CHARACTERISTICS OF CLIFFS AND NEST SITES USED BY BREEDING PRAIRIE FALCONS

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Abstract - Data from over 400 Prairie Falcon (*Falco mexicanus*) eyries in 8 states show a consistent pattern of eyrie placement relative to height and aspect of nest cliffs. Mean eyrie height averaged 63% of mean cliff height. Mean exposure of eyries and nest cliffs tended to be southerly with no significant difference between eyrie and cliff exposures. Potholes were the most frequently used nest sites. Patterns of occupancy and nest success in Wyoming were statistically independent of physical habitat variables measured. However, eyries on tall exposed buttes consistently had high failure rates that appeared weather related. Attributes of Wyoming eyries are presented and suggestions made for creating new eyries for Prairie Falcons as a management tool.

We summarized and compared data on nest cliffs and eyries used by the Prairie Falcon *(Falco mexicanus)* in the western United States. Included are data available in the literature and original data from eyries active between 1982 and 1984 in Wyoming. Our objective was to document the variation in nest cliffs and eyries used by these falcons and to identify consistent patterns of use. In our study, we examined the association between physical nesting habitat and patterns of eyrie occupancy and nest success. We discuss attributes of Prairie Falcon nest cliffs and eyries, and suggest guidelines for creating new falcon eyries.

Study Area and Methods

Data from 8 states were considered: Washington (Decker 1931), Wyoming-Colorado (Enderson 1964), Montana (Leedy 1972), Utah (Porter and White 1973), New Mexico (Platt 1974), Oregon (Denton 1975), Idaho (Ogden 1973; Ogden and Hornocker 1977), and Colorado (Williams 1981).

We collected data from eyries and associated cliffs in southern Wyoming known to have been active between 1982 and 1984. We define *eyrie* as the area in and immediately around the nest scrape. *Nest cliff* was the rock formation above and below the eyrie. A single nesting territory may contain several separate nest cliffs and eyries that are occupied and defended in different years. We climbed to eyries by ladder or rope; nest cliff measurements were taken from below.

Variables measured at eyries centered on the nest scrape, if recognizable, or on the approximate center of the eyrie. These included roof (or overhang) height, width, length, and percent coverage of nest scrape by roof or overhang. We measured area of both entrance and floor with a transparent 25 cm^2 grid. Slope of both floor and ceiling were measured with a clinometer. Eyrie exposure was measured by placing a compass in the nest scrape and taking readings along a horizontal plane to both outside edges. From these azimuths (corrected for declination) we calculated mean and extent of horizontal exposure. Finally, eyries were classed as either potholes, horizontal ledges or shelves, vertical cracks or crevices, and stick nests.

Nest cliff measurements focused on that portion of the cliff directly above and below the eyrie. Variables included cliff and eyrie height, inclination of the toe slope below cliff (determined by clinometer), and aspect perpendicular to the cliff. Verticality of each cliff was estimated with a large protractor and was either vertical (85-95°), overhung (<80°) or underhung (>100°). Cliffs were classed as: canyon walls, buttes or mountains, rimrock or ridges, and isolated rock outcrops.

Standard statistics are presented for most variables. Statistics from other studies, if not reported, were calculated from frequency tables or raw data. We analyzed our data using one-way ANOVA and Chi-square (χ^2) to examine relationships between physical variables and histories of nest success and occupancy within and among years. In among-year analyses, we only included sites with complete 3-yr histories.

Data suitable for circular statistical analysis (Batschelet 1981; Zar 1984) were available for Montana, Utah, New Mexico, Idaho, Colorado and Wyoming. Grouped data were analyzed as suggested by Batschelet (1981); 954 confidence intervals were estimated by interpolation (Batschelet (1981: Fig. 5.2 1). We used used Rayleigh's test to determine statistical significance of mean exposures to infer nonrandom orientations (Zar 1984). Concentration (r), or length of the mean vector as calculated by circular methods, ranges from 0 to 1 and is affected by variation in circular data, sample size, and grouping. Values of r near l indicate data points closely concentrated about the mean angle.

Results

Eyries. — Dimensions of eyries from the present study were summarized (Table 1), and comparable to Williams (1981) and Porter and White (1973). Williams (1981) reported eyrie lengths and widths which averaged 78.9 cm (SE = 7.63) and 81.1 cm (SE = 9.52), respectively. Both means were significantly less than measurements from Wyoming (t-Test; P<0.01). Roof heights of Colorado eyries (Williams 1981) averaged 83.2 cm (SE = 12.04), and were significantly greater (t-Test; P < 0.01) than we found. The Colorado data yielded an average floor area of 6821 cm^2 (SE = 1198.22). Area within 8 eyries averaged 15,000 cm^2 in Utah (Porter and White 1973). Our estimate of area lies between these, but statistical comparisons could not be made.

Floors of most (80%) Wyoming eyries sloped downwards towards the front at 5-10°. Conversely, most (84%) eyrie roofs or overhangs sloped to the

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Table 1. Attributes of Prairie Falcon eyries in southern Wyoming, 1982 to 1984.

VARIABLE	MEAN	SE	RANGE	N
Height (cm)	47.9	3.62	11-193	68
Width (cm)	91.2	7.45	18.313	70
Length (cm)	135.4	8.82	43-400+	71
Floor (cm^2)	9325	769.83	1600-29275	70
Entrance (cm^2)	5375	975.12	875-53500	56
Floor Slope (°)	7.4	0.78	-10-35	67
Roof Slope (°)	-12.3	2.23	-65-45	56

rear at a wide range of angles (Table 1). All eyries we examined, except for 2 (3%), had overhanging rock or ceilings protecting the nest scrape. Percent coverage of nest scrapes was frequently 100%, and averaged 93%.

Across their range, Prairie Falcons nested most frequently in potholes or on cliff ledges. Crevices and stick nests were used less frequently (Table 2).

Nest cliffs. — Heights of eyries and nest cliffs varied widely. Relative to mean cliff heights, mean eyrie heights varied from 60-70% (Table 3). Mean heights of eyries from 8 studies were highly correlated with mean heights of cliffs ($R^2 = 0.99$; $P < 0.001$), and averaged 63% of mean cliff height. Minimum cliff and eyrie heights reported in these studies were 2.1 m and 0.8 m, respectively. Signifi-

Table 2. Types of eyries used by nesting prairie falcons.

STATE	POTHOLE[1]		CREVICE[2]		LEDGE[3]		STICKNEST		REFERENCE
	n	(%)	n	(%)	n	(%)	n	(%)	
WY	29	(41)	17	(24)	18	(25)	7	(10)	This study
CO	2	(14)	9	(64)	3	(21)	--	--	Williams (1981)[4]
ID	76	(60)			24	(19)	26	(21)	Ogden and Hornocker (1977)
OR	15	(42)	14	(39)	7	(19)	--	--	Denton (1975)[4]
NM	8	(39)			4	(19)	9	(43)	Platt (1974)
UT	26	(36)	7	(10)	23	(32)	(16)	22	Porter and White (1973)
MT	18	(37)	18	(37)	9	(18)	4	(8)	Leedy (1972)
CO-WY	20	(56)			16	(44)			Enderson (1964)
WA	6	(43)			1	(7)	7	(50)	Decker (1931)
	200	(45)	65	(15)	105	(24)	69	(16)	

[1]Includes sites listed as caves, holes and cavities.
[2]Includes sites listed as vertical cracks.
[3]Includes sites listed as horizontal shelves. Includes a few sites with sticknests present.
[4]Data not reported but sticknests used.

Table 3. Mean heights of Prairie Falcon eyries and nest cliffs.

Cliff Height (m)			Eyrie Height (m)				
Mean	(n)	Range	Mean	(n)	Range	Percent[1] Height	Reference
14.6	(71)	4.3 - 34.6	9.8	(71)	2.9 - 30.6	67	This study
53.7	(14)	15 - 140	32.1	(14)	10 - 90	60	Williams (1981)
36.9	(49)	3.7 - 122+	22.9	(41)	2.1 - 61+	62	Denton (1975)[2]
14.0	(21)	6 - 35	8.6	(21)	3 - 30	61	Platt (1974)
30.4	(126)	2.3 - 122+	19.8	(126)	2.4 - 122+	65	Ogden (1973)[2]
31.0	(44)	2.1 - 154.4	19.6	(51)	0.8 - 137.2	63	Porter and White (1973)
38.1	(57)	9.2 - 92+	24.4	(57)	3.1 - 76.2	64	Leedy (1972)[3]
15.8	(36)	7.7 - 38.7	11.1	(36)	-- - --	70	Enderson (1964)
29.3	(418)	2.1 - 154.4	18.5	(417)	0.8 - 137.2	63	Grand Mean

[1]Percent height = $\frac{\text{Mean eyrie height}}{\text{Mean cliff height}}$ x 100%

[2]Values biased low as some very tall eyries and cliffs were excluded.

[3]Approximate values.

cantly more Wyoming eyries were in the upper one-half of the cliffs than in the lower one-half (χ^2; $P < 0.005$). But the upper and middle one-third of cliffs were used equally.

Inclination of toe slopes ranged from 0-36°. Most (57%) cliffs were vertical (85-95°), though many (34%) sloped back into the hill (> 100°). Only 9% were overhung (< 80°).

We found nest cliffs fairly evenly distributed among volcanic buttes or mountains (34%), sandstone canyons (30%) and isolated rock outcrops (25%). Few occurred on low rimrock (11%). In Oregon, Denton (1975) reported eyries on bluffs (38%), ridges (29%), canyons (24%) and outcrops (9%).

Exposure of eyries and cliffs. — Exposure data from 6 of the 8 western states are shown in Figure 1 (Appendix). Except for Utah and New Mexico, aspects of both cliffs and eyries was reported. In no case did the distributions of eyrie and cliff aspects differ significantly (χ^2; $P > 10$). When 95% confidence intervals could be calculated, intervals for eyrie exposure and cliff aspect overlapped extensively (Appendix; Fig. 3) Overall, mean eyrie aspects averaged 161.2° (r = 0.24); mean cliff aspects averaged 158.3° (r = 0.19). Due to large disparities in sample sizes, these grand means are biased toward our data from Wyoming.

Aspects of cliffs and eyries in Wyoming ranged from 0 - 360° (Fig. 2). We lumped eyrie exposures into 2 groups (northeast and southwest facing) and found that 70.2% faced southwest; close to the percentage (69.4%) of eyries that faced southwest in Utah (Porter and White 1973; Fig. 16). Extent of horizontal exposure of eyries we examined (Fig. 3) ranged from 5 - 160°, and averaged 54 ± 12° (r = 0.83). Williams (1981) reported "angles of view" ranging from 30 - 170° and averaging 122 ± 3° (r = 0.74).

Neither ANOVA nor χ^2 tests revealed any significant ($P > 0.05$) relationships among physical traits, including exposures, of Wyoming eyries and histories of nest occupancy and success. This held true both within and among years.

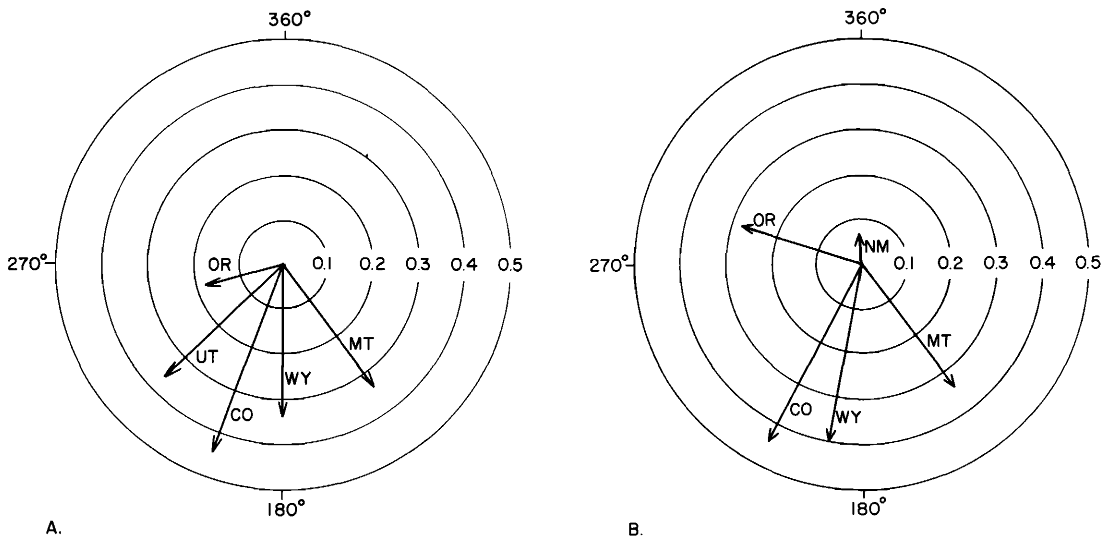

Figure 1. Mean aspect of Prairie Falcon eyries (A) or nest cliffs (B) in Montana, Colorado, Wyoming, Utah, Oregon and New Mexico. Vector lengths are proportional to degree of concentration (r) about mean aspect (Appendix).

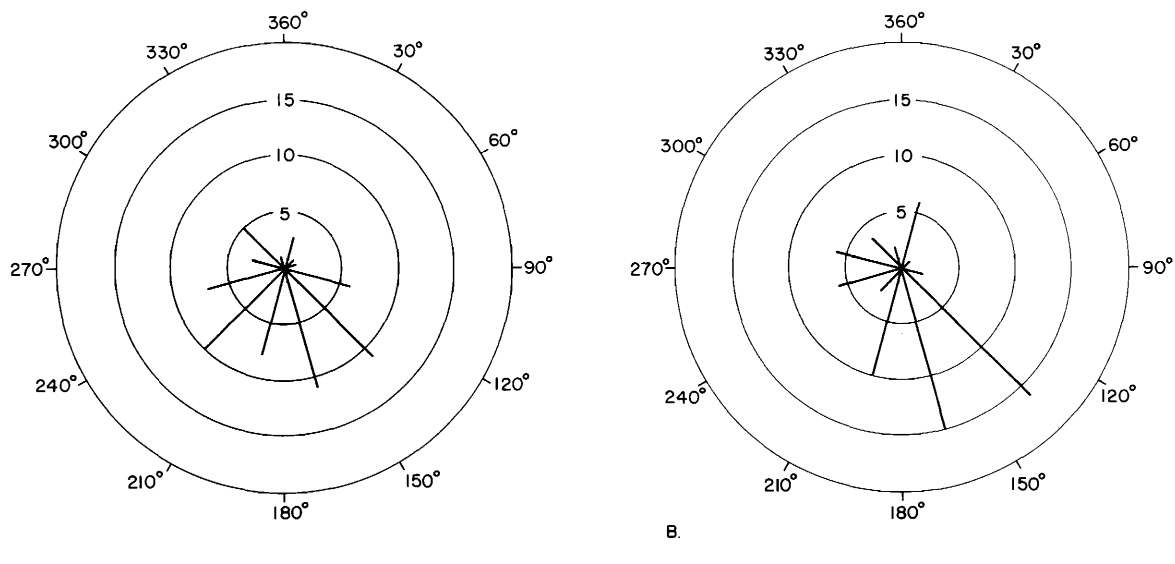

Figure 2. Frequency histograms of eyrie exposure (A) and cliff aspect (B) for Prairie Falcons in southern Wyoming, 1982-1984.

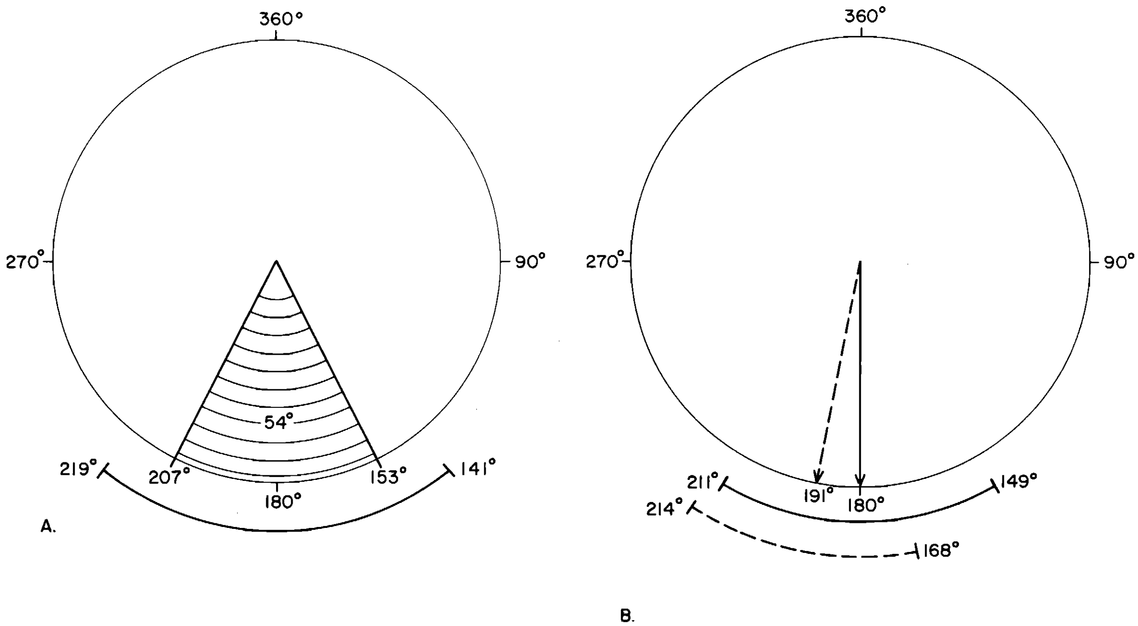

Figure 3. Means and 95% confidence intervals for (A) extent of exposure and (B) cliff aspect (broken line) and eyrie exposure (solid line), for Prairie Falcons in southern Wyoming, 1982-1984.

DISCUSSION

Compared to other western raptors, Prairie Falcons have narrow nest site requirements. They nest almost exclusively on rock cliffs (cf., MacLaren et al. 1984). Nest cliffs used vary widely in height, location and aspect. Yet in the studies examined, Prairie Falcons demonstrated some consistent patterns in their use of eyries. Mean eyrie and cliff heights were strongly correlated and distributions of eyrie and cliff aspects were similar. We do not infer habitat selectivity because data on availability of potential eyries and nest cliffs have neither been collected by us nor presented in the studies we cite.

Eyries. — Potholes, reported most frequently, provide excellent shelter from both inclement weather and direct sunlight, but are not always available. In our experience, potholes occur most frequently in sandstone, while ledges and vertical cracks are more common in granite, basalt and conglomerate cliffs. Vertical cracks and crevices also provide excellent shelter and shade, but may be subjected to chilling drafts. Nests in crevices were reported infrequently in the literature but were common in our study area.

Nest cliffs. — Mean eyrie heights, as percentage of mean cliff heights, were surprisingly consistent and indicate extensive use of nest sites 60 - 70% up cliff faces. Further study is needed to explain this narrow range of eyrie heights relative to cliff heights. By nesting in the upper reaches of vertical cliffs, Prairie Falcons should be safe from mammalian predators. Such a location also provides a commanding view of the territory and of potential prey or predators. Depending on aspect and prevailing winds, updrafts along cliffs may aid the falcons when leaving the nest to hunt or defend territory. Convective updrafts may form more frequently on south-facing cliffs as they radiate more heat than cliffs with other aspects.

Exposure. — Prairie Falcons have long been known to nest on cliffs with southerly aspects (e.g., Dawson 1913). Sixty-one and 42% of the eyries studied by Enderson (1964) and Ogden (1973) faced south. But their data, as reported, could not be included in our circular statistics analyses. With 2 exceptions (Platt 1974; Denton 1975), the studies examined indicated southerly mean aspects (Fig. 1). Although cliff and eyrie exposure varied widely in most studies, Rayleigh's test indicated significant nonrandomness in most cases (Appendix). Mean exposures were often only weakly significant ($P < 0.10$) due to wide ranges of exposures and because most data from the literature were grouped into broad exposure classes. Aspects of nest cliffs in New Mexico and eyries in Oregon were random (Rayleigh's test; $P > 0.10$). Excluding these, mean cliff aspect ranged from 144 - 288°, and mean aspect of eyries ranged from 143 - 226°. Prairie Falcons do use north-facing cliffs and eyries (Figs. 1 and 2). In fact, Tyler (1923) reported that most Prairie Falcon eyries in southern California had northerly aspects and none were southerly. He attributed this to a scarcity of south-facing cliffs and an abundance of north-facing cliffs. Our results demonstrate a tendency for Prairie Falcons to use southerly aspects, but do not demonstrate any benefit in terms of nest success. Eyrie configuration and location on the cliff may override efforts of cliff aspect (Ellis 1982). Data on availability of potential cliffs and eyries with differing aspects are needed to conclude that falcons actively select south-facing cliffs.

The microclimate within an eyrie is affected by its exposure and cliff aspect; southerly exposures likely help to moderate cold temperatures during incubation and brooding. Solar heating of nest scrapes may lessen the energy requirements of incubating and brooding falcons. The majority (97%) of eyries we examined had overhead protection. Most eyries examined by Enderson (1964), Leedy (1972), Platt (1974), Ogden and Hornocker (1977) and Williams (1981) were similarly sheltered. Overhead shade may be important during midday since nestlings exposed to direct sun when temperatures are near 32° C may die (Nelson 1969). Such temperatures are unusual during the nestling period in our study area, but use of shaded eyries may increase nestling survival at lower elevations and latitudes.

We believe shelter from late spring storms to be more important than protection from heat stress in our Wyoming study area. Such storms were associated with a high rate (64%) of nesting failure on buttes in 1983. A spring snowstorm this same year was followed by desertion of all 5 active nests on buttes in a small area of northeastern Wyoming (J. Squires pers. comm.). In our study area, territories on tall exposed buttes consistently suffered higher rates of nest failure (43 - 64%) than those located on lower sheltered canyons, rims and outcrops (18 - 38%). However, χ^2 tests failed to confirm a significant association ($P > 0.10$) between nest success and cliff location.

In our study, neither cliff nor eyrie aspect appeared to determine patterns of eyrie occupancy or nest success (see also Ogden and Hornocker 1977). Eyrie, but not cliff, aspect apparently affected nest success in Colorado (Williams 1981) where all 5 southwest-facing eyries failed in 1980. Williams attributed this to local weather patterns.

Biotic factors likely play a larger role than physical habitat in determining occupancy and nest success in Prairie Falcons. Though not confirmed by statistical analyses (χ^2; $P > 0.10$), nesting Great-horned Owls (*Bubo virginianus*) were often associated with unoccupied and unsuccessful falcon territories in our study area. Although we did not quantify accessibility of eyries to mammalian predators, this may be an important factor (Ogden and Hornocker 1977). Abundance of prey clearly affects Prairie Falcon productivity and nest success. Townsend's Ground Squirrel (*Spermophilus townsendi*) densities in Idaho accounted for over 98% of the annual variation in Prairie Falcon productivity (USDI-BLM 1979).

Management implications. — Mitigation for loss of suitable nesting cliffs due to energy, urban, or recreational development may be needed in some areas. An obvious solution is the creation of new nest sites. Such sites were rapidly colonized in California (Boyce et al. 1980) and Alberta (Fyfe and Armbruster 1977). Because the size of the non-breeding population of Prairie Falcons may be as high as 25% of the breeding population (Runde in prep.) substantial population increases seem possible, but will depend upon the local availability of prey and foraging habitat.

The data presented here suggest locating new nest sites on south-facing cliffs about two-thirds up the cliff. Area of the floor should be at least 7,000 cm^2, and slope gently (5-10°) to the front. Overhead cover should be present, and horizontal exposure should be about 54° (Fig. 3A). If eyries are to be created on mine highwalls as part of habitat reclamation or mitigation, their legal, hydrological, and physical constraints must first be addressed (Tessman 1984). The data in Table 3 suggest that cliffs, or highwalls, selected for eyrie creation be at least 2.1 m tall.

We suggest that newly created eyries be clustered together to mimic nesting territories with several alternate nest sites. These new territories could be spaced approximately 1-2 km apart unless visual barriers are present to separate them. In this situation, we have seen successful nests as close as 150 m. Our data show that in a 3-yr period over one-half of the eyries were only occupied 1 yr, and 23% were occupied 2 yrs. Similar findings were reported by Enderson (1964) and Ogden (1973). We suggest that 2 or 3 nest sites be provided per cliff. The ability to use alternate eyries within a nesting territory may help to reduce direct competition for nest sites with owls, and may decrease the frequency of parasitic infestations.

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LITERTURE CITED

BATSCHELET, E. 1981. Circular statistics in biology. Academic Press. New York. 366 pp.

BOYCE, D.A., JR., L. FISHER, W.E. LEHMAN, B. HIPP AND J. PETERSON. 1980. Prairie falcons nest on an artificial ledge. *Raptor Res.* 14:46-50.

DAWSON, W.L. 1913. The nesting of the prairie falcon in San Luis Obispo County. *Condor* 15:56-62.

DECKER, F.R. 1931. Prairie falcon's nest. *The Oologist* 48:96.

DENTON, S.J. 1975. Status of prairie falcons breeding in Oregon. M.S. Thesis. Oregon State Univ., Corvallis. 58 pp.

ELLIS, D.H. 1982. The peregrine falcon in Arizona: Habitat utilization and management recommendations. Inst. Raptor Stud. Res. Pap. No. 1.

ENDERSON, J.H. 1964. A study of the prairie falcon in the central Rocky Mountain region. *Auk* 81:332-352.

FYFE, R.W. AND H.I. ARMBRUSTER. 1977. Raptor management in Canada. Pages 282-293. *In* R.D. Chancellor (Ed.). Proc. of the World Conference on Birds of Prey. Vienna, 1975. ICBP. 442 pp.

LEEDY, R.R. 1972. The status of the prairie falcon in western Montana: special emphasis on possible effects of chlorinated hydrocarbon insecticides. M.S. Thesis. Univ. of Montana, Missoula. 96 pp.

MACLAREN, P.A., D.E. RUNDE AND S.H. ANDERSON. 1984. A record of tree-nesting prairie falcons in Wyoming. *Condor* 86:487.

NELSON, M.W. 1969. Status of the peregrine falcon in the Northwest. Chp. 4 *In* J.J. Hickey (Ed.). Peregrine Falcon Populations: Their biology and decline. Univ. of Wisconsin Press, Madison. 596 pp.

OGDEN, V.T. 1973. Nesting density and reproductive success of prairie falcons in southwestern Idaho. M.S. Thesis. Univ. of Idaho, Moscow. 39 pp.

OGDEN, V.T. AND M.G. HORNOCKER. 1977. Nesting density and reproductive success of prairie falcons in southwestern Idaho. *J. Wildl. Manage.* 41:1-11.

PLATT, S.W. 1974. Breeding status and distribution of the prairie falcon in northern New Mexico. M.S. Thesis. Oklahoma State Univ., Stillwater. 68 pp.

PORTER, R.D. AND C.M. WHITE. 1973. The peregrine falcon in Utah, emphasizing ecology and competition with the prairie falcon. *Brigham Young Univ. Sci. Bull.* 28:1-74.

TESSMAN, S. 1984. Habitat reclamation procedures for surface mines in Wyoming. Pages 185-195. *In* R.D. Comer et al. (Eds.). Proc. of the Symposium: Issues and Technology in the Management of Impacted Western Wildlife. Steamboat Springs, Colo. Nov. 15-17, 1982. *Thorne Ecol. Inst. Tech. Pub. 14.* Boulder, Colo. 250 pp.

TYLER, J.G. 1923. Observations on the habits of the prairie falcon. *Condor* 25:95-97.

U.S.D.I. - B.L.M. 1979. Snake River Birds of Prey Special Research Report to the Secretary of Interior. Boise, Idaho. 142 pp.

WILLIAMS, R.N. 1981. Breeding ecology of prairie falcons at high elevations in central Colorado. M.S. Thesis. Brigham Young Univ. Provo, Utah. 44 pp.

ZAR, J.H. 1984. Biostatistical Analysis. Second Edition. Prentice Hall. Englewood Cliffs, NJ. 736 pp.

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Appendix: Mean aspect of Prairie Falcon eyries and Prairie Falcon nest cliffs.

STATE	MEAN ASPECT[1]	r VALUE	SIGNIFICANCE LEVEL[2]	N	REFERENCE
Eyries					
Wyoming	180°±31°	0.41	$P<0.001$	67	Present study
Colorado	200°±60°	0.44	$P<0.10$	14	Williams (1981)
Oregon	255°	0.18	$P>0.10$	36	Denton (1975)
Utah	226°±34°	0.36	$P<0.01$	49	Porter and White (1973)
Montana	143°±33°	0.34	$P<0.001$	49	Leedy (1972)
Cliffs					
Wyoming	191±23°	0.40	$P<0.001$	71	Present study
Colorado	200°±60°	0.44	$P<0.10$	15	Williams (1981)
Oregon	288°±51°	0.28	$P<0.10$	36	Denton (1975)
New Mexico	353°	0.07	$P>0.10$	21	Platt (1974)
Montana	144°±35°	0.34	$P<0.01$	45	Leedy (1972)

[1]With 95% confidence interval, when calculable.
[2]Rayleigh's test.