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PHYSIOGRAPHIC CHARACTERISTICS OF PEREGRINE FALCON NESTING HABITAT ALONG THE COLORADO RIVER SYSTEM IN UTAH

Brandon L. Grebence^{1,2} and Clayton M. White¹

ABSTRACT.—Portions of the Colorado, Dolores, Green, and San Rafael rivers in Utah were surveyed for the breeding Peregrine Falcon (*Falco peregrinus anatum*) from 1986 to 1988. Eleven physical variables were measured at nest cliffs (N = 22) and nonnest cliffs (N = 22) to discern descriptors of cliff choice and subsequent occupancy by breeding peregrines in unexplored habitat within the Colorado River and its tributaries. Ratio scale measurements were subjected to discriminant function analysis or the Mann-Whitney test to determine significant differences between cliff types. At nest cliffs, Rayleigh's and Kuiper's tests were applied to compass directions to ascertain mean direction and circular uniformity. None of the variables we selected revealed any appreciable descriptive ability, which suggests that certain physical attributes of a nest cliff are of questionable value in forecasting occupancy by breeding peregrines within that particular habitat.

Historical breeding density of the Peregrine Falcon (*Falco peregrinus anatum*) west of the Rocky Mountains was perceived as "extremely low, and this surely is not due to lack of knowledge" (Bond 1946: 107). In the early 1970s an analysis of Utah revealed 40 historical or recent breeding sites, but the majority (80%) were located within the Great Basin. Five of the 8 locations (65%) within the Colorado Plateau were suspected but not verified (Porter and White 1973). The 1975 North American Peregrine Survey suggested the possibility of only 6 additional breeding sites along major drainages of the Colorado Plateau (Fyfe et al. 1976). A survey of Glen Canyon National Recreation Area (GCNRA) in 1983 located 2 additional sites on the lower end of Lake Powell (USFWS report 1983). One year later U.S. Park Service lands occurring within Utah were comprehensively surveyed, and peregrine breeding density within GCNRA was more completely described (Enderson 1984). In 1987 a follow-up survey of GCNRA revealed 5 previously unknown sites (Peregrine Fund Inc., unpublished report 1987). Six additional sites along the Colorado (2), Dolores (1), Green (2), and San Rafael (1) rivers were located during the 1986–1988 breeding seasons (Utah Division of Wildlife Resources, unpublished reports 1986, 1988).

Habitat evaluation near known breeding sites in Arizona revealed an apparent commonality of several traits and led to the forma-

tion of a predictive model for cliff occupancy by breeding adults (Ellis 1982). The habitat within Arizona, however, was very heterogeneous. A characterization of total peregrine breeding habitat in a more uniform habitat than Arizona has been attempted for the Colorado Plateau (Teresa 1989). Our study objective has been to identify within a more homogeneous habitat physiographic variables that reliably predict cliff choice and occupancy in previously unexplored habitat of the Colorado River and its tributaries.

STUDY AREA

The state of Utah is divided into four physiographic provinces: Basin and Range, Rocky Mountain, Colorado Plateau, and Basin and Range–Colorado Plateau Transition (Stokes 1977). The Colorado Plateau (eastern and southern one-third of Utah) has many subdivisions but, for the sake of simplicity, is further subdivided into two sections: the Uinta Basin and Canyonlands (Murphy 1981). The Canyonlands section comprises the southeastern quarter of Utah and is dissected by three major rivers: Colorado, Green, and San Juan. Only the San Juan River remains essentially unsurveyed for the presence of peregrines.

Between 14 and 17 June 1988 one of us (BLG) surveyed the Green River from the mouth of the San Rafael River to Mineral Bottom, and during 9–14 July 1987 from Mineral

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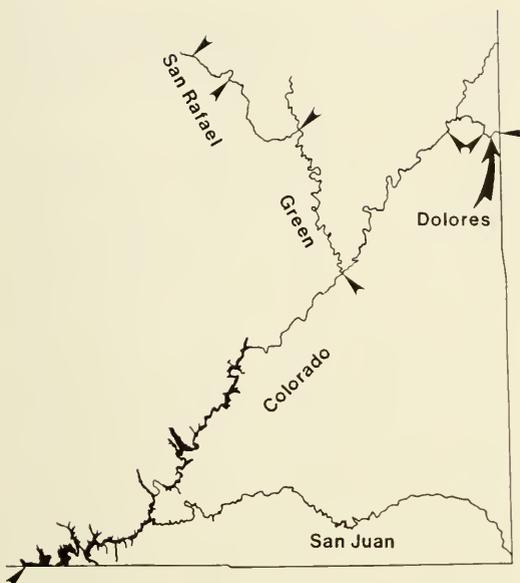


Fig. 1. River sections surveyed (denoted by arrows) on the Colorado, Green, Dolores, and San Rafael rivers for Peregrine Falcons in southeastern Utah.

Bottom to its confluence with the Colorado River (ca 163 km). One of the Green River's main tributaries, the San Rafael River, was surveyed from Buckhorn Wash to Swazy's Leap on 5–6 May 1988 (ca 49 km). Between 18 April and 16 June 1987 the Colorado River was surveyed from the eastern end of Professor Valley (ca 47 km east of Moab, Utah) to Page, Arizona (ca 462 km). The Dolores River (another Colorado River tributary) was surveyed from the Colorado border to the mouth of Fisher Creek on 22–23 April 1986 (ca 9 km; Fig. 1). Each of the aforementioned rivers probably contains nesting peregrines not observed in these surveys.

The majority of the Canyonlands section is classified as part of the Great Basin Desert (Larson 1970), with an annual precipitation of 13–20 cm (U.S. Dept. of Commerce NOAA-EDS 1973). Maximum and minimum recorded temperatures 1 April–30 June 1987 ranged from -3.3 C (1 April) to 40 C (14 June; NOAA Utah Climatological Data 1987).

Fremont cottonwood (*Populus fremontii*), the dominant tree along the Green, Dolores, and Colorado rivers, forms irregularly clustered communities in riparian zones. Thick vegetation typifies this riparian zone, primarily tamarisk (*Tamarix ramosissima*) inter-

persed with narrowleaf willow (*Salix exigua*), black willow (*S. gooddingii*), singleleaf ash (*Fraxinus anomala*), desert olive (*Forestiera pubescens*), Emory seepwillow (*Baccharis emoryi*), Rio Grande seepwillow (*B. salicina*), squawbush (*Rhus trilobata*), arrowweed (*Pulchella sericea*), and common reed (*Phragmites australis*). Floodplain regions along the Colorado and Green rivers have their own distinct community of shrubs, including four-wing saltbush (*Atriplex canescens*), torrey seepweed (*Suaeda torreyana*), greasewood (*Sarcobatus vermiculatus*), rubber rabbitbrush (*Chrysothamnus nauseosus*), viscid rabbitbrush (*C. viscidiflorus*), and skunkbush (*R. aromatica*). Vegetative communities above the cliff walls are dominated by blackbrush (*Coleogyne ramosissima*) and shadscale (*Atriplex confertifolia*). Tamarisk is ubiquitous in GCNRA where shoreline regions have sufficient soil to support vegetative cover. Rocky hillsides are dominated by xerophytic vegetation, predominantly blackbrush and shadscale (Flowers 1959). The diversity of plants promotes a diversity of prey species that may be a critical factor for peregrine numbers.

Persistent flooding of the Dolores River has prevented thick vegetative communities in its riparian areas. Talus slopes above the river and the communities above cliff walls are dominated by Utah juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus edulis*).

The dominant tree along the San Rafael River is also Fremont cottonwood, and the understory communities are predominantly tamarisk, greasewood, and four-wing saltbush. Talus slopes and areas above cliff walls are dominated by pinyon pine and Utah juniper (Foster 1968).

METHODS

A breeding site, or eyrie, is defined as a ledge or pothole in association with a nest scrape. A nest cliff is defined as the rock formation surrounding the eyrie (see Runde and Anderson 1986). Cliff brink is defined as that point where a rope is necessary for further downward travel. Cliff base is defined as that point of the talus slope where climbing skills are necessary for further upward travel.

Adult peregrines were initially located with a spotting scope or binoculars. Once a presumed breeding territory was located, a second visit was undertaken in order to confirm

eyrie occupancy and location. Eyrie locations were plotted on USGS 7.5' or 15' topographic quadrangle maps by positioning a compass at an obvious land feature and recording azimuth to the eyrie. Eight of the nest cliffs were surveyed on land and the remaining 14 from a boat.

Actual eyrie location was determined by observing one adult relieve its mate from incubation. Once the exact eyrie location was ascertained, an azimuth (EYAZI) could be determined. A clinometer (Suunto PM-5/360 PC, Finland) was used to record percentage readings of the cliff brink, eyrie position, boundary between sandstone layers, and cliff base (Mosher et al. 1987, Runde and Anderson 1986). Each cliff section, together with its corresponding percentage reading, was multiplied by the cliff height (CHEIGHT: distance from the cliff brink to the cliff base) to yield estimates of eyrie height (EHEIGHT: distance from the cliff brink to the eyrie), eyrie to base height (EYBASE: distance from the eyrie to the cliff base), and sandstone layer height. Initially, a rangefinder was used in conjunction with the clinometer to determine CHEIGHT. When the calculated CHEIGHT was compared with the estimated CHEIGHT taken from a topographic map, a lack of consistency in rangefinder distances was evident. Apparently, excessive vibrations altered distance calibrations, which then produced erroneous measurements. Subsequently, estimated CHEIGHTs derived from topographic maps were used exclusively to determine EHEIGHT and EYBASE (Table 1).

In Britain, Ratcliffe (1962:25) observed, for peregrines and common raven (*Corvus corax*), that "in the most rugged country each species reaches a maximum breeding density and there is usually a large excess of suitable nesting cliffs." The Canyonlands section of southern Utah contains some of the most rugged terrain in the United States (Murphy 1981). Accordingly, nonnest cliffs (N = 22) were selected arbitrarily along the same river corridors that had nest cliffs, the sole criterion being the presence of at least one obvious ledge or pothole that could function as an eyrie. Identical measurements were taken at nest and nonnest cliffs (Tables 1, 2). Nonnest cliffs were not selected at random because randomly selected sites could not always be

included from a logistical standpoint. Furthermore, random selection could not always include cliff faces that contained ledges or potholes, which would render comparisons with nest cliffs meaningless.

A 5-km distance was used as a radius for each eyrie, based on the work of Enderson and Kirven (1983) and Mearns (1985), for the determination of total elevational gain (TOTGAIN), defined as the maximum elevation minus the minimum elevation found within that circle. Additional map measurements included the shortest distance to water (DWATER) and the corresponding azimuth (AWATER), cliff azimuth (CLAZI), cliff brink elevation (CELEV), and eyrie elevation (EELEV; Table 1). CHEIGHT estimation was determined from eyrie location-azimuth, which also provided CELEV. The cliff base reading on 15' maps was determined from a land-area and slope-indicator template (Reproduction Specialties Inc.).

At nest cliffs, CLAZI, EYAZI, and AWATER were tested for significant mean directions by employing Rayleigh's test (Zar 1984), and for circular uniformity by using Kuiper's test (Mardia 1972). At both nest and nonnest cliffs, EHEIGHT, EYBASE, TOTGAIN, DWATER, and CELEV were subjected to a stepwise discriminant function analysis (DFA) using the SPSS statistical package (Nie et al. 1975) to determine differences between cliff types. CHEIGHT (the sum of EHEIGHT and EYBASE) and EELEV (equivalent to EHEIGHT) were determined to be confounding variables and were excluded from the analysis. The five variables entered into the DFA were well within the recommended sample size of at least three times the number of variables to be measured (Williams and Titus 1988).

Of the three sandstones of the Glen Canyon Group (Navajo-Kayenta-Wingate), the Kayenta Sandstone layer was utilized most frequently for eyrie placement (80%). An attribute of the Kayenta Sandstone layer is erosion into ledgy slopes (Baars 1972), which presumably provides a variety of nest sites from which to choose. Three variables of Kayenta Sandstone cliffs were compared for significant differences by using the Mann-Whitney test (Conover 1980; nest cliffs N = 12 and nonnest cliffs N = 11). These variables were Kayenta

TABLE 1. Characteristics of nest cliffs.

Site no.	Height (m)			Elevation (m)			Azimuth			Distance to water ^k (m)
	Cliff ^a	Eyrie ^b to brink	Eyrie ^c to base	Cliff ^d	Eyrie ^e	Total ^f gain	Cliff ^g	Eyrie ^h	To water ^j	
1	110	15	95	1341	1326	395	103	107	140	168
2	305	45	260	1524	1479	529	163	201	188	411
3	98	27	71	1780	1753	638	204	183	208	2478
4	122	19	103	1536	1517	418	131	90	134	518
5	79	5	74	1207	1202	444	108	125	124	74
6	274	17	257	1402	1385	303	14	55	48	257
7	183	54	129	1402	1348	340	214	217	223	183
8	98	28	70	1500	1472	566	110	68	90	808
9	122	45	77	1402	1357	354	60	51	48	91
10	140	45	95	1268	1223	517	97	25	112	152
11	134	28	106	1841	1813	595	170	153	135	2981
12	146	31	115	1487	1456	436	46	26	43	305
13	110	3	107	1329	1326	445	42	34	49	107
14	158	101	57	1621	1520	654	60	43	55	290
15	165	70	95	1292	1222	648	20	350	20	94
16	116	10	106	1640	1630	538	135	125	132	274
17	134	44	90	1353	1309	507	307	241	306	107
18	122	13	109	1402	1389	515	95	83	72	229
19	116	74	42	1244	1170	275	83	65	90	42
20	104	16	88	1232	1216	401	78	69	90	88
21	97	21	76	1865	1844	531	222	190	207	457
22	171	49	122	1609	1560	710	118	105	115	335
\bar{x}	141	35	107	1467	1433	489	101	90	103	475
SD	54	24	53	189	191	116	67	71	66	738

^aCHEIGHT, ^bEHEIGHT, ^cEYBASE, ^dCELEV, ^eELEV, ^fTOTGAIN, ^gCLAZI, ^hEYAZI, ^jAWATER, ^kDWATER (as referenced in text)

TABLE 2. Characteristics of nonnest cliffs.

Site no.	Height (m)			Elevation (m)			Azimuth			Distance to water ^k (m)
	Cliff ^a	Eyrie ^b to brink	Eyrie ^c to base	Cliff ^d	Eyrie ^e	Total ^f gain	Cliff ^g	Eyrie ^h	To water ^j	
23	146	35	111	1731	1696	829	293	246	307	442
24	61	11	50	1768	1757	638	62	32	204	3164
25	49	5	44	1585	1580	600	111	119	44	2012
26	61	6	55	1463	1457	611	135	107	115	351
27	146	6	140	1426	1420	390	64	63	64	76
28	110	14	96	1877	1863	594	205	158	222	640
29	122	9	113	1829	1820	589	203	181	157	1975
30	85	11	74	1853	1842	582	156	125	34	792
31	43	18	25	1323	1305	394	223	257	180	122
32	195	49	146	1780	1731	715	88	101	96	671
33	110	24	86	1451	1427	654	253	270	274	305
34	293	6	287	1634	1628	799	135	129	119	335
35	55	11	44	1183	1172	233	7	1	10	54
36	73	9	64	1280	1271	427	95	84	103	107
37	158	26	132	1560	1534	398	110	105	110	168
38	85	8	77	1244	1236	397	86	82	86	91
39	128	28	100	1256	1228	329	345	330	311	101
40	79	31	48	1207	1176	648	277	272	295	61
41	219	15	204	1499	1484	471	30	63	30	244
42	195	33	162	1402	1369	460	82	76	82	229
43	226	9	217	1353	1344	374	65	70	72	244
44	122	47	75	1402	1355	340	80	97	106	259
\bar{x}	126	19	107	1505	1486	521	97	94	85	566
SD	65	13	64	218	219	156	85	79	85	776

^aCHEIGHT, ^bEHEIGHT, ^cEYBASE, ^dCELEV, ^eELEV, ^fTOTGAIN, ^gCLAZI, ^hEYAZI, ^jAWATER, ^kDWATER (as referenced in text).

TABLE 3. Characteristics of Kayenta-Wingate Sandstone nest cliffs.

Site no.	Height (m)					Eyrie (as a % of Kayenta)
	Cliff	Wingate	%	Kayenta	%	
3	98	62	63	36	37	75
4	122	90	74	32	26	60
5	79	47	60	32	40	18
8	98	70	71	28	29	100
9	122	77	63	45	37	100
11	134	106	79	28	21	100
12	146	90	62	56	38	56
13	110	107	98	3	2	100
16	116	97	83	19	17	50
17	134	90	67	44	33	100
18	122	83	68	39	32	33
21	97	67	69	30	31	70
\bar{x}	115	82	71	33	29	72
SD	18	17	10	13	10	28

TABLE 4. Characteristics of Kayenta-Wingate Sandstone nonnest cliffs.

Site no.	Height (m)					Eyrie (as a % of Kayenta)
	Cliff	Wingate	%	Kayenta	%	
23	146	101	69	45	31	78
24	61	47	77	14	23	83
26	61	50	82	11	18	52
27	146	117	80	29	20	22
28	110	76	70	34	30	43
29	122	111	91	11	9	80
30	85	74	87	11	13	100
31	43	25	58	18	42	100
36	73	61	83	12	17	71
37	158	99	62	59	38	44
38	85	56	66	29	34	27
\bar{x}	99	74	75	25	25	64
SD	38	28	10	15	10	26

Sandstone height (KSH), EHEIGHT expressed as a percentage of the KSH, and the KSH expressed as a percentage of CHEIGHT (Tables 3, 4).

RESULTS

Traditional utilization of nest cliffs is a well-known aspect of peregrine breeding biology (Hickey 1942, Ferguson-Lees 1951, Cade 1960, Ratcliffe 1962, Newton 1976, White and Cade 1971, Mearns and Newton 1984). The persistence of the phenomenon has been hypothesized to involve prey specialization (Cade 1960), territorial familiarity and con-

comitant reproductive success (Newton 1979), the reduction of competition and stability of populations (White and Cade 1971), and insolation considerations (Cade 1960, Porter and White 1973, Kuyt 1980, Pruett-Jones et al. 1981). This habituation to specific nest cliffs was used to census and relocate 10 eyries discovered prior to 1986 (Enderson 1984).

Spacing regularity in unbroken habitat is an additional feature that describes peregrine breeding distribution (Beebe 1960, Cade 1960, Ratcliffe 1962, Newton 1976). A consistent minimum distance presumably is related to population stability (Ratcliffe 1962), the regulation of breeding density in accord with available resources (Newton et al. 1977), and the reduction of intraspecific conflicts during breeding or hunting (Newton 1979). Six additional eyries were discovered in 1986–1987 by assuming this regular spacing between eyries.

All four rivers contain sections characterized by a nearly continuous line of cliffs on either side, which face virtually every azimuth of the compass. Of the nest cliffs surveyed, 12 were Wingate and Kayenta sandstones and 3 were Navajo Sandstone. On lower Lake Powell, from Wahweap Marina to Mountain Sheep Canyon, 3 nest cliffs were Morrison Formation sandstones and 1 was Entrada Sandstone. Remaining nest cliffs ($N = 3$), located from Hite Marina to the mouth of the Green River, were Cedar Mesa Sandstone. Eleven of the nonnest cliffs were Wingate and Kayenta sandstones, 3 were Navajo Sandstone, 4 were Cedar Mesa Sandstone, and 4 were of sandstones of the Morrison Formation (Hintze 1973).

Univariate Analysis

Means and standard deviations of the three measured variables of Kayenta-Wingate sandstone cliffs are shown in Tables 3 and 4. No significant differences were revealed between nest cliffs and nonnest cliffs for the KSH ($p > .50$, Mann-Whitney), KSH expressed as a percentage of the CHEIGHT ($p > .15$, Mann-Whitney), and EHEIGHT expressed as a percentage of KSH ($p > .35$, Mann-Whitney).

For nest cliffs, CLAZI, EYAZI, and AWATER revealed significant mean directions (101° , 90° , and 103° ; $p < .005$, $p < .01$, and $p < .005$, respectively; Rayleigh's test; Tables

TABLE 5. Classification results of discriminant analysis of physiographic characteristics of Peregrine Falcon nesting habitat along the Colorado River.

Actual group	N	Predicted group membership	
		Nest	Nonnest
nest	22	10 45.5%	12 54.5%
nonnest	22	5 22.7%	17 77.3%
[61.4% of grouped cases were correctly classified]			

TABLE 6. Summary of stepwise discriminant analysis including the standardized canonical discriminant function coefficients for two of the five variables measured at nest cliffs and nonnest cliffs.

Variable	Step	Wilks' Lambda	Significance level	Standardized Discriminant Function Coefficients
EHEIGHT	1	.86	.01	.95
TOTGAIN	2	.84	.02	-.42

1, 2), and in each case azimuths were not uniform about the compass ($p < .05$, $p < .05$, and $p < .005$, respectively; Kuiper's test).

Discriminant Analysis and Classification

The key objective of the DFA is to predict group membership given a particular linear measurement (Williams 1983). The relative strength of this predictive ability is displayed on the classification table (Table 5). A cursory scan reveals the lack of a satisfactory separation between nest cliffs and nonnest cliffs. This effect may be the result of a violation of equality of the variance-covariance matrices, which distorts predictive ability, or the result of the arbitrary selection of nonnest cliffs. A test for the equality of two population correlation coefficients indicated that correlation coefficients of the two cliff types were equal. The implication of this result is a difference in variances. The variability in TOTGAIN and EHEIGHT is shown in Figure 2.

Two of the five variables, EHEIGHT and TOTGAIN, revealed significant group separation (Table 6). However, since the variance-covariance matrices were significantly different from each other ($p = .03$), a key assumption of discriminant analysis was violated. This may have compromised the ability of the DFA to effectively separate nest cliffs from nonnest cliffs.

DISCUSSION

While the relative importance of cliff height in determining breeding occupancy has been contested, Hickey (1942) maintained that, for the peregrine population east of the Rockies, extremely high cliffs represented an "ecological magnet" and were the single most important factor for occupancy. This concept was disputed as an "oversimplification when one tries to apply it in the west" (Bond 1946:107). Cade (1960) argued that the concept detracted from other factors that were better determinants. High cliffs were not considered requisite for nesting (Beebe 1960), nor were they preferred or related to nesting success (Herbert and Herbert 1965). Cliff height was discounted as unimportant for Colorado eyries, but total elevational gain was deemed to be significant (Enderson and Craig 1979). Ratchiff (1962) countered that in Great Britain cliff height was an attractant and hypothesized that an increased choice of nest sites and security from intervention were responsible. He further suggested that total elevational gain as well as lateral extent were more important than the verticality of the nest cliff itself.

Figure 2 indicates that a wide range of topographical relief occurred at nest cliffs; it also shows that outlier cliffs had eyries positioned lower on the cliff face. This wide range reflects contrasts between the relationship of geological formations from location to location. TOTGAIN may be related to the stoop mode of hunting, where the peregrine "usually needs a considerable advantage in height over its intended prey" (Ratchiff 1980:153). EHEIGHT has a rather narrow range with three exceptions (see Fig. 2). Again this effect is the result of geology. The majority (82%) of the nest cliffs had a sandstone layer (particularly Kayenta Sandstone), with numerous ledges less than 50 m from the brink of the cliff (Figs. 2, 3). It is possible that the arbitrary manner in which potential ledges were designated on noneyrie cliffs resulted in the weak separation of cliff types in the DFA.

Availability of a bathing site was considered requisite for cliff occupancy (Bond 1946, Cade 1960). Rivers were considered essential components of peregrine habitat in Alaska because they provided the erosional agent for formation of cliffs and they supplied the riparian habitat necessary for some of the preferred

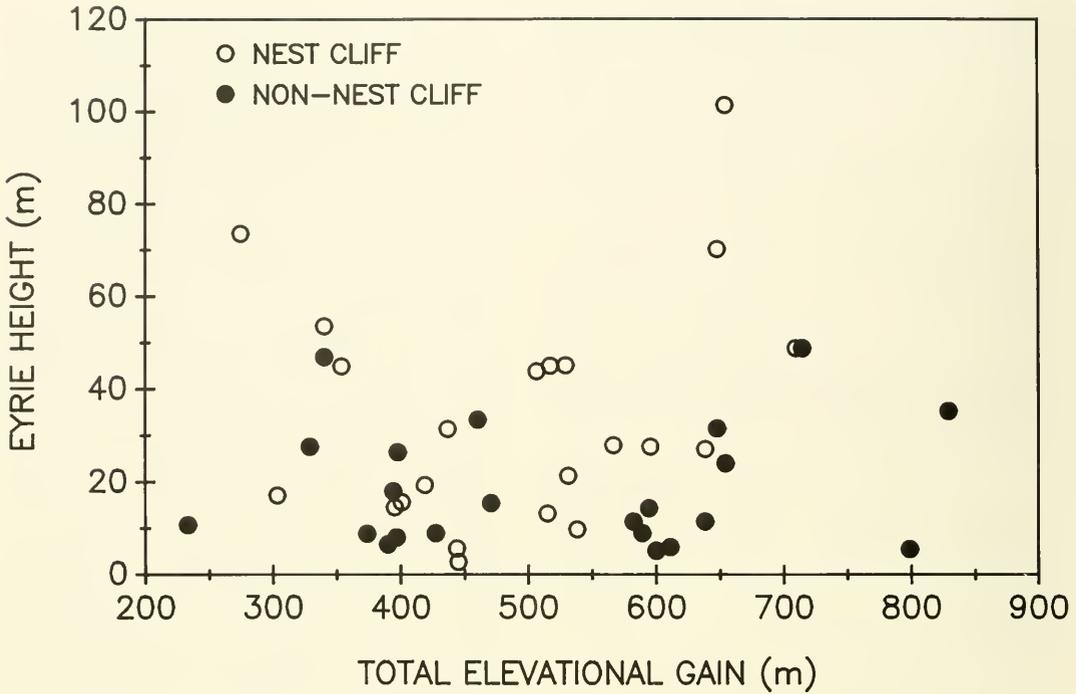


Fig. 2. Total elevational gain (TOTGAIN; X-axis) plotted against the distance from the cliff brink to the eyrie (EHEIGHT; Y-axis). The scales for both axes are in meters. Open circles represent nest cliffs, and closed circles represent nonnest cliffs. Those values separated from the main cluster of circles represent outliers.

prey (White and Cade 1971). Proximity to a perennial source of water was considered an attribute of most peregrine eyries (Porter and White 1973, Enderson and Craig 1979, Ellis 1984, White and Porter 1986), but the alleged property was not ubiquitous as suggested for Oregon (Gabrielson and Jewett 1940).

In our study, DWATER was biased in favor of nest cliffs that were confined to a river corridor, and the DFA suggests that this variable was not a significant predictor of cliff occupancy. Perhaps as additional nest cliffs within the Colorado Plateau are discovered, especially in side canyons of major river corridors, in Capitol Reef National Park, and in the San Rafael Reef, this variable will attain more predictive power.

In Alaska an avoidance of north-facing cliffs was noted by Cade (1960). He hypothesized that this was an adaptive response to summer storms that approached from the north. Canadian nest sites had a predominantly southern or western exposure, and it was suggested that early snowmelt freed those cliffs for breeding use (Kuyt 1980). Porter and White

(1973) found that most eyries in Utah were on east- or north-facing cliffs (data were heavily weighted by the large proportion of eyries in the northern half of Utah). They suggested this represented a directional preference for the avoidance of insolation. In Australia most nest sites faced north or west, but directional variations were not significantly different from random (Pruett-Jones et al. 1981). However, when cliffs were grouped as north facing or south facing, a significant preference ($p < .01$) for north-facing cliffs emerged, and exposure was significantly related to fledging success ($p < .05$; Pruet-Jones et al. 1981). Climatic extremes were therefore postulated to cause the directional selection of the eyrie (Porter and White 1973, Pruet-Jones et al. 1981).

In Great Britain suitable nest cliffs faced all directions, and no directional preferences were detected (Ratcliffe 1962). Similarly, Colorado eyries revealed no consistent directional pattern other than an avoidance of the southern quadrant ($135\text{--}225^\circ$; Enderson and Craig 1979). Ellis (1984) found that Arizona



Fig. 3. View of cliff containing peregrine eyrie showing interface of Kayenta-Wingate Sandstone (arrow). The region of interface was also the region of eyrie placement.

nest cliffs faced predominantly north and west, with very few facing southward. However, when Ellis combined the Utah data (Porter and White 1973) with Arizona data, his resulting data indicated clearly that nest cliffs could face any direction. Ellis thus concluded that directional preference of cliffs could not be used as the sole criterion for occupancy even in a desert environment.

In our study nest cliffs had significant mean directions for both cliff and eyrie azimuths, and both were not uniformly distributed about the compass (Fig. 4). This implies a strong preference for the eastern quadrant ($45\text{--}135^\circ$). However, our results are consistent with Ellis's contention that cliff orientation (and in this study eyrie orientation as well) cannot be used by itself as a predictor of occupancy.

Based on observations of Golden Eagle (*Aquila chrysaetos*) mortality, Nelson (1969) hypothesized that peregrines were particularly vulnerable to insolation extremes because of their habit of late seasonal nesting. Evidence of heat stress in both adult and

nestling peregrines was noted at a south-facing eyrie in Alaska (Enderson et al. 1972). Golden Eagle eyries in Alaska and Utah revealed statistically significant directional preferences ($p = .01$), south-southeast in the arctic and north-northwest in the Utah desert. These results implied an avoidance of cold and heat, respectively (Mosher and White 1976). Ellis (1984) suggested that composition and arrangement of a peregrine eyrie, rather than directional orientation, were dictated by total insolation. Williams (1984) demonstrated the existence of an eyrie microclimate for the Prairie Falcon (*Falco mexicanus*) at an east-facing eyrie (95°) that presumably protected nestlings from ambient temperature extremes. Microclimate requirements should be progressively more exacting as the azimuth changed from east to south.

In our study 5 of 22 (23%) nest cliffs and their respective eyries were situated in the southern quadrant (Fig. 4). All 5 eyries were deeply recessed ledges, and 4 of 5 had a large rock on the brink of the eyrie, which provided additional shade (Fig. 5). The structure of

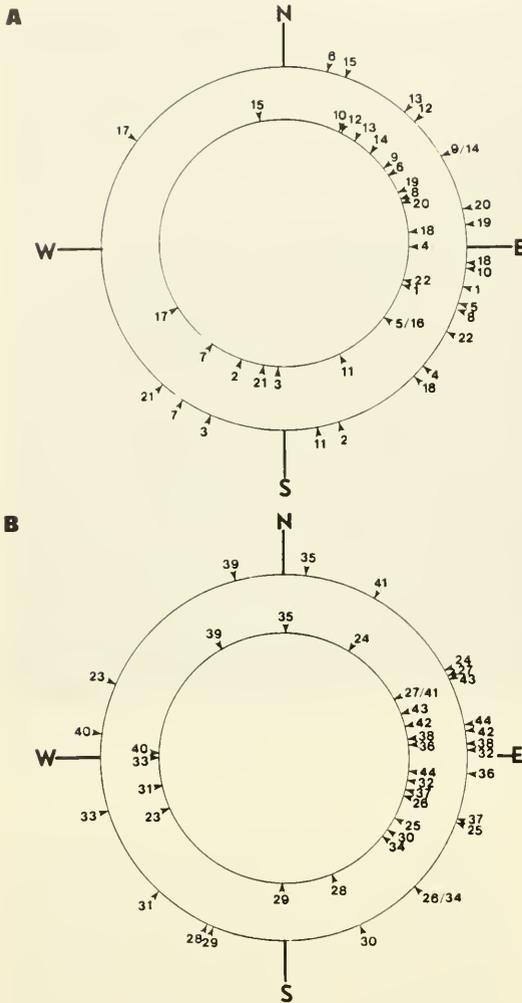


Fig. 4. Cliff and eyrie azimuths of nest cliffs (A) and nonnest cliffs (B) along the Colorado River and its tributaries 1986-88. Arrows on inner circles (N = 22) indicate eyrie azimuths, and arrows on outer circles indicate cliff azimuths (N = 22). Numerical values correspond to specific sites listed in Tables 1 and 2.

these south-facing eyries probably provided a microclimate that ameliorated total insolation and maintained a critical level of atmospheric humidity essential for successful hatching (Ratcliffe 1980), as 11 young fledged from these 5 sites (2.2 young/occupied site, unpublished data). These reproductive values compare favorably with normal fledging rates (Ratcliffe 1980). Fledging success at southern quadrant eyries in a desert environment implies that a similar microenvironment is real-

ized within deeply recessed ledges such as those produced by northern and eastern cliff azimuths.

Additionally, desert environments frequently have considerable wind. This is especially true in canyons. We were unable to measure the effect of wind, but it may also ameliorate temperatures and allow some otherwise seemingly unsuitable cliffs to be used. Also, rain, especially when driven by prevailing winds, may influence the use of certain cliff facings or cliff and eyrie variables as shown in Australia (Olsen 1988). But, likewise, we gathered no data on this in our study.

Our results suggest that peregrines select eyries that ameliorate solar radiation in one of two ways: by selecting a cliff or eyrie with a northern or eastern azimuth, or by selecting an eyrie that nullifies insolation (e.g., deeply recessed ledges). The overall results of our study are in accord with the contention of Cade (1960:238) that "there is no very convincing evidence of so close a correlation between the physical characteristics of cliffs and the history of their occupancy by peregrines."

Finally, we conclude with three salient observations of the "red rock country" of the southern third of Utah: (1) Nest cliffs composed of all three sandstones of the Glen Canyon Group will usually have eyries situated in the Kayenta Sandstone. (2) Spacing regularity appears to be a useful attribute for locating additional nesting peregrines. So far, this spacing seems to be on the order of 6-14 km between sites. (3) Cliffs should not be excluded from a breeding survey because of a preconceived notion concerning azimuth.

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Fig. 5. Close up of a south-facing eyrie. Note the deep recess containing the eyrie (arrow) and large rock characteristic of eyrie ledges on south-facing cliffs.

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