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THE INFLUENCE OF HABITAT, PREY ABUNDANCE, SEX, AND BREEDING SUCCESS ON THE RANGING BEHAVIOR OF PRAIRIE FALCONS¹

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Abstract. We studied the ranging behavior and habitat selection of radio-tagged Prairie Falcons (*Falco mexicanus*) during the breeding season in southwestern Idaho. The distribution and numbers of Townsend's ground squirrels (*Spermophilus townsendii*), the primary prey of Prairie Falcons in our study area, varied in response to drought during the study period. Prairie Falcons ranged over large areas (ca. 300 km²) and increased their foraging ranges in response to declining ground squirrels. Reptiles and birds were preyed upon most frequently when squirrels were rare. Males and females differed little in their use of space. Successful pairs ranged over smaller areas than non-nesters and unsuccessful pairs. Falcons nesting near habitat most suitable for ground squirrels ranged over smaller areas than those nesting farther from such habitat. Home ranges contained significantly more winterfat (*Ceratoides lanata*) and native perennial grasses (especially *Poa secunda*), and significantly less salt desert shrubs and exotic annual grasses than expected based on availability. Salt desert shrubs were found less than expected, based on availability in core areas within home ranges. Selection for winterfat and bluegrass in core areas was contingent upon selection at the larger scale of the home range; falcons with home ranges containing more winterfat and bluegrass than expected based on availability were less selective in their placement of core areas with respect to these habitats. We believe salient features of Prairie Falcon home ranges result largely from patchy distribution of landscape features associated with different densities and availabilities of Townsend's ground squirrels.

Key words: *Prairie Falcon, Townsend ground squirrel, home range, habitat selection, radio telemetry, conservation.*

INTRODUCTION

Prairie Falcons (*Falco mexicanus*) are one of the most common raptors of montane desert and shrub habitats of western North America. Numerous studies have documented their nest site characteristics (Runde and Anderson 1986, Allen 1987), abundance (Platt 1974, 1981), foraging behavior (Phipps 1979, Haak 1982), habitat

requirements (Hunt 1993, Squires et al. 1993), wintering behavior (Beauvais et al. 1992), nesting behavior (Kaiser 1986, Holthuijzen 1990), and productivity (Ogden and Hornocker 1977, Allen et al. 1986). Despite this research, our knowledge of Prairie Falcon ranging habits and habitat use remains limited because these birds range over large, remote areas where observing them is difficult. Some of this difficulty can be overcome by the use of radio-telemetry, but previous work involved relatively small sample sizes of radio-tagged Prairie Falcons (≤ 14 ; Dunstan et al. 1978, Hunt 1993).

The most intensive studies of Prairie Falcons have been conducted in the Snake River Birds of Prey National Conservation Area (NCA) of

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southwestern Idaho, where abundance and productivity have been measured continuously for 21 years. The NCA has the densest concentration of nesting Prairie Falcons in the world; approximately 200 pairs nest on basalt cliffs that border 100 km of the Snake River. Falcons specialize on Townsend's ground squirrels (*Spermophilus townsendii*) to such an extent that their arrival on, and departure from, nesting areas is closely correlated with ground squirrel emergence and estivation, and their productivity is closely correlated with indices of squirrel abundance (U.S. Dept. Interior 1979, Steenhof et al., unpubl. data).

In this paper we investigate behavioral linkages between Prairie Falcons and Townsend's ground squirrels that help explain why ground squirrel population dynamics influence Prairie Falcons. We measured the behavior of falcons during four years of varying squirrel abundance to determine: (1) the degree to which falcons relied on ground squirrels for prey, (2) whether the degree of reliance on ground squirrels influenced ranging behavior and habitat use, (3) how sex and breeding success influenced the relationships between prey abundance and ranging behavior, and to (4) provide managers with a prescription for optimal falcon habitat.

METHODS

STUDY AREA

We studied Prairie Falcons in a 198,616 ha portion of the NCA selected for an investigation of the effects of military training on falcons. It included relatively homogenous areas east and west of a military training area and extended north enough to encompass foraging ranges of falcons (U.S. Dept. Interior 1996). The terrain and vegetation were dominated by shrub (*Artemisia tridentata*, *Chrysothamnus nauseosus*, *Ceratoides lanata*, and *Atriplex confertifolia*) and grassland (*Poa secunda* and *Bromus tectorum*) flats punctuated by buttes and rolling hills surrounding the Snake River Canyon. Falcons nested in the Snake River Canyon and hunted surrounding plains to the north and east.

TERMINOLOGY

"Nesting area" is a stretch of cliff where nests are found year after year, but where no more than one pair has ever bred in one year. Falcons nest in potholes, cracks, and ledges on cliffs in nesting areas. A nesting attempt was "success-

ful" if ≥ 1 chick reached an estimated age of 30 days (80% of actual age to fledging, Steenhof 1987). We rappelled to nests when chicks were at least 30 days old to obtain brood counts, which reliably discriminate successful from failed breeders (Marzluff and McFadzen 1996). We did not always know if falcons using a nesting area successfully laid eggs. We therefore established three categories for analyses: (1) "Unsuccessful pairs" were pairs found throughout the breeding season in a previously documented nesting area that did not produce 30-day-old young, (2) "Non-nesters" were nonbreeding individuals not associated with a previously documented nesting area, and (3) "Successful pairs" produced 30-day-old young. For some analyses, unsuccessful pairs and nonbreeders were lumped for comparison with successful pairs. In all analyses of travel distance, breeding pairs were classified as successful until the time they lost their clutch or brood.

DIETS

We observed a sample of nests each year to document falcon reliance on Townsend's ground squirrels. From 1991 through 1994, we observed prey delivered to breeding females and nestlings at 62 nests during 235 days between late April and mid-June. Nests were constantly observed from 20 min before sunrise to 15 min after sunset by two observers, one in the morning and another in the afternoon. Observations were made with 10 × 50 binoculars and 15–45× spotting scopes from blinds or vehicles at distances between 70 and 300 m (see Holthuijzen 1990). Observers were trained before making observations and were rotated among nest sites to minimize observer bias. We classified prey delivered by species or class (mammal, bird, reptile, insect) when possible. Only fresh items (blood usually visible, prey supple and not dehydrated) were included in counts of deliveries to reduce multiple counting of cached items.

RADIOTELEMETRY

Selection and capture of falcons. The Prairie Falcons radio-tagged for this study were randomly selected from approximately 200 pairs breeding in the 110-km stretch of the NCA from Walters Ferry to Bruneau. This area was stratified based on position of nesting areas relative to a military training area into a west, central, and east region (Fig. 1). We attempted to ra-

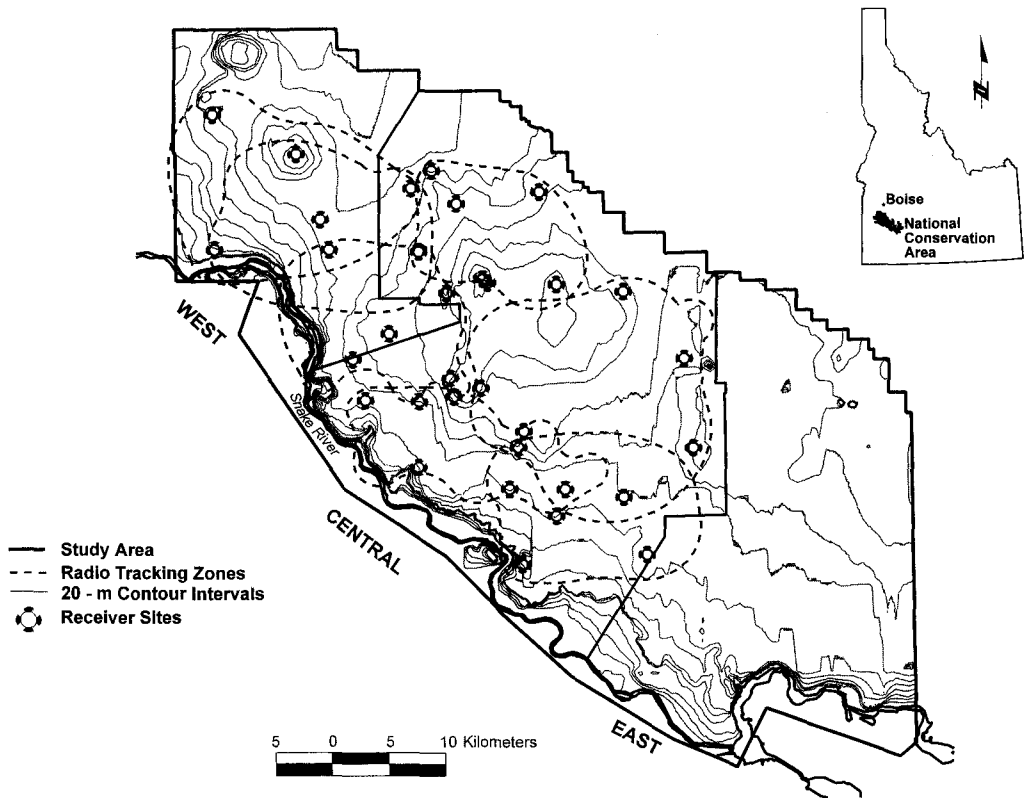


FIGURE 1. Topography and location of study area. Receiver sites where radio tracking was conducted and generalized tracking zones are indicated. Bold lines from river to northeastern border of study area delineate three sampling strata (west, central, east).

dio-tag equal numbers of falcons in the west and central strata, and approximately equal numbers of males and females each year. Falcons from the east stratum were radio-tagged only in 1992 (1 falcon) and 1993 (5 falcons).

We investigated 68 randomly selected nesting areas for the possibility of trapping Prairie Falcons in 1991, 52 in 1992, 86 in 1993, and 76 in 1994. We rejected nesting areas if: (1) adults were not present or not exhibiting territorial behavior ($n = 142$), (2) sites were heavily disturbed by human recreational activities ($n = 1$), (3) sensitive raptors, primarily Ferruginous Hawks (*Buteo regalis*), would be disturbed by trapping ($n = 10$), (4) trap placement sites were unavailable ($n = 4$), or (5) falcons were not responsive to the trapping methods ($n = 30$). We trapped during courtship, egg-laying, incubation, and brooding, and captured 34 adult Prairie Falcons in 1991, 37 in 1992, 40 in 1993, and 41 in 1994. We radio-tagged 28 of these in 1991, 34

in 1992, 36 in 1993, and 31 in 1994. These samples are independent as no individuals were radio-tagged in more than one year.

Two 2-person teams trapped each year from March to May. They observed each nesting area until a falcon exhibited signs of occupying the nesting area (perching, courting, copulating, or defending the area), and then placed traps as close as possible to the cliff containing the nest. To avoid trap placements dangerous to personnel and possibly disruptive to falcons (Clugston 1990), we captured falcons away from the nest using noose harnesses or dho-gazas (Bloom 1987). We lured falcons to the traps with live Rock Doves (*Columba livia*), European Starlings (*Sturnus vulgaris*), House Sparrows (*Passer domesticus*), or Great Horned Owls (*Bubo virginianus*).

When an individual was captured, it was hooded immediately (Bloom 1987). We placed a radio transmitter (12–16 g with Teflon® straps

and leather sternum patch) on each captured falcon that we believed resided in the preselected nesting area where we were trapping, unless we felt eggs in the abdomen (1992–1994), or the individual had received a transmitter in a previous year (1992–1994). The general configuration of the harness followed Buehler et al. (1995), with the modification of a leather sternum patch added to distribute the pull of the backpack evenly across the breast (Vekasy et al. 1996). We also weighed, measured, and banded each bird. Sex was determined by wing chord length (U.S. Dept. Interior 1977).

We monitored each falcon for at least 1 hr after release to determine if the transmitter package and/or handling adversely affected the bird's flight or behavior. Each bird was monitored again for 2 hr (in most cases on the next day) to ensure that the transmitter was still on and that the bird's behavior appeared normal. Comparisons of radio-tagged birds to untagged, control birds indicated no significant effects of tagging on productivity or behavior (Vekasy et al. 1996).

Tracking protocol. We radio-tracked falcons from fixed sites in seven zones ranging in size from 50 to 80 km² that covered foraging areas on benchlands adjacent to canyon nesting areas. After conducting a series of tests on transmitters placed throughout the study area (beacons) during winter 1992, we further divided the study area into eight zones (70–120 km²) which were small enough to allow detection from 4–6 fixed receiver sites of most radio-tagged falcons using the zone (Fig. 1). Receiver sites were located with a global positioning system (GPS) accurate to within 5 m. Most receiver sites were on prominent buttes, ridges, and outcroppings, but some were on flat terrain (Fig. 1). Receiver sites were typically > 6 km from the falcons being tracked and were positioned in a zone to allow the taking of simultaneous bearings that minimized triangulation error (White and Garrott 1990).

Teams of four to six persons radio-tracked falcons in each zone from approximately 15 April–15 July each year from 1991 to 1994. Each zone was sampled in random order with the constraint that each be sampled once in the morning (30 min before sunrise until 13:30) and once in the afternoon (13:30 until approximately sunset) every 14–16 days. Two zones usually were sampled each day (one in the morning and one in the afternoon). Each year all radio-tagged

falcons were tracked relatively evenly throughout the season and through the daylight hours. Tracking sessions were suspended when lightning or heavy rain threatened personnel or receiving equipment.

Radio-tracking teams used 4-element, Yagi antennas and programmable scanning receivers (Advanced Telemetry Systems, Isanti, MN) to sample sequentially for radio frequencies of instrumented falcons. Antennas were hand-held or placed on 2–7-m towers to increase the reception range. Bearings were obtained by sighting hand-held compasses toward signals in 1991 and 1992. In 1993 and 1994, compass rosettes bolted to towers enabled us to eliminate the use of hand-held compasses and increased the consistency of orientation from each site. Null-peak antenna arrays were not used because they did not increase bearing accuracy (Clugston 1990).

Trackers used 2-way radios to alert other team members of the presence of a falcon in a zone. When ≥ 3 trackers had a bird's signal, they took simultaneous bearings to the signal. All bearings to falcons were entered into laptop computers to determine the error associated with a given triangulation and to identify systematic errors resulting from misaligned compasses, electrical interference, etc. We repeated triangulation attempts on each bird until either a 95% confidence ellipse around the location was < 1,000 ha, the bird was deemed out of range, or the bird's signal was detected by < 3 trackers. We allowed at least 30 min between successive location estimates with ellipses < 1,000 ha on the same bird to reduce dependency among estimates. Although multiple estimates of the same bird's locations are not truly independent, location estimates 30 min apart should be representative of a falcon's use of the study area (White and Garrott 1990). Furthermore, these locations should not include diurnal or seasonal bias in home range estimation because they were evenly distributed throughout the study period (Andersen and Rongstad 1989).

The design of our zones may bias home range estimation because falcons could not be tracked while they were at their nests below the canyon rim (Marzluff et al. 1994). However, our goal was to define ranges and habitat use while foraging, therefore activities at the nest were less important. Radio-tracking in each zone twice every two weeks (once in the morning and once in the evening) minimized potential biases as

sociated with falcons foraging outside of a zone on a particular day.

Selecting location estimates and falcons for analysis. Subsamples of location estimates for individual falcons were selected for use in home range analyses based upon their accuracy. Because confidence ellipses associated with location estimates (Lenth 1981) are weakly correlated with actual accuracy of an estimate (Marzluff and Kimsey, unpubl. data), we developed a regression model to estimate accuracy based on beacon tests. The model was verified by predicting accuracy of remote estimates when falcons were simultaneously observed by mobile ground crews independent of crews at fixed locations. Using Andrew's estimator to produce a point estimate relatively insensitive to signal bounce (Lenth 1981), we accounted for 55% of variation associated with distance between estimated and actual locations (linear error) by using the distance from the estimated location to the center of a "tracking region." The tracking region is a dynamic polygon with vertices formed by positions of trackers involved in a particular location estimate. We used location estimates with estimated linear errors smaller than the upper 75% quartile of the error distribution in our calculations of home range. This allowed us to objectively censor estimates with large linear errors while keeping accurate and precise estimates.

The adequacy of radiotelemetry sampling of individual falcons was assessed by relating increase in home range size to successively larger samples of locations for each falcon (incremental analysis; Kenward 1987). Individual males with ≥ 40 location estimates were considered to be adequately sampled because incremental analysis indicated that 85% of the area used by males was sampled by these first 40 fixes (Marzluff et al. 1992). Location estimates for females were more difficult to obtain because they spent most of their time out of radio contact below the canyon rim until their nestlings were ready to fledge. Incremental analysis indicated that 25 estimates of a female's locations defined 75% of the total area used by the female (Marzluff et al. 1992). We therefore considered females to be adequately sampled if they had ≥ 25 location estimates with at least 65% taken from the time of fledging to post-fledging independence (1 month after fledging; McFadzen and Marzluff 1996) when females ventured farthest from their

nests. Our definitions of adequately sampled males and females are further justified because correlations between home range size and the number of location estimates used to calculate home range size were very weak (r 's < 0.20 , P 's > 0.40 ; Marzluff et al. 1992). This implies that less frequently (but "adequately") sampled ranges were not unusually small, as one might expect if the intensity of sampling influenced determination of home range size.

HOME RANGE AND RANGING BEHAVIOR

Home range size, use of area within ranges, and travel distance from nests and other centers of activity were computed with Ranges V (Kenward and Hodder 1995). We estimated home ranges with harmonic mean methods, convex polygons, and hierarchical incremental cluster analysis (Dixon and Chapman 1980, Kenward 1987). Nest sites were not used in the delineation of home ranges. For harmonic mean isolines, we reduced plotting error by using a 40×40 grid and location estimates in the center of the grid squares (Spencer and Barrett 1984). Telemetry location point estimates were used without accounting for telemetry error in all calculations of area. This may lead to slight underestimates of home ranges and core areas, especially using convex polygons, but relative differences in range size among individuals are not affected (Senchak 1991).

We used the minimum convex polygon to represent the maximum home range size and the 95% harmonic mean range as a general representation of the area typically used by falcons. The 95% harmonic mean range was probably the best estimator because it excluded infrequently used outlying points, and matched, with only slight distortion, the area in which we obtained location estimates (Squires et al. 1993). We used minimum convex polygons for estimation of habitat available to falcons within their home range because it described the maximum area used, minimized inclusion of areas where we never located birds, and did not rely on statistical distributions of locations. Cluster techniques (Kenward 1992) produced the best representations of "core areas" (areas of disproportionately high use within ranges).

We investigated effects of year, sex, nest location, and breeding success on ranging habits with multivariate analyses of variance (MANOVAs). Measures of spatial use were partitioned

into three groups for use as dependent variables in separate MANOVAs as follows: (1) average travel distance from the nest to telemetry locations and 95% harmonic mean home range as indices of average area use, (2) maximum travel distance from the nest to telemetry locations, minimum convex polygon home range, and maximum width of home range for maximum area use, and (3) 90% and 95% cluster-based home ranges for core area use. Sample sizes were insufficient to investigate all four factors (year, sex, nest location, breeding success) in any single analysis because there were few unsuccessful pairs in 1992 and few successful pairs in 1993. Therefore, we initially subdivided the sample into successful pairs and unsuccessful pairs plus non-nesters. Sample size was sufficient for the use of a two-factor (year and sex) MANOVA to analyze successful pairs, but the smaller sample of unsuccessful pairs was adequate only for two, single-factor (1 for year, 1 for sex) MANOVAs. The influence of breeding success was investigated separately for males and females. For all analyses, the nest site universal transverse mercator (UTM) coordinates (or trap site coordinates, if no nest was established) were included as covariates in the MANOVAs.

We combined each adequately sampled, successfully breeding individual's travel distances to test the influence of sex, year, and stage of nesting cycle on travel in a three-factor ANOVA (nest location was used as a covariate). Four stages of the nesting cycle were determined by back-dating from estimated age at banding or from the last date of observation before nest failure as follows: (1) territory establishment/incubation, (2) early brood rearing (nestlings < 21 days old), (3) late brood rearing (nestlings \geq 21 days old), and (4) postfledging (the first month after fledging). Because the number of locations per individual for each stage of the nesting cycle was not equal, each location estimate in the ANOVA was assumed to be independent. Any pseudoreplication (Hurlbert 1984) in the analysis may increase Type I error, but assessments of the relative importance of each factor should be valid.

HABITAT SELECTION

We investigated habitat selection at three scales. First, to document general associations between falcons and underlying vegetation, we correlated

the number of telemetry locations per km² with the percent cover of shrubs and grasses in each km² of the study area. These large grid cells were used because of the error associated with telemetry locations. Second, to document selectivity in the location of home ranges by individual falcons, we compared the proportion of habitats used in convex polygon home ranges to the proportion of habitats available within the usual flight range of falcons (the area from 21 km north of the Snake River Canyon [the average maximum travel distances observed for radio-tagged birds] to 7 km south of the canyon [the full extent of vegetation sampling south of the canyon]). Third, to document selectivity within the home range by individual falcons, we compared the proportion of habitats used within core areas (defined by cluster analysis) to the proportion of habitats available within each individual's convex home range. We examined habitat in clusters that included 95% of locations because ranges showed little change in the rate of area increase for cluster polygons that included from 20% to 95% of the locations, but typically increased sharply thereafter both in area within ranges and size variation between ranges, which indicated that the remaining 5% of locations were outliers.

We quantified habitat (vegetation) in two ways. First, we calculated percent cover of shrub and grass sampled at 684 sites from 1990 through 1994. Percent cover at each site was estimated by point frame interception (Floyd and Anderson 1982) at 252 points randomly distributed along seven, 50-m transects. Percent cover of 16 plant species (*Artemisia spinescens*, *Artemisia tridentata*, *Atriplex canescens*, *Atriplex confertifolia*, *Atriplex nuttallii*, *Bromus tectorum*, *Ceratoides lanata*, *Chrysothamnus nauseosus*, *Chrysothamnus viscidiflorus*, *Grayia spinosa*, *Poa secunda*, *Salsola iberica*, *Sarcobatus vermiculatus*, *Sitanion hystrix*, *Tetradymia glabrata*, *Vulpia* spp.) per 1 km² of the study area was derived by interpolating between sites using a GIS-based kriging procedure (technique that assigns plant cover for areas not sampled based on cover of nearby sampled areas). This measurement of habitat was used to test for selection at all three scales discussed above. Second, we determined the types and areas of habitats from Landsat thematic mapper satellite imagery. Habitats were classified on the basis of dominant vegetation and included sagebrush/rabbitbrush,

winterfat, salt desert shrub, grassland, cliff, and water habitats (Knick et al. 1997). In addition, we delineated all areas used for agriculture since 1979 (including fallow fields) from a composite of the 1979 Snake River Birds of Prey vegetation map (U.S. Dept. Interior 1979), 1993 Bureau of Reclamation agriculture maps, and the classified satellite imagery. Resolution of the habitat map was 50 m \times 50 m (resampled from 30-m pixels in the satellite image). We 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). Because falcon locations were least closely correlated with this quantification of habitat, we only used it to investigate selection at the first scale discussed above.

We determined significance of selectivity in the location of home ranges and location of core areas within home ranges by calculating 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. The sampling unit was the individual falcon and average selection ratios were calculated for our sample of falcons. We calculated a 95% confidence interval around each ratio average after a Bonferroni adjustment for multiple comparisons. Selection ratios that did not include 0 in their confidence interval indicated significant ($\alpha = 0.05$) selection for (ratio > 0) or against (ratio < 0) particular habitats.

The error associated with telemetry locations may bias tests of habitat selection, especially if error is large relative to habitat patch size (White and Garrott 1986, Nams 1989). We reduced this potential bias by basing our assessments of habitat use on entire home ranges and core areas rather than basing them on individual location estimates. Although sizes of such areas are influenced by telemetry error, this influence is less than the bias created by using individual locations to determine habitat use (Senchak 1991). Areas estimated without accounting for telemetry error may underestimate actual area (Senchak 1991), which might lead to overestimates of the significance of habitat selection. However, this is unlikely in our study because we used conservative methods to assign significance to habitat selection (individual falcons as experi-

mental units and Bonferonni-adjusted confidence intervals). Values presented are $\bar{x} \pm SE$.

RESULTS

DIETS

Townsend's ground squirrels comprised the majority of prey utilized by Prairie Falcons each year, but the proportion of prey types delivered fresh to the territory differed significantly among years ($G_4 = 88.6$, $P < 0.001$). Parents delivered more Townsend's ground squirrels in 1992 than in 1993 or 1994 (Fig. 2). Conversely, more reptiles and birds were delivered in 1993 and 1994 than in 1992 (Fig. 2).

RADIO TELEMETRY

As a result of large areas covered by Prairie Falcons, we were between 141 m and 14.6 km ($\bar{x} = 7.7$ km \pm 38 m, $n = 7,213$ locations) from them when we obtained acceptable location estimates. Bearings obtained by tracking moving falcons across such large distances were relatively imprecise (SD of bearing errors = 16.4°), but unbiased (\bar{x} deviation of estimated bearings from true bearings = 1.03°, $n = 584$ estimates of beacon locations; not significantly different from 0, paired $t_{583} = 1.52$, $P = 0.13$). Estimated linear error between location estimates and falcon positions ranged from 0–6.7 km ($\bar{x} = 3.0$ km \pm 20 m, $n = 7,213$). Although the errors are large (approximately 10% of maximum distance between points in a falcon's range), their unbiased nature means that comparisons of relative differences between groups of birds are meaningful.

HOME RANGE AND RANGING BEHAVIOR

Average home range size was ca. 300 km², depending upon calculation method (Table 1). Falcons traveled 7 km on average, and an average maximum of 21.7 km from their nests (Table 1). The greatest distance a falcon was located from its nest was 38.3 km. Falcon use of these large ranges was not distributed in an even manner. Rather, 90% of locations were confined to 1–7 core use areas that included only 38% of the total range.

Average Prairie Falcon home range size was nearly twice as large in 1993 and 1994 compared to 1991 and 1992 (\bar{x} 95% harmonic mean range \pm SE for: 1991 = 227 km² \pm 22; 1992 = 204 km² \pm 26; 1993 = 341 km² \pm 36; 1994 = 400 km² \pm 38). Year-to-year changes in use of

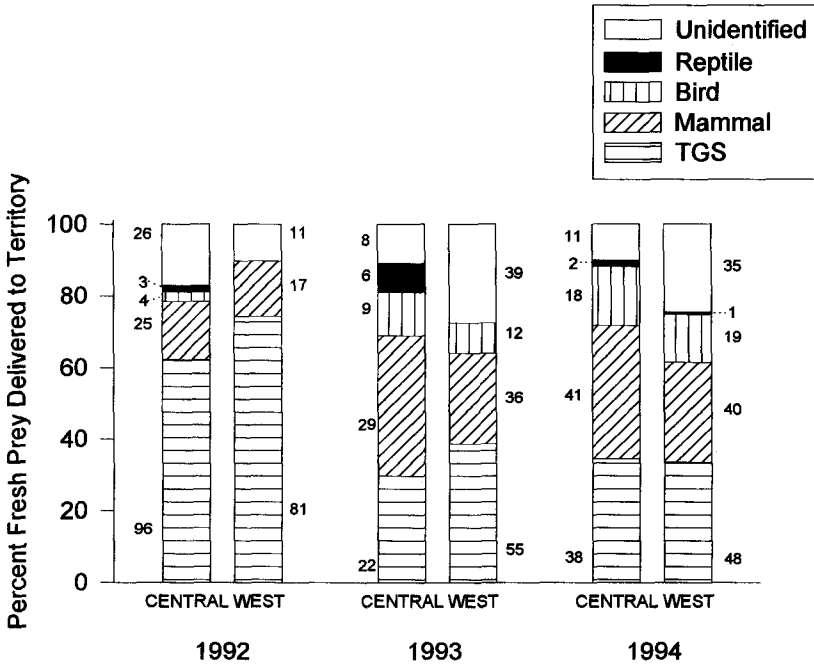


FIGURE 2. Percentage of fresh prey items delivered by adult Prairie Falcons to their territories in the central and western sampling areas (see Fig. 1 for area locations) in 1992–1994. Unidentified prey items presented here were excluded from the analysis of annual variation in prey items. Numbers of prey of each type are adjacent to histograms. TGS = Townsend’s ground squirrel.

TABLE 1. Travel distances and home range characteristics of radio-tagged Prairie Falcons. Measures are averaged for the entire sample and a variety of subsamples. Table entries are mean, sample size, and standard error.

Sample	Average distance traveled from nest (m)	Maximum distance traveled from nest (m)	Maximum distance across home range (m)	Size of home range (ha)		Size of core use area (ha)	
				convex polygon	95% harmonic mean	95% cluster	90% cluster
All falcons	7,031	21,748	27,561	31,472	29,757	16,203	11,351
	77	77	93	95	95	95	95
	290	738	909	1,570	1,772	893	718
Successful pairs	7,021	21,253	26,773	29,113	25,959	14,865	10,597
	58	58	58	58	58	58	58
	352	815	1,175	1,882	1,887	1,115	860
Unsuccessful pairs	7,063	23,259	28,675	34,536	36,753	16,488	11,985
	19	19	19	19	19	19	19
	484	1,651	2,020	4,322	5,298	2,065	1,631
Non-nesters	N/A	N/A	29,094	35,838	34,613	20,233	13,146
			18	18	18	18	18
			2,056	3,164	3,824	1,942	1,933
Males	7,044	23,384	29,075	34,187	31,935	16,999	12,338
	45	45	53	53	53	53	53
	350	909	1,221	2,016	2,436	1,099	907
Females	7,013	19,447	25,553	28,045	27,009	15,219	10,128
	32	32	40	42	42	42	42
	501	1,127	1,310	2,400	2,542	1,464	1,132

area were significant for falcons that successfully reared 30-day-old young, and these differences were apparent in average, maximum, and core use of area (Table 2). Unsuccessful pairs and non-nesters did not exhibit significant annual differences in ranging habits regardless of the type of travel or range considered (Table 2).

Males and females did not differ greatly in their use of area (Table 1). Average, core, and maximum use of area varied little between males and females that successfully reared 30-day-old young (Table 2). Travel during the nesting cycle by males and females differed significantly among years (3-way interaction between stage of nesting cycle, sex and year in ANOVA comparing travel distances of adequately sampled birds: $F_{9,4247} = 4.0$, $P < 0.001$). Males traveled farther than females during territory establishment/incubation except in 1992 (Fig. 3). Females typically traveled farther than males during late brood rearing, except in 1992 when they traveled extensively during incubation/territory establishment (Fig. 3). The greatest change in travel distance during the nesting cycle occurred in 1992 when both sexes greatly reduced travel during brood rearing and post-fledging.

Non-nesters and breeders after nest failure ranged over larger areas than successful breeders (Table 1), but this difference was significant only for average area use by males (Table 2). Female use of core area was similarly related to breeding success, but the trend only was marginally significant (Table 2). Maximum area used did not differ with respect to breeding success for males or females.

Falcons that nested in the northwest portion of the study area ranged over smaller areas than those that nested in the southeast portion. This trend was significant for average travel of successful and unsuccessful pairs and for use of core area by unsuccessful pairs (Table 2). Maximum area used did not vary significantly with nest location, regardless of breeding success (Table 2).

HABITAT SELECTION

General association between falcons and vegetation. Habitat features explained a significant, but moderate ($< 1/3$) portion of the variation in the abundance of falcon locations (Table 3). The number of telemetry locations per km² was more sensitive to variation in percent cover of individual plant species than to variation in the dom-

inant vegetation (compare R^2 for models in Table 3).

The distribution of falcon location estimates per km² was heavily skewed to the northwest portion of the study area where Sandberg's bluegrass (*Poa secunda*) and big sagebrush (*Artemisia tridentata*) were most common (Figs. 4 and 5). Greasewood (*Sarcobatus vermiculatus*), four-winged saltbush (*Atriplex canescens*), and Russian thistle (*Salsola iberica*) also were positively correlated with the occurrence of falcon locations (Table 3). In contrast, falcon location estimates were rarest in habitats with abundant rabbitbrush (*Chrysothamnus nauseosus* and *C. viscidiflorus*), cheatgrass (*Bromus tectorum*), and bottlebrush squirreltail (*Sitanion hystrix*; Table 3). The general association of falcons with habitats dominated by sagebrush, winterfat (*Ceratoides lanata*), and grassland was confirmed in the analysis of habitat classes defined from satellite imagery (Table 3).

Areas used by falcons (≥ 1 location km⁻²) averaged 5% cover of big sagebrush, 8% cover of Sandberg's bluegrass, and 2% cover of winterfat (Fig. 6). Bluegrass was the dominant vegetation in areas used by falcons. In contrast, cheatgrass dominated areas where falcons were not located. Areas containing many falcon locations (≥ 10 locations km⁻²) had 12% cover of bluegrass, 5% cover of big sagebrush, 2.5% cover of winterfat, 5.5% cover of cheatgrass, and 6.7% cover of Russian thistle (Fig. 6).

Amount of land in agriculture was weakly and positively associated with falcon abundance (Table 3). Agricultural lands are primarily interspersed throughout sage, winterfat, and bluegrass habitats in the northwest portions of the study area.

Placement of home range. Prairie Falcons' home ranges contained a high percent cover of plant species associated with Townsend's ground squirrels. Home ranges contained over twice the percent cover of winterfat and bluegrass than was available within the usual flight range of falcons (see Methods). Likewise, ranges contained significantly more of the annual grass *Sitanion hystrix* than expected based on availability (Table 4). In contrast, falcon home ranges had fewer salt-desert shrubs (*Atriplex canescens*, *A. confertifolia*, *Grayia spinosa*, *Sarcobatus vermiculatus*, *Tetradymia glabrata*) and grasses (*Bromus tectorum*, *Agropyron spicatum*) than expected based on availability.

TABLE 2. Influence of year, sex, nest location, and breeding success on use of area by Prairie Falcons. Table entries are results of MANOVAs comparing use of average, maximum, and core area among various factors. Average use of area is tested by comparing 95% harmonic mean home range and mean travel distance simultaneously across factors. Maximum use of area is tested by comparing the 100% convex polygon, maximum travel distance and maximum width of the convex polygon simultaneously across factors. Core use of area is tested by comparing the 90% and 95% core areas across factors. Nest location effects on spatial use were tested by including nest coordinates (or capture location coordinates for non-nesters) as covariates in MANOVAs. Effects of breeding success were tested by comparing pairs that successfully reared young to 30 days of age to pairs that failed to rear 30-day-old young or that did not breed. Table entries are Wilks' multivariate *F*-statistics, degrees of freedom and probability values. No interactions were significant.

Sample	Factor	Average use of area			Maximum use of area			Core use of area		
		<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
Successful breeders	Year	4.56	6, 94	<0.001	3.25	9, 112	0.01	3.19	6, 94	0.01
	Sex	0.003	2, 47	0.99	0.70	3, 46	0.56	0.03	2, 47	0.97
	Location (east-west)	5.53	2, 47	0.01	1.66	3, 46	0.19	1.49	2, 47	0.24
	Location (north-south)	7.74	2, 47	<0.001	1.34	3, 46	0.27	2.94	2, 47	0.06
Unsuccessful breeders	Year	1.21	6, 24	0.33	0.82	9, 26	0.61	0.98	6, 58	0.45
	Sex	2.54	2, 14	0.11	2.28	3, 13	0.13	2.09	2, 31	0.14
	Location (east-west)	4.28	2, 14	0.04	1.93	3, 13	0.18	2.89	2, 31	0.07
	Location (north-south)	6.00	2, 14	0.01	1.92	3, 13	0.18	6.68	2, 31	0.01
Maales	Breeding success	3.29	2, 34	0.05	1.15	3, 33	0.35	1.41	6, 82	0.22
Females	Breeding success	0.25	2, 27	0.78	0.80	3, 26	0.51	2.77	2, 37	0.08

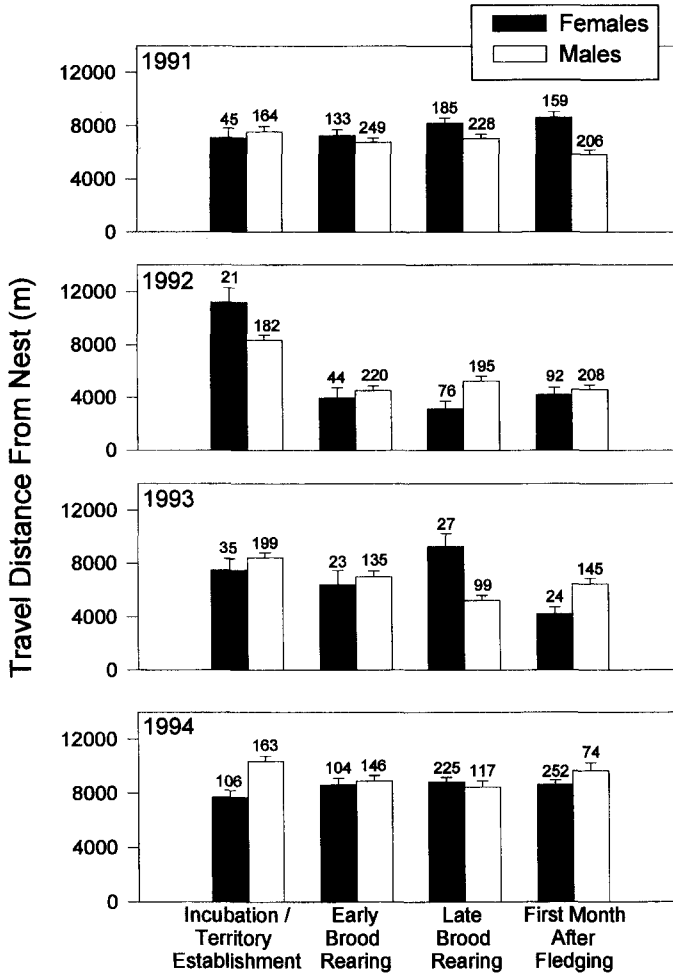


FIGURE 3. Average distance traveled from their nests by males and females each year throughout the nesting cycle. Nesting cycle periods are defined in the Methods. Error bars are SE. Sample sizes are given above error bars.

Falcons nesting in the northwestern portion of the study area were more selective for sagebrush and bluegrass than those nesting in the southeast. Correlations between nest location (UTM coordinates) and each individual falcon's selection coefficient for vegetation were strongest for sagebrush ($n = 98$; North UTM: $r = 0.52$, $P < 0.001$; East UTM: $r = -0.58$, $P < 0.001$), and also significant for bluegrass ($n = 98$; North UTM: $r = 0.22$, $P = 0.03$; East UTM: $r = -0.26$, $P = 0.01$). Selection for winterfat decreased significantly from north to south ($n = 98$; North UTM: $r = -0.25$, $P = 0.02$).

Selection within the home range. Falcons were less selective within home ranges than they were

in the placement of the home range (Table 4). Most salt desert shrubs (*Atriplex confertifolia*, *A. nuttalli*, and *Sarcobatus vermiculatus*) occurred in core areas less than expected. However, *Atriplex canescens* occurred in core areas more frequently than expected based on availability.

The degree of selectivity within home ranges was related to the location of the home range in the study area. Individual falcons that had more bluegrass than expected based on availability in their home range were less selective for bluegrass in their placement of core areas ($r = -0.52$, $n = 98$, $P < 0.001$). Selection within ranges for winterfat also was less in relation to the extent of selection for winterfat in the place-

TABLE 3. Importance of plant species coverage (determined by kriging between data obtained from vegetation transects) versus habitat categories (defined by dominant plant species classified from satellite imagery) in explaining variation in number of Prairie Falcon radiotelemetry locations per square kilometer. Table entries are significant ($P < 0.05$) t -statistics testing the importance of each variable in a stepwise multiple regression of vegetation on the number of falcon radiotelemetry locations for 1991–1994 combined. Variables not remaining in model had nonsignificant (ns) t -values. Summary statistics for regression models are listed at bottom of each column.

Plant species coverage		Dominant habitat category	
Species	t -value	Habitat	t -value
<i>Artemisia tridentata</i>	6.3	Sagebrush/rabbitbrush	9.7
<i>Atriplex canescens</i>	5.6	Salt desert shrubs	ns
<i>Atriplex confertifolia</i>	1.9	Winterfat	9.1
<i>Atriplex nuttallii</i>	-2.3	Grassland	4.9
<i>Bromus tectorum</i>	-7.5	Agriculture	2.7
<i>Ceratoides lanata</i>	13.4	Water	ns
<i>Chrysothamnus nauseosus</i>	-5.0	Cliff/rock outcrop	8.2
<i>Chrysothamnus viscidiflorus</i>	-9.8		
<i>Grayia spinosa</i>	-4.8		
<i>Poa secunda</i>	23.3		
<i>Salsola iberica</i>	5.4		
<i>Sarcobatus vermiculatus</i>	5.7		
<i>Sitanion hystrix</i>	-6.4		
<i>Tetradymia glabrata</i>	-4.2		
<i>Vulpia</i> spp. ¹	ns		
<i>Agropyron spicatum</i>	ns		
F	110.2		54.3
df	14, 3465		5, 3005
P	<0.001		<0.001
R^2	0.31		0.08

¹ *Vulpia octiflora* and *V. michrostachys* were not reliably delineated in the field.

ment of the home range ($r = -0.39$, $n = 98$, $P < 0.001$). Selection for bluegrass and winterfat within ranges with less than expected percent cover of these plants increased the overall percent cover of bluegrass and winterfat within core areas. Percent cover within core areas of bluegrass and winterfat increased significantly with the degree of selectivity within home ranges for bluegrass and winterfat (all P s < 0.001).

DISCUSSION

During four years of study, in which weather and prey abundance varied greatly (U.S. Dept. Interior 1996, Van Horne et al., in press), we documented the ranging behavior and habitat use of 98 radio-tagged Prairie Falcons. Previous studies of Prairie Falcon behavior and habitat use investigated few birds and usually only lasted two years. Despite these limitations, many conclusions previously reported were confirmed in our study, specifically: (1) greater reliance on alternate prey when ground squirrel populations declined (Phipps 1979, Steenhof and Kochert 1988), (2) use of slightly larger areas by males than females and increased use of area when

prey abundance declined (Dunstan et al. 1978, Harmata et al. 1978, Squires et al. 1993), (3) long travel distances and large home ranges for males and females during incubation and territory establishment (Dunstan et al. 1978, Haak 1982), (4) increased length of travel distances for females as the nesting cycle progressed (Dunstan et al. 1978), (5) use of many distinct core areas within the foraging range (Hunt 1993), and (6) the importance of native grassland habitats (Hunt 1993).

We believe the size and use of area within Prairie Falcon home ranges in the NCA results largely from the patchy distribution of landscape features associated with different densities and availabilities of Townsend's ground squirrels. In years of normal rainfall, ground squirrels reach their highest densities in habitats with abundant cover of the native Sandberg's bluegrass (*Poa secunda*; Van Horne et al., in press). Following a drought, Townsend's ground squirrels survive better in native sagebrush habitats, and congregate around agricultural fields (Van Horne et al., in press). We located Prairie Falcons most frequently in areas with high percent cover of

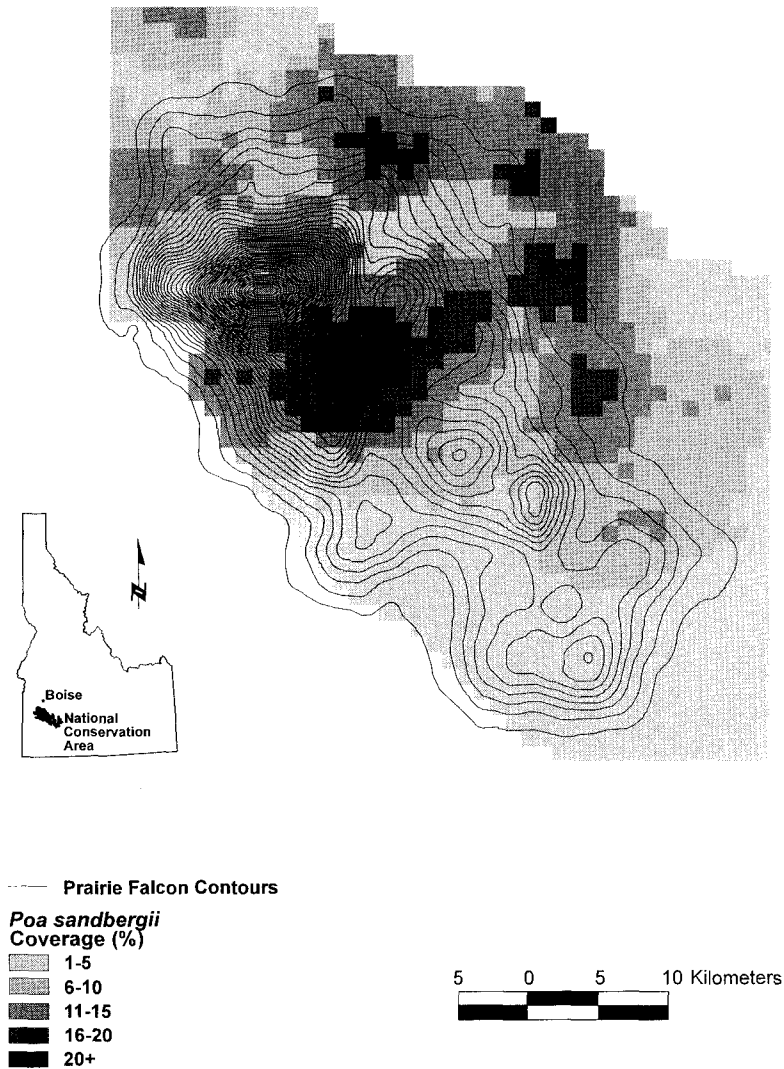


FIGURE 4. Association of Prairie Falcons and Sandberg's bluegrass throughout the study area. Percentage coverage of bluegrass is indicated by shading as determined by kriging between vegetation transects. Falcon abundance for 1991–1994 is portrayed by contours determined by splining (a spatial interpolation method) between counts of radiotelemetry locations obtained per km².

Sandberg's bluegrass, winterfat, and big sagebrush, probably because of the greater abundance of ground squirrels there. Moreover, individual falcons in the northwest portion of the study area, where bluegrass/sage/winterfat habitats are close to nesting areas, brought more ground squirrels to their nestlings and ranged over significantly smaller areas than falcons nesting in the southeast where bluegrass/sage/winterfat is less common and far from the nesting cliffs (Figs. 2, 4, and 5).

Effects of the 1992 spring drought support the importance of ground squirrel distribution as a determinant of Prairie Falcon foraging behavior. The drought strongly influenced Townsend's ground squirrel densities and distributions (Van Horne et al., in press), and we saw these changes reflected in falcon ranging habits and habitat use. Ground squirrel populations increased from moderately high in 1991 to extremely high in 1992, then crashed to the lowest levels recorded in the NCA in 1993 and 1994 (Van Horne et al.,

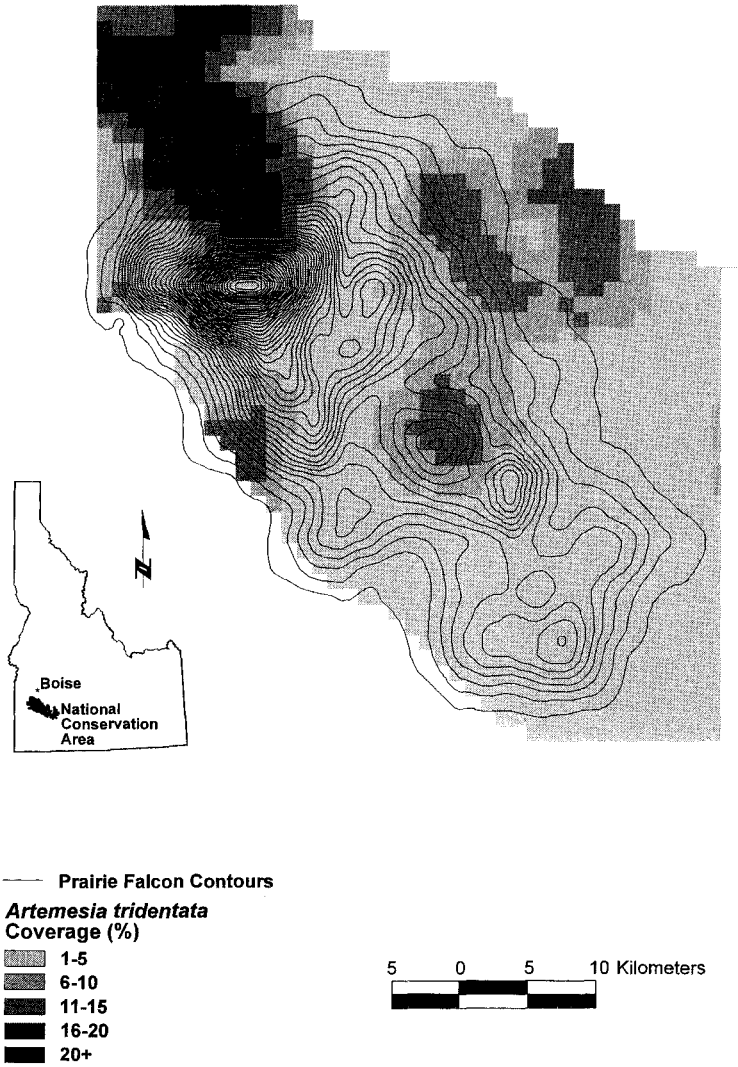


FIGURE 5. Association of Prairie Falcons and big sagebrush throughout the study area. See Figure 4 for details.

in press). As expected, falcons used relatively small areas in 1992 and large areas in 1993 and 1994. However, the extreme reduction in area used and reduced use of bluegrass habitat in 1992 was likely accentuated because a drought caused senescence of bluegrass by early May, and ground squirrels, especially juveniles, moved as bluegrass senesced (Van Horne et al., in press). Ground squirrels also congregated near alfalfa fields close to falcon nesting areas, where they could forage, although the fields themselves did not provide burrows for refuge. The abundance of available prey close to falcon

nests apparently allowed falcons to dramatically reduce travel during brood rearing and post-fledging periods in 1992, and rely on winterfat habitats more than in previous years (Table 3). Similar weather conditions in 1994 caused bluegrass to again senesce early (Van Horne et al., in press), but squirrels were rare, and falcons continued to range far from their nests throughout the nesting cycle, concentrating their activities in habitats likely to contain ground squirrels (e.g., bluegrass and sagebrush).

Prairie Falcons used habitats likely to contain ground squirrels more frequently during years of

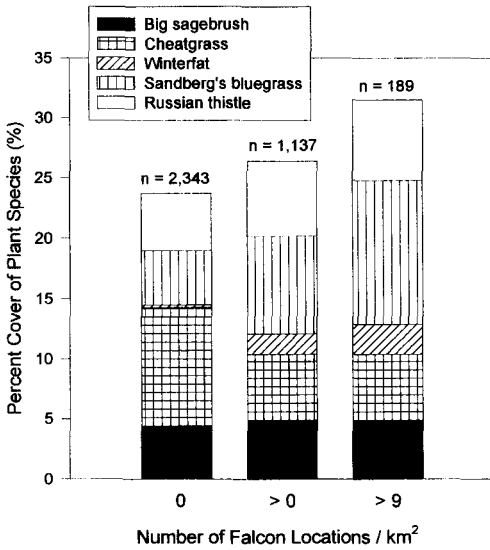


FIGURE 6. Coverage of dominant plant species per km² where no falcon radiotelemetry locations were obtained, where at least one location was obtained, and where 10 or more locations were obtained. Coverage of cheatgrass decreases while bluegrass and winterfat increases in areas with progressively more falcon locations. n = number of km² cells with appropriate number of falcon locations.

low squirrel abundance than during years of high squirrel abundance. Apparently bluegrass/sage/winterfat habitats may support the highest abundances of squirrels when populations are low. Thus, maintenance of bluegrass/sage/winterfat habitat is probably important to the management of Prairie Falcon populations. Even though falcons routinely consumed other prey types (birds and reptiles) in years of low squirrel abundance, Townsend's ground squirrels make up the majority of falcon diets, especially in years when falcon productivity is high (Fig. 2).

Variation in habitat accounted for only 1/3 of the variation in the observed locations of radio-tagged falcons in the study area. However, the reliance of falcons on native shrub and grassland mosaics may be greater than reported here because our estimated locations were associated with large error. This should have little effect on our assessments of habitat use in home ranges and core areas because these area measurements rely, not a single location, but on a collection of locations which are unbiased. Obtaining locations remotely also prevented us from knowing what the falcons were doing at the time a location was determined. Although falcons forage

TABLE 4. Habitat selection for home range placement and use of space within home ranges by Prairie Falcons. Selection coefficients equal $\ln(\text{habitat used}/\text{habitat available})$, and entries in body of table are averaged for n = 98 falcons. Habitats used in the convex polygon home range are compared to habitats available in the typical flight range of falcons within the area sampled for vegetation (from 21 km north of the Snake River Canyon to 7 km south of the canyon) to test selection for placement of the home range. Selection for placement of core areas is tested by comparing habitats used within the core to habitats available within the convex polygon home range. Asterisks indicate significant (* = P < 0.05, ** = P < 0.01) selection for (ratio > 0.0) or against (ratio < 0.0) habitats.

Plant species	Selection by individuals for placement of:	
	Home range	95% core area
<i>Artemisia tridentata</i>	-0.06	-0.12
<i>Atriplex canescens</i>	-0.63**	0.31*
<i>Atriplex confertifolia</i>	-1.52**	-0.46**
<i>Atriplex nuttallii</i>	0.11**	-0.47**
<i>Bromus tectorum</i>	-0.58**	0.04
<i>Ceratoides lanata</i>	0.71**	-0.10
<i>Chrysothamnus viscidiflorus</i>	-1.74**	-0.13
<i>Grayia spinosa</i>	-0.89**	-0.06
<i>Poa secunda</i>	0.51**	-0.09
<i>Salsola iberica</i>	-0.09	-0.04
<i>Sarcobatus vermiculatus</i>	-1.01**	-2.92**
<i>Sitanion hystrix</i>	0.20**	-0.06
<i>Tetradymia glabrata</i>	-3.82**	-0.15
<i>Vulpia</i> spp. ¹	-0.10	-0.07
<i>Agropyron spicatum</i>	-0.86**	-0.15

¹ *Vulpia octoflora* and *V. michrostachys* were not reliably delineated in the field.

continuously when away from their canyon nests (Phipps 1979), we suspect that observations of actual foraging would show an even stronger use of bluegrass/sage/winterfat mosaics by falcons.

Prairie Falcons in the NCA had larger home ranges than Prairie Falcons in other areas (Dunstan et al. 1978, Harmata et al. 1978, Hunt 1993, Squires et al. 1993). Only Haak (1982) reported ranges (228 km²) close to the size we documented (298 km²). Some of the differences may be methodological: (1) we did not record location estimates at nests because of topography (such locations were, however, also excluded by Squires et al. [1993] and Hunt [1993]), (2) our study included years of low prey abundance, (3) we tracked birds throughout the nesting cycle from territory establishment to dispersal, and (4) we used fixed tracking sites at varying distances from the nest sites that allowed us to wait for birds to visit all parts of their range.

Beyond the methodological factors, it also is

possible that home ranges are larger in the NCA because of the way in which high-quality-prey habitat is distributed. Schoener (1968) reported that Prairie Falcons had much larger home ranges than expected for birds their size. He speculated, and Harmata et al. (1978) concurred, that this was possibly due to dispersion of habitats containing prey and constraints of the falcon's hunting style. Our results support this idea. Native grass habitats most likely to contain Townsend's ground squirrels were 5–20 km from nest sites (Fig. 4), home range size increased with declining prey, and home range size increased from northwest to southeast within the study area in parallel with reduced percent cover of perennial grass.

Because of the mosaic structure of prey habitat in the NCA, increased foraging areas required during years of low prey abundance may be too large for effective brood rearing. Falcons in the NCA apparently cannot range over more than 300 km² and still provide the required food and vigilance to their nestlings. Falcons traveled over areas of 350–400 km² in years when their reproduction was poor (1993, 1994), but only covered 200–280 km² in years when their reproduction was good (1991, 1992; Table 1). Moreover, when prey declined those falcons nesting in the southeast, who ranged over areas \geq 300 km² even when squirrels were abundant, were the first to show poor reproduction and usually had poorer reproduction than pairs nesting in the northwest where squirrel habitat was abundant close to nests (Steenhof et al., unpubl. data).

Ideal habitat for foraging falcons probably includes a mosaic of shrubs and grasses, in which shrub patches \geq 10 ha provide cover and forage for squirrels, particularly during drought periods (Van Horne et al., in press). Our observation that sagebrush and winterfat covers approximately 8% of the ground used most by falcons should not be interpreted to mean a continuous shrub coverage. Rather, areas of perennial grasses should be interspersed with stands of winterfat and big sagebrush. Open areas are apparently needed by falcons to catch squirrels (Haak 1982), but shrub cover may reduce squirrels' abilities to detect raptors making it potentially easier for falcons to surprise their prey (Sharpe et al. 1994).

Agricultural borders may be especially important habitats for Prairie Falcons in drought years because ground squirrels in these areas

may be the only productive breeders in the population (Smith and Johnson 1985). The openness of agricultural habitats, especially pastures and hayfields, may be conducive to successful falcon foraging (Haak 1982) and may provide a variety of prey types, such as voles and passerines, to supplement falcon diets when ground squirrel populations crash. These possible advantages may explain the slight positive association of falcons with agriculture during our study, which occurred during years of mild to severe drought. However, the advantage of agriculture in our study area may be unique because agricultural fields are sparsely dispersed among native habitats thereby increasing habitat diversity. Conversion of large tracts of native vegetation to agriculture would adversely impact falcons because overall prey abundance is much lower in agricultural lands than in native shrubland (U.S. Dept. Interior 1979).

Controlling wildfire is perhaps the most important management practice beneficial for Prairie Falcons. Shrubsteppe habitats are vulnerable to fire, which converts shrub and perennial grass communities into exotic annual communities which are eventually dominated by cheatgrass (Yensen 1982). Cheatgrass communities can support ground squirrel populations, but populations in such areas are more susceptible to drought and therefore provide less stable prey populations than those in shrub/perennial grass mosaics (Yensen et al. 1992, Van Horne et al., in press).

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