).

Selection for sagebrush/rabbitbrush and the avoidance of agriculture and grassland resulted in most eagles foraging in habitats that had the potential to contain jackrabbits. Although our measure of habitat potential to support jackrabbits comes from the spring/summer season during a low population phase of jack-

rabbits, this is unlikely to influence our assessment of habitats because jackrabbits are found in the habitats rated as highest quality throughout the year, regardless of population cycling (Knick and Dyer 1997). However, the scale at which eagles selected jackrabbit habitats differed depending on the season and the characteristics of the home range. Outside of the breeding season, when even core areas were large, eagles selected foraging points in the

best available jackrabbit habitat. During the breeding season, when ranges were smaller, entire core areas were in jackrabbit habitat, and foraging points within cores were in cliff, winterfat, and agriculture where other prey types (notably Townsend's ground squirrels and Rock Doves) occurred. Jackrabbit habitat was used frequently within breeding-season core areas, but use at the scale of foraging points was not selective because territories or core areas were already in the best jackrabbit habitat available. Eagles may be selective in good jackrabbit habitat, but our inability to partition habitat quality more finely precluded testing selection within the best jackrabbit habitat. The importance of selection at one scale to selection at other scales was further illustrated by the lack of selectivity for sagebrush/rabbitbrush within territories that already had a high percentage of sagebrush/rabbitbrush. Habitat selection needs to be investigated at several levels to understand fully how animals allocate their time among various habitats (Wiens et al. 1986, Aebischer et al. 1993).

Although the use of area varied widely among individuals in the nine territories, the use of area by eagles in a given territory varied little regardless of nest location, prey abundance, or identity of breeders. All of these factors varied among years, but home range size and range boundaries did not vary significantly among years. In fact, home-range boundaries changed little from the 1970s to the 1990s. Continued residency by at least one, and usually both, members of the pair, their individual use of perching and foraging habits, and the constraining effects of neighboring pairs on territory shape likely contributed to the stable patterns of spatial use within a territory. Long-term studies of marked individuals are necessary to accurately contrast variation in use of space between territories with variation within territories.

Despite annual stability in territory size and shape, physical defense of territories was rarely observed. Defense of boundaries against neighboring breeders was adequately accomplished by undulating flights (Harmata 1982, Collopy and Edwards 1989). Undulating flights were most often given at the edge of territories, rather than near nests (Fig. 1) and were least frequently given by pairs that had just formed (territory d, e; individuals were banded), sug-

gesting that their function was territory maintenance rather than pair bonding. We routinely captured eagles that were not the tagged offspring of the present territory owners at food items we placed in territories during the nonbreeding season for trapping. Rather, these eagles were vagrant nonbreeders or winter residents. Lack of defense against nonterritorial eagles also was observed in Wyoming (Phillips and Beske 1982) and may be rare because eagles are not breeding and the risks of injury from fighting (Harmata 1982) outweigh any costs of losing foraging opportunities.

We documented the largest home-range sizes reported for this species. Many of the ranges in our study were within values previously reported for this study area and elsewhere (i.e. 500 to 9,000 ha; Dixon 1937, Tjernberg 1977, Dunstan et al. 1978, Phillips and Beske 1982, Collopy and Edwards 1989), but three individuals occupied much larger areas (individuals b, c, f; Fig. 2A, B). Increased size of home ranges often resulted from excursions, especially during the nonbreeding season. Core areas and 95% harmonic-mean ranges, which exclude excursions, are more similar in size to published home ranges. Excursions may have been accentuated during our study, which included a period (winter 1992-93 through 1994) when jackrabbit numbers were low and declining (Steenhof et al. 1997). However, excursions also may represent searches for breeding, as well as foraging, opportunities. They were not synchronized forays by the pair, and in one case the female from territory "f" included territory "e" in her travels; she settled and bred there the following spring. Like any estimate of home range, ours is dependent upon decisions made during data collection and selection of individual points for inclusion in analyses. However, our intensive, long-term observations that include several individuals occupying a given territory allowed us to make realistic estimates of actual space use by eagles.

MANAGEMENT IMPLICATIONS

Management of a healthy population of Golden Eagles in shrubsteppe habitats must focus on maintaining the native shrub community. Stands of sagebrush/rabbitbrush interspersed with grassland harbor sizeable populations of an important prey item, black-tailed

jackrabbits (Knick and Dyer 1997). Our analysis demonstrates that eagles forage in areas without shrubs less than expected based on availability. Eagles were especially dependent upon shrub habitats when these shrub habitats were rare in the landscape.

Managers must recognize that although eagles range over large areas (>170,000 ha were used by one eagle), many concentrate their foraging in shrub habitats. Shrub (especially sagebrush/rabbitbrush) patch size appears to be an essential feature of all home ranges. Mean patch size for jackrabbit use of this habitat type was 5,000 ha, and the likelihood of observing jackrabbits increased with both increasing patch size and number of patches in the landscape (Knick and Dyer 1997). In managing the remaining large shrub areas in the landscape for eagles, we recommend that fragmentation by any disturbance not reduce the size of shrub patches below the mean patch size selected by jackrabbits. Patches slightly larger than this also should be maintained to accommodate maximum core areas during the nonbreeding season (6,387 ha; Table 2) and to provide habitat for vagrant and wintering eagles (observed in patches averaging 2,117 to 3,502 ha; Atkinson et al. unpubl. data). Individual variation in space use by eagles argues against using average values of home-range size in management recommendations. Rather, a variety of large and small areas could be suitable for eagles if they are managed to provide large shrub patches or rich alternative foraging areas (e.g. riparian zones).

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