THE PEREGRINE FALCON IN UTAH, EMPHASIZING ECOLOGY AND COMPETITION WITH THE PRAIRIE FALCON

by

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ABSTRACT

This study was undertaken to record the known history of the Peregrine Falcon (*Falco peregrinus*) in Utah as we have been able to construct it from both the literature and from our original research that extends over about a 30-year period in the state. The present total population of the peregrine in Utah is possibly only 10 percent of what it has been in historic times. In an effort to find explanations for the decline, we have explored hypotheses of climatic changes, impact of pesticides, disease, and human disturbances. We conclude that pesticide contamination and climatic changes may have been the major reasons for their decline in Utah.

A general background of the geographical and ecological distribution of the species in Utah is provided as are also details of its nesting behavior from some Wasatch Mountain eyries. Our data suggest that its nesting density along the Wasatch Mountains was about the same order of magnitude as nesting densities in other regions of North America that are generally considered more favorable to the peregrine.

We have considered some of the environmental factors that may limit the species in Utah and especially its relationship with a congener, the Prairie Falcon (*Falco mexicanus*). We conclude that the peregrine may live jointly with the Prairie Falcon with a minimum of intraspecific competition. We present evidence which suggests that the peregrine has been in Utah since the late Pleistocene and that it has had a long history of sympatric existence with the Prairie Falcon.

INTRODUCTION

Breeding populations of the Peregrine Falcon (*Falco peregrinus*) have declined sharply over much of its historic range in North America and Europe during the last two decades. Although this decline has been well documented for many areas (Hickey, 1969), little has been published on the status, past or present, of the species in the Great Basin, especially as a breeding bird in Utah, an area encompassing 84,916 sq miles (219,932 km^2).

We wish, therefore, to place on record our observations of the peregrine in Utah from data collected over the past 30 years. In presenting these data, it is our purpose to: (1) describe the ecological distribution of the species in the state, (2) delineate the ecological factors which may have limited its distribution and breeding success there, (3) describe its food and habitat niches, (4) discuss its competition with related species, especially the Prairie Falcon (*Falco mexicanus*), and (5) compare its present levels of population with those formerly known, since peregrines in Utah have not been immune to the decline that afflicted its populations elsewhere. Because the known active eyries of this species in the state are now only about 10 percent of those known to have been present earlier in the century, another of our objectives is to (6) discuss and evaluate the factors which may have led to the near extirpation of this species in the state.

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GEOGRAPHIC DISTRIBUTION

Historic Records

The peregrine was not mentioned in the ornithological literature for Utah until 1871, when it was reported by Allen (1872) to prey on waterfowl about the marshes of the Great Salt Lake near Ogden. He found it to be common there in September. The next to mention the presence of the species was Henshaw (1874), who with Yarrow, collected 600 specimens of birds representing 165 species on a trip from Salt Lake City to St. George between July and December 1872. The peregrine was considered by Henshaw to be a rather common resident in Utah and to nest in the state. Henshaw's later account (1875) mentions only an observation of this species by Allen (1872) in the vicinity of Ogden, thus opening to question the source of his data supporting the status of the species in Utah.

The lack of observations by Allen (1872) of the Prairie Falcon in the Great Salt Lake Valley and the complete absence of this species in his account of the birds encountered in Kansas, Colorado, Wyoming, and Utah is difficult to understand, since the peregrine apparently was noted at all but two of Allen's collecting localities and a specimen (young bird) was obtained by him (ibid.) at Fairplay (South Park), Colorado Territory. Did Allen (ibid.) overlook the Prairie Falcon or did he consider all large falcons to be peregrines? Nevertheless, his observations of the peregrine along the Great Salt Lake marshes probably were accurate, as the species has been seen there many times since then. Although Ridgway (1874, 1877) found the Prairie Falcon to be common in the rocky canyons of the Wasatch Mountains and a rare breeder along cliffs of canyons and valleys in Salt Lake City and neighborhood in 1869, he apparently made no observations of the peregrine in Utah. Several earlier naturalists and explorers (Fremont, 1845; Stansbury, 1852; Baird, 1852; and Remy and Brenchley, 1861) also failed to mention the presence of the peregrine in Utah.

Specimen Records

Specimens from both the arctic tundra population (*F. p. tundrius*) and the more southern population (*F. p. anatum*) have been taken in Utah during the winter months. A specimen of the *tundrius* race, identified by C. M. White (CMW), was found shot and wounded by R. Vern Bullough on 15 December 1956, near Farmington Bay, Davis County. (For a discussion of peregrine systematics, see White, 1968b.)

A male specimen of unknown racial affinity was collected by Wolfe (1928) near St. George, Washington County, on 5 February 1926. John Hutchings (Bee and Hutchings, 1942) collected a specimen of *anatum* (*sensu lato;* western subgroup) (CMW) near Pelican Point, Lake Mountains, Utah County (date not given, Woodbury, Cottam and Sugden, unpubl. ms, indicate specimen was taken alive, 2 August 1935). Five specimens (Twomey, 1942)—a male, molting into adult plumage; an adult female, collection date not given; and three males, collected on 23 April and 5 and 23 August in 1935 at the Ashley Creek marshes, Uintah County—were assigned to the race *anatum* (*sensu lato;* western subgroup) (CMW).

Woodbury et al. (unpubl. ms) record the following additional specimens by county: **Box Elder,** at Bear River marshes, specimens taken 1 July and 6 September 1914; 14 September 1915; 28 July and 28 September 1916 (U.S. Biol. Surv.); 18 August and 7 September 1927 (Phil. Acad. Sci.); all *anatum* (*sensu lato;* western subgroup) (CMW). **Davis,** Jordan Fur Farm, W of Bountiful, 5 January 1939 (Univ. Utah Coll.; UU) *anatum* (*sensu lato*). **Salt Lake,** near Salt Lake City, 4 September 1947 (UU). **Iron,** near Cedar City, 12 May 1936 (Chicago Field Mus.; LBB), *anatum* (*sensu lato;* western subgroup) (CMW). **Uintah,** Ashley Creek marshes, a young male in 1937 (Carnegie Mus.). **Washington,** Zion Canyon (Zion National Park), 16 July 1939 (Zion Park Museum) *anatum* (*sensu lato;* western subgroup) (CMW).

Additional specimens of *F. p. anatum* (*sensu lato;* western subgroup) have been examined by C. M. White for Emery County, two specimens, July; and Salt Lake County, two specimens, January and November.

Nesting Records

Historically, the peregrine is known to have nested in 13 counties of Utah and is suspected of nesting in at least three others. Figure 1 shows the pattern of known and suspected breeding distribution in Utah, and Table 1 gives their known histories in the state.

The first recorded eyrie for the state was an observation by Johnson (1899), who in May 1898, found three young peregrines in a shallow cave under an overhanging rock of an 80-foot (24 m) cliff [Land Rock] in Lake Mountains, west of Utah Lake, Utah County, and five eggs

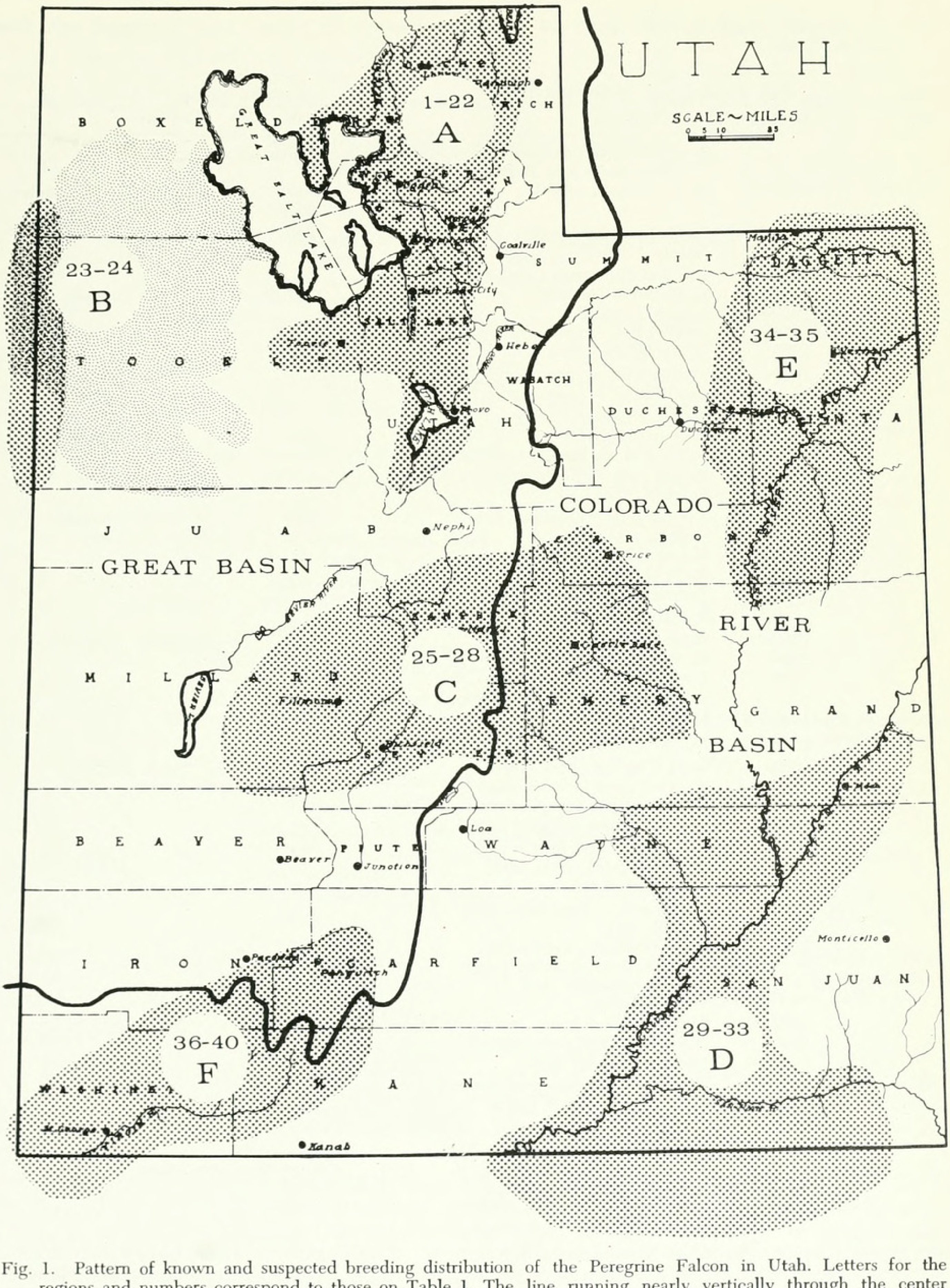

Fig. 1. Pattern of known and suspected breeding distribution of the Peregrine Falcon in Utah. Letters for the regions and numbers correspond to those on Table 1. The line running nearly vertically through the center of the state separates the Great Basin from the Colorado River Basin. The west face of the Wasatch Mountains bisects area A and is encompassed within the northern and southern boundary of the area. Lightly stippled area between regions A and B delimits the Great Salt Lake Desert, although there are also other areas of salt flats at the southwest edge of the Great Salt Lake that are not classified within the confines of the desert.

Table 1. Peregrine eyries in Utah. Eyrie site numbers and letters for regional areas correspond with those given in Figure 1.

Site No.	First Located and Subsequent History: Date	Observer	Last Known to be Active: Date	Observer
		A—Great Basin Region—Surrounding Utah and Great Salt lakes, and North Central Utah		
1	1898	H. C. Johnson (1899)	Early 1900s	H. C. Johnson (field notes of R. G. Bee)
2[1]	1940	R. G. Bee (field notes)	1940	R. G. Bee (field notes)
	1939-42	Nelson (1969)°		Nelson (1969)
3	1935	Bee and Hutchings (1942)		
4	*ca.* 1926-27	L. R. Wolfe (in letter)	1957-58	C. M. White (unpubl. data)
	1939-42	Nelson (1969)°		
	1954	Porter et al. (unpubl. ms)		
	1956	C. M. White		
5	1940s	Morlan Nelson (pers. comm., 1971)		
		Boyd Shaeffer (pers. comm.)		
6	1939-42	Nelson (1969)°		
7	1939-42	Nelson (1969)°	1953	R. J. Erwin (unpubl. data)
	1943	R. D. & R. L. Porter		
		R. J. Erwin, J. F. Poorman (unpubl. data)		
8	*ca.* 1900-20?	Treganza (in Woodbury et al., unpubl. ms)	1969	C. M. White (unpubl. data), single bird
	1939-42	Nelson (1969)°		
	1943	R. D. Porter & R. J. Erwin (unpubl. data)		
9	1939	Morlan Nelson (pers. comm., 1971)		
10	1939-42	Nelson (1969)°	1956	C. M. White (unpubl. data)
	1950	C. Wilson (pers. comm.)		
	1955	Lorin Carsey (pers. comm.), one young female taken for falconry		
11	1939-42	Nelson (1969)°		
12	1939-42	Nelson (1969)°		
13	1940s	Boyd Shaeffer (pers. comm.) reported eyrie to have been found and photographed in the 1930's by a different party	1952	R. J. Erwin (unpubl. data)
	1951	R. D. Porter and Jack Hagan (unpubl. data), birds seen, eyrie not located		
14	*ca.* 1900-20	Treganza (in Woodbury et al., unpubl. ms)		
	1926-27	L. R. Wolfe (in field notes of R. G. Bee), seen carrying food toward cliffs, and Wolfe (1928)		
	1939-42	Morlan Nelson (pers. comm., 1971)		
	1940s	Boyd Shaeffer (pers. comm.), took young from eyrie		
15	1930	Dr. Harold Austin (pers. comm.)		
16	1943	R. D. & R. L. Porter, and R. J. Erwin (unpubl. data)		
	1940s	Boyd Shaeffer (pers. comm.)		
17	1930s	Clyde Ward (pers. comm.)	1968?	Clyde Ward
	1940s	Boyd Shaeffer (pers. comm.)		
	1950s	C. M. White (unpubl. data)		
	1967	Del Diamond (pers. comm.)		
18	1930s	Clyde Ward (pers. comm.)	1954	Clyde Ward
	1939-46?	Morlan Nelson (pers. comm.)	1969	H. Austin and L. Wakefield one adult seen.
19	1930-32	Clyde Ward (pers. comm.)	1930-32	Clyde Ward (pers. comm.)
20	1946-?	Boyd Shaeffer (pers. comm.) Marcus Nelson?		

Table 1 (Continued)

21 (SNV)[2]	*ca.* 1926-27	L. R. Wolfe (in field notes of R. G. Bee)		
22 (SNV)	1939-42	Morlan Nelson (pers. comm., 1971)	1970	C. M. White (unpubl. data)
		B—Great Basin Region—Great Salt Lake Desert		
23[3]	1942	H. Webster (letter, 1961)	1959-60	C. M. White and Gary D. Lloyd (unpubl. data)
24	1942	H. Webster (letter, 1961)		
		C—Central Utah, eastern edge Great Basin, western edge Colorado River Basin (Plateau)		
25	*ca.* 1939	Gunther and Nelson (in Woodbury et al., unpubl. ms.)		
26	1969	C. M. White (unpubl. data)	1969	C. M. White (unpubl. data)
27 (SNV)	1960	G. G. Musser, A. D. Stock, and C. M. White (unpubl. data)		
28	1961	White and Lloyd (1962)	1964	C. M. White and G. D. Lloyd (unpubl. data)
		D—Colorado Plateau and Navajo Country		
29 (SNV)	1916 & 1936	Woodbury and Russell (1945)	1961	C. M. White and G. D. Lloyd (unpubl. data), pair seen in area
30 (SNV)	1958 1959	R. J. Erwin (unpubl. data) R. D. Porter (unpubl. data)	1962	G. D. Lloyd (unpubl. data), adult in general area
31 (SNV)	1953	Behle (1960)		
32	1958	G. L. Richards (pers. comm.), saw fledged young		
33 (SNV)	1958-59	C. M. White (pers. comm. from M. Hopkins, unpubl. data)		
		E—Uinta Basin and Upper Colorado River Basin		
34	1937	Twomey (1942)	1961	G. L. Richards (pers. comm.), at nearby locality
35 (SNV)	1935-? 1965-66	Twomey (1942) E. Peck, W. Pingree, and J. Gaskill (pers. comm.)		
		F—Southwestern Utah, edge Great Basin; and Virgin River Valley		
36 (SNV)	1961	C. M. White and G. Worthen (unpubl. data)	1961	C. M. White (unpubl. data)
37	1936	W. S. Long (breeding female collected)	1962	C. M. White and G. D. Lloyd (unpubl. data), an adult in area
38	1939	Grater (1947)	1964 1966	Wauer and Carter (1965) C. M. White (unpubl. data), lone adult seen
39 (SNV)	1963	Wauer and Carter (1965)		
40 (SNV)	*ca.* 1926	Wolfe (1928)		

[1]May be an alternate site for number 1; located only 2 or 3 miles (3.2 or 4.8 km) from site number 1, but nearly 40 years later.

[2]SNV, (suspected, but not verified) adults were observed at these localities, but eyrie sites not actually located; although adult birds have been seen one or more times, in the authors' opinions, the sites need further verification. The validity of these sites is probable.

[3]The eyrie proper is about 0.5 mile (0.8 km) into Nevada.

•These sites are the ones referred to by Nelson (1969); their locations were communicated to us in a letter from Nelson dated 25 April 1969.

on the same ledge on 30 March 1899 (Figs. 1-5; Table 1, site 1). While circling Utah Lake, Johnson (ibid) noted Long-billed Curlew (*Numenius americanus*), snipes (*Capella gallinago*), bitterns (*Botaurus lentiginosus*), and a goodly number of ducks of various species which probably served as a food supply for the peregrines.

Bee and Hutchings (1942) report finding a nest containing four fresh eggs on a ledge overlooking Utah Lake, (5 miles south of the Land Rock site) near Pelican Point in the Lake Mountains, 20 May 1935 (Fig. 1, Table 1, site 3). They collected the adults to verify identification. Local residents report that peregrines had been observed nesting there for many years (ibid.). A visit to the sites on 22 April 1950 by R. D. Porter and R. J. Erwin revealed no indications of recent occupancy. In recent years lime mining

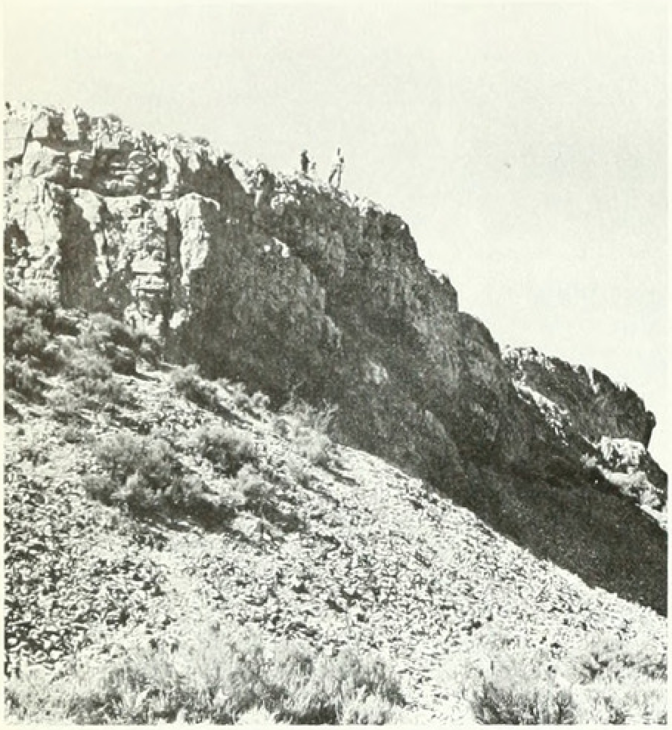

Fig. 2. Land Rock, west side of Utah Lake; location of first known peregrine eyrie site in Utah. It is a marginal site, which in some recent years has been occupied by Prairie Falcons. Note scrubby nature of vegetation in foreground. Photo by Kim Despain, 1971.

operations have destroyed the Pelican Point site (Fig. 6) and Prairie Falcons have occasionally occupied the Land Rock site.

Nelson (1969) located 9 or 10 eyries (*in letter,* 25 April 1969, Nelson gave 9 eyrie locations) in the area surrounding the Utah and Great Salt lakes during the period 1939–1942. This area included parts of Box Elder, Weber, Davis, Salt Lake, Utah, and Tooele counties. Treganza (*in letter,* 5 January 1930; Woodbury et al., unpubl. ms) found the species breeding on the cliffs fronting the lake from Brigham to Ogden [at least four eyries overlooked the Bear River Marshes in the 18 miles from Ogden to Brigham City (Woodbury, pers. comm., *in* White, 1969b)]. Although he located nests, he was unable to negotiate the cliffs; one was over 1,000 feet (305 m) high (Fig. 7). Females were collected off the nests, but precise nesting data were not obtained.

Gunther and Nelson (Woodbury et al., unpubl. ms) noted the species nesting at a site in the Great Basin Desert of west central Utah during the nesting season (year not given). Gunther (Woodbury et al., unpubl. ms) saw the species at a large reservoir in Wasatch County in the summer of 1938.

Fig. 3. Utah Lake and adjacent habitat as presently seen from atop the Land Rock eyrie site; marshes formerly were more extensive than today and came closer to the eyrie. Photo by Kim Despain, 1971.

Fig. 4. A view of Land Rock eyrie showing nature of terrain and vegetation. Photo by Kim Despain, 1971.

Grater (1947) recorded peregrines at Angel's Landing in Zion Canyon, Washington County, from March to August 1939, where adults frequently were seen carrying food to a high ledge on the face of the peak. On 16 July 1939 (the more precise dates from Woodbury et al., unpubl. ms) a young female, only a few weeks old, was accidentally killed in the canyon (Figs. 1 and 8, Table 1, site 38). Wauer and Carter (1965) reported this site to be active as late as 1964.

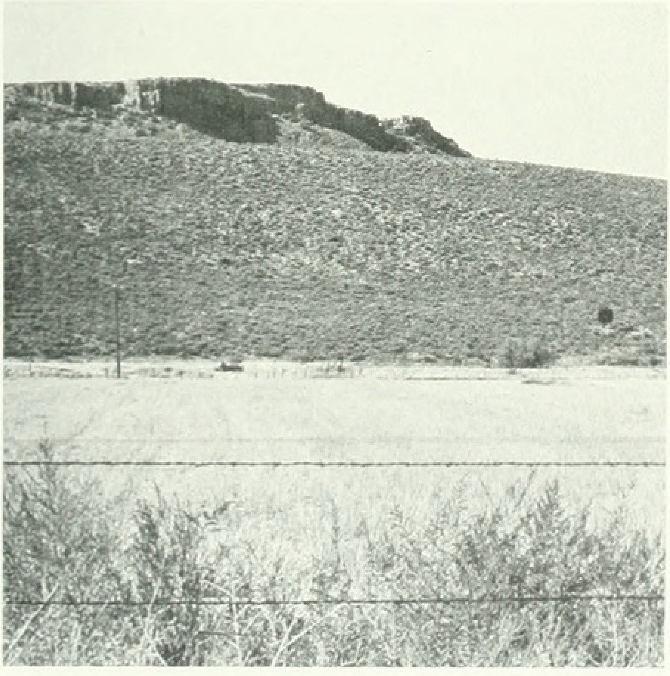

Fig. 5. A different view of the Land Rock eyrie showing terrain. Flat area formerly contained some marsh habitat. Photo by Kim Despain, 1971.

In the Uinta Basin, Twomey (1942) reported an inaccessible eyrie about 40 feet (12.2 m) up on a deep shelf of a cliff, east of the Green River, near Vernal (Fig. 1; Table 1, site 34), Uintah County. Actions of the adults indicated that young were in the nest and immature birds were seen at the Ashley Creek marshes in early August and in the vicinity of Jensen from August through September. G. L. Richards (pers. comm.) saw a pair in the marshes in 1961, the most recent evidence of activity at this eyrie.

In southern Utah, single falcons were seen at Kanab, Kane County, on 28 April 1935, and 6 April 1947, and two were recorded along Kanab Creek on 20 May 1947 (Behle, Bushman, and Greenhalgh, 1958). Behle (1960) also noted the species near the Colorado River at Dewey on 21 May 1953 (Fig. 1; Table 1, site 31), and in Glen Canyon on 6 August 1958. Peregrines were seen several times in July and August at Navajo Mountain, San Juan County, by Woodbury and Russell (1945) in 1936, and by C. M. White and G. D. Lloyd (unpubl. data) in 1960 and 1961 (Fig. 1; Table 1, site 29). White and Lloyd (1962) reported on the predation of young peregrines which had not yet fledged from an eyrie in the Colorado River Basin (Figs. 1, 9, and 10; Table 1, site 28).

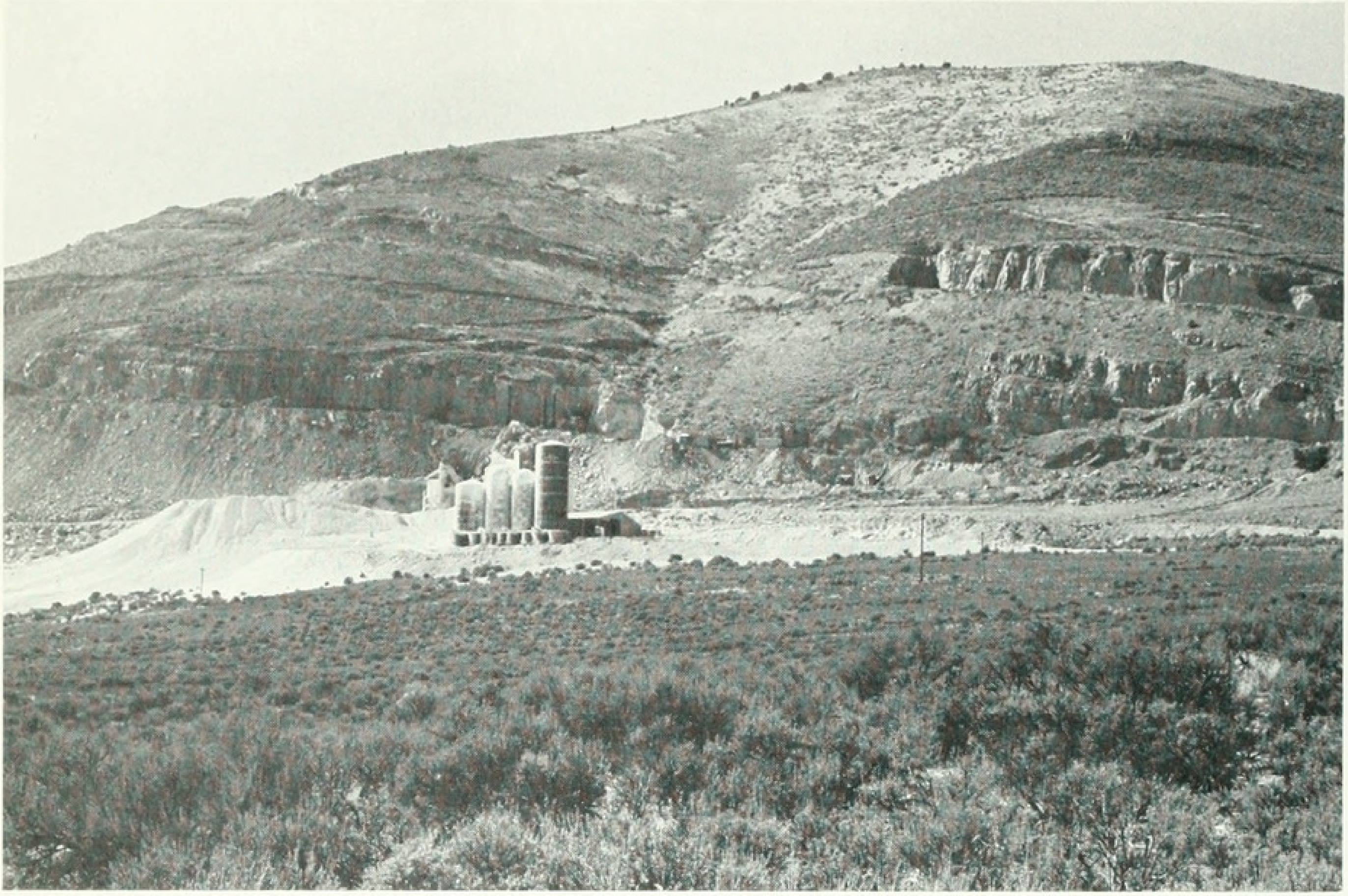

Fig. 6. Pelican Point eyrie site (Table 1, site 3, Fig. 1) showing lime mining operation, which in recent years destroyed the nesting cliff. Photo by Kim Despain, 1971.

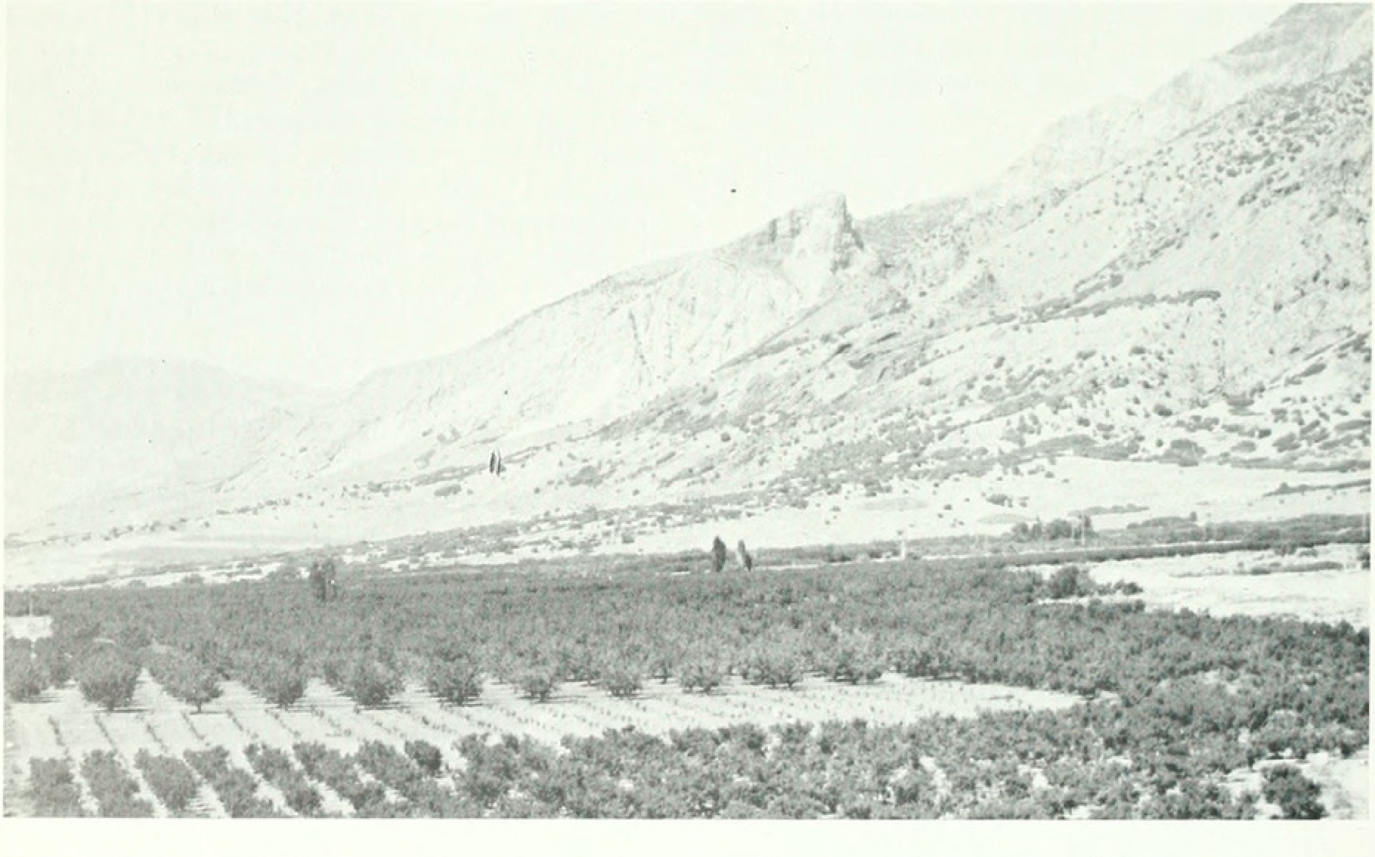

Fig. 7. Treganza noted a pair of peregrines nesting on the distant 1,000 ft. (305 m) cliff in the early 1900s, but he was unable to reach the eyrie site (Woodbury et al. unpubl. ms). Photo by R. J. Erwin, 1971.

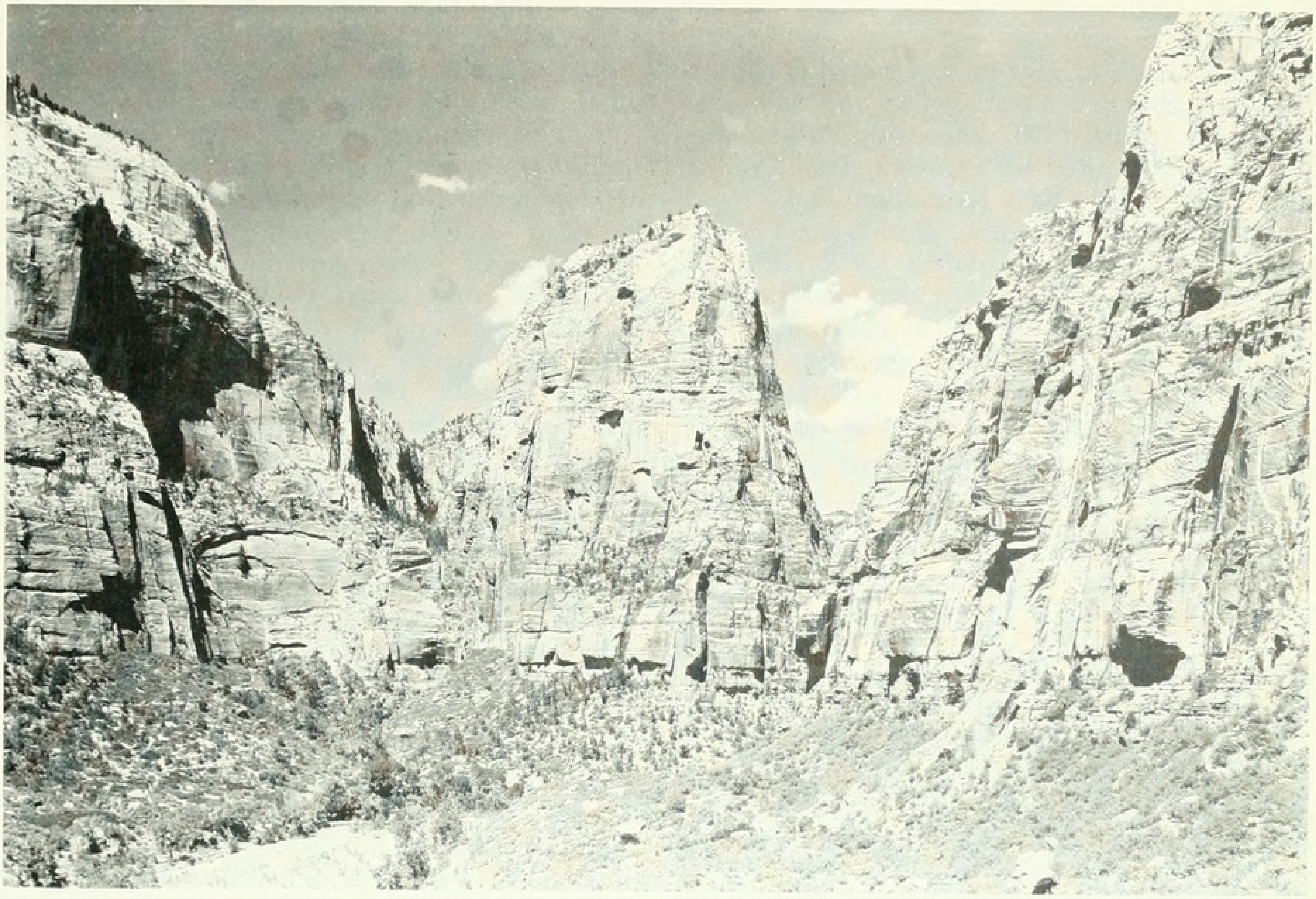

Fig. 8. Angel's Landing, Zion Canyon. Cliff in center where Grater (1947) saw peregrines nesting high on face of peak (Fig. 1, Table 1, site 38). Photo by Grant, 1 September 1929, Courtesy U. S. National Park Service.

Postnesting Season and Winter Records

The species is present in the state throughout the year (Woodbury, Cottam, and Sugden, 1949). Postbreeding adults, immatures, migrants, and wintering falcons congregate near marshes where a plentiful supply of food is available, especially near the marshes of the Great Salt Lake (Woodbury, Cottam, and Sugden, unpubl. ms). At the Bear River marshes, for example, records extend back to 1915, when Alexander Wetmore found the peregrine to be a regular and frequent visitor after mid-July (ibid.). The Christmas bird censuses taken by Vanez T. Wilson et al. (in *Bird Lore* 42, 1940; *Audubon Magazine* 43-48, 1941-1946; and *Audubon Field Notes* 1-24, 1947-1970) at the Bear River Migratory Waterfowl Refuge, indicate that the species wintered there in small numbers until the early 1960s (Fig. 11). The greatest number of peregrines seen during the seven- to eight-hour censuses was seven, in 1940. The Christmas bird counts at the Bear River marshes were exceptionally consistent from one year to the next beginning in 1939 through 1960 as regards the number of participants, the area covered, and the party hours afield. Additionally, V. T. Wilson directed and participated each year until 1960, after which other observers were involved and a greater area was covered, although the number of party hours afield remained essentially the same.

The racial affinity of specimens taken at the Bear River marshes between 1 July and 28 September (*anatum, sensu lato;* western subgroup), suggest that most of the postbreeding and fall peregrines in these marshes were from local eyries. The steady decline in the numbers of peregrines recorded at the Bear River marshes during the Christmas bird counts (ibid.) from 1939 to the early 1960s (Fig. 11) closely corresponded with the decline in the number of active eyries in the area surrounding the marshes. This correspondence suggests that most peregrines wintering in the marshes of Great Salt Lake probably were from local breeding populations, although they also may have been from some other sharply declining population of the *anatum* race. It is probable that only a small percentage of these wintering birds were from the arctic populations (*F. p. tundrius*), because arctic birds normally winter farther south, and because the arctic populations were not known to have declined between 1939 and the late 1960s.

Peregrines also have been reported on Christmas bird counts both at Ogden and Salt Lake City over the past 30 years. In addition, they have been recorded at Parowan, Iron County, on 27 December 1963 (*Audubon Field Notes* 18; 1964) and at St. George, Washington County, on 1 January 1969 (*Audubon Field Notes* 23; 1969). Christmas bird count data for the areas other than the Bear River marshes are either too spotty or are too heterogeneous in their method of collection to be evaluated statistically.

The peregrine was recorded at Clear Lake State Waterfowl Management Area by R. Williams on 16 September 1939, and by Gunther and Nelson on 24 October, 10 November, and 4 December 1941 (Woodbury et al., unpubl. ms), indicating that the species winters at other marshes as well as at those near the Great Salt Lake. Members of arctic populations (*F. p. tundrius*) apparently utilize Utah's marshes both as stopping places during migration and, sparingly, as wintering grounds. This is suggested by Lincoln's (1933) report of a peregrine banded as a juvenile at King's Point, Yukon Territory, within the geographic range of *tundrius* on 30 July 1924; by its recovery at Duchesne, Duchesne County, Utah, on 20 February 1925; and by the collection in December of the previously mentioned specimen of *tundrius* from Farmington Bay.

Late summer sightings, which could represent either resident birds or early migrants, have been recorded from several other areas. Twomey (1942) reported peregrines at Hill Creek, 40 miles (64.4 km) south of Ouray, Uintah County, on 5 August [1935?], at Strawberry Reservoir, Wasatch County, on 17 August [1935?], and Behle (1960) recorded the species at Glen Canyon near Wahweep Creek, Mile 17, on 6 August 1958 and at 10,500 feet (3,200 m) on the north slope of Mt. Ellen, Henry Mountains, on 8 September 1957. Finally, a subadult was seen near Park City, Wasatch County, in late August 1959 (M. Nelson and F. Welch, pers. comm.).

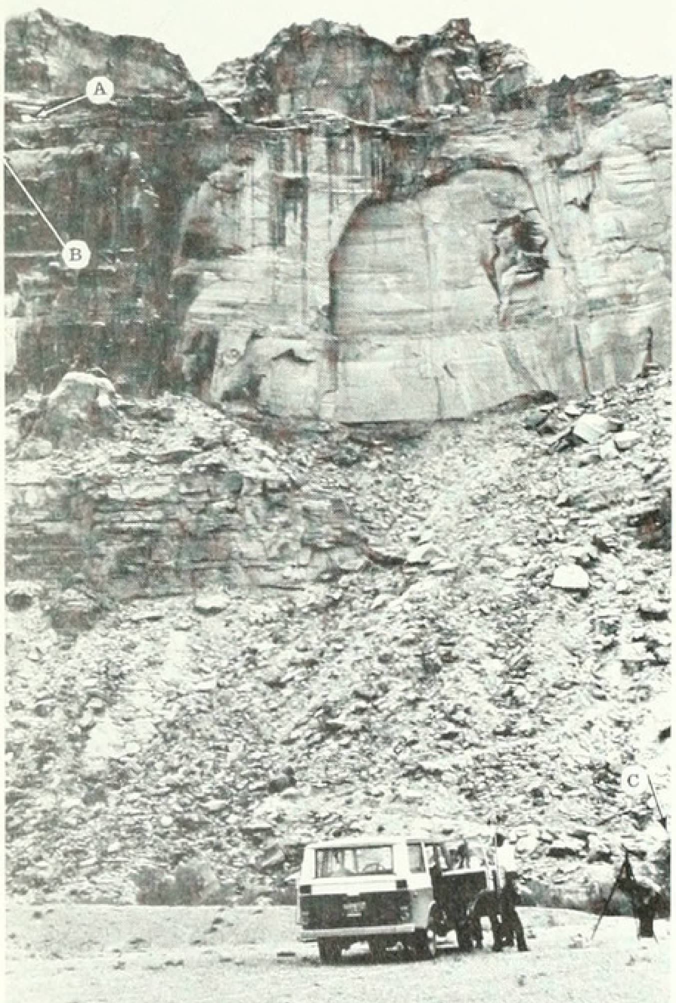

Fig. 9. Peregrine cliff in desert of Colorado Plateau, reported by White and Lloyd (1962) (Fig. 1, Table 1, site 28). Distance from the rock at point A to the eyrie ledge at point B is 70 ft (21.3 m). Poplar trees (*Populus fremontii*), along a water course in foreground (*C*) are 40–50 ft (12.2–15.2 m) in height. Photo by J. B. Platt, May 1971.

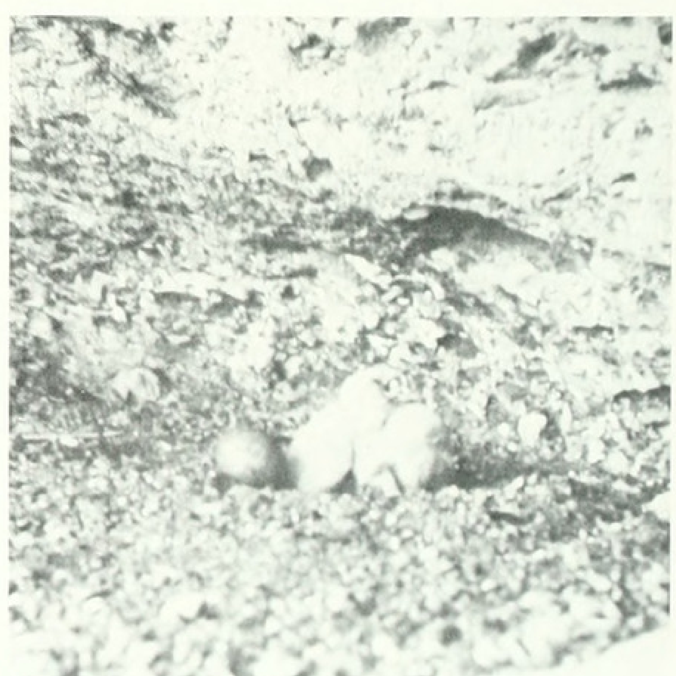

Fig. 10. Two-day-old young and an addled egg on nesting ledge at desert eyrie in Colorado Plateau (site 28) shown in Figure 9. Photo by G. D. Lloyd and C. M. White, 10 June 1961.

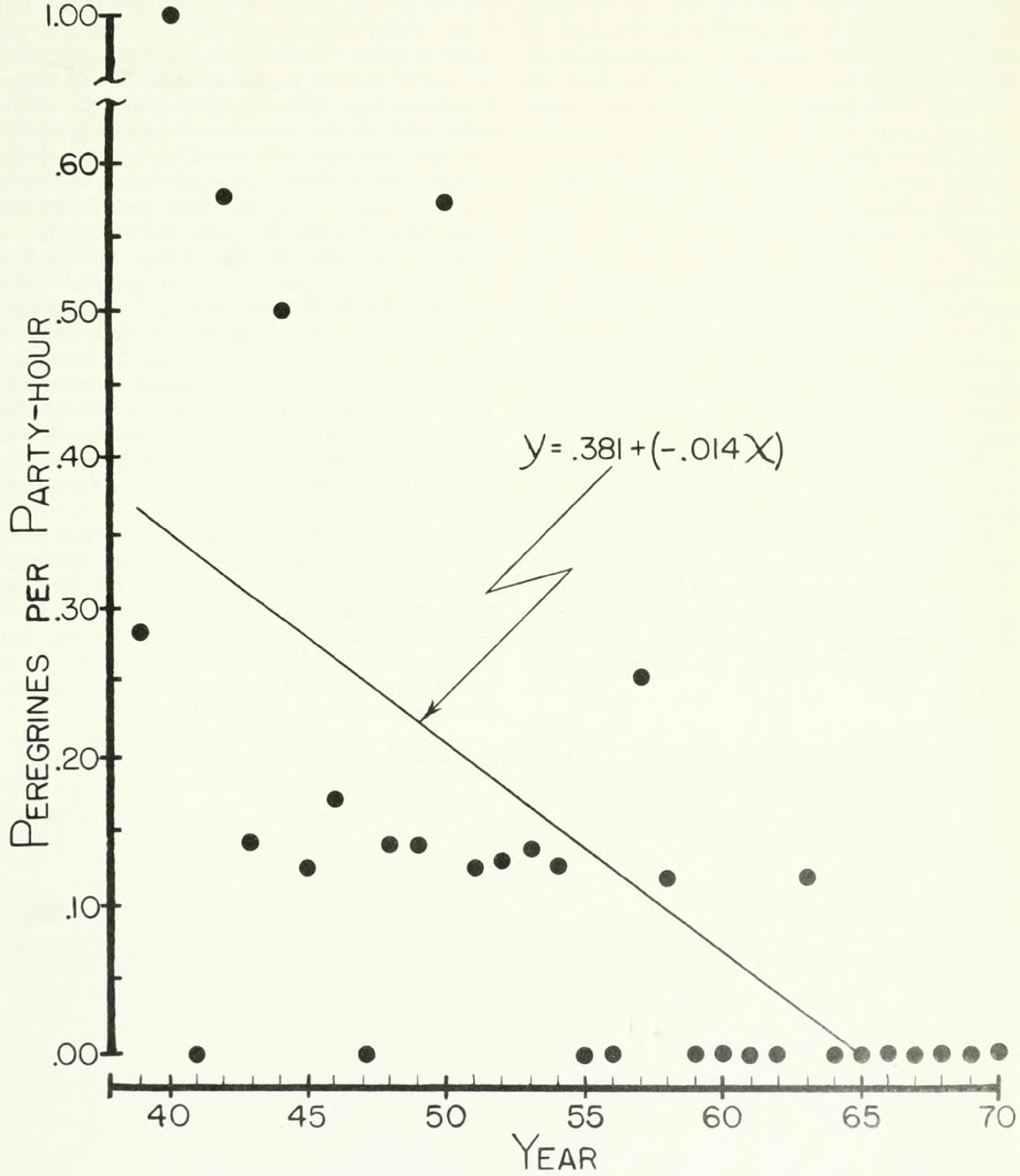

Fig. 11. Linear regression analysis of the number of Peregrine Falcons recorded per party hour, during Christmas bird counts at the Bear River Migratory Waterfowl Refuge between 1939 and 1970. Each circle represents the observations for one Christmas bird count. Downward trend is statistically significant ($p<0.01$). This analysis suggests that the peregrine had essentially disappeared as a wintering bird in the Bear River marshes by 1965.

DENSITY DISTRIBUTION OF PEREGRINE EYRIES IN UTAH

Utah's desert climate should seem to be a significant barrier to the nesting of the peregrine, yet we have compiled a list of about 40 eyries in the state (Table 1), which appear to have been active at one time or another. On the basis of density, if all 40 eyries were active simultaneously, there would be about 2,123 sq miles (5,499 km^2) per eyrie site. If the 11 suspected but unverified eyries (SNV, Table 1) are excluded, the density would be reduced to one eyrie site for every 2,928 sq miles (7,584 km^2).

Density of peregrine nesting sites in Utah appears to be directly related to the availability of food and suitable cliffs for nesting. The importance of these two factors to the distribution and density of the peregrine in the state will be discussed separately in a later section. Eyrie sites usually were situated near marshes, lakes, or rivers, where there was a plentiful supply of prey species. Where the nesting habitat was extensive, such as in the area of the Great Salt Lake (Fig. 1, Table 1), eyrie sites were clustered around the marshes in a pattern conforming to the availability of nesting sites (Fig. 12). Elsewhere in the state, where suitable habitat is greatly restricted, each eyrie site usually was located many miles from its closest known neighbor (Fig. 1).

The density of peregrine eyries in Utah, exclusive of the area surrounding the Great Salt Lake (4,500 mi^2; 11,655 km^2), is one site per 4,232 sq miles (10,962 km^2), if the 19 additionally known and suspected eyries were all active simultaneously. If the 10 suspected eyries in the remainder of the state are excluded, the average area per nest site would be 8,935 sq miles (23,142 km^2). There were 20 known eyries in the area surrounding the Utah and Great Salt lakes (Fig. 1, Table 1, eyrie sites, 1–20). This is exclusive of eyrie site 22 (Table 1) which is outside of the region. One other probable eyrie is suggested by the presence of adults on each of several visits by L. R. Wolfe (field notes of R. G. Bee) to one other site (site 21, Table 1). If all 20 known eyries were active concurrently, there would have been one eyrie site for about every 225 sq miles (583 km^2) in an area covering about 4,500 sq miles (11,655 km^2), surrounding and including the Utah and Great Salt lakes (Fig. 1, Table 1).

The average distance between 13 eyries (sites 5, 7-10, 12-19, Table 1) located along 130 linear miles (209 km) of the west face of the Wasatch Mountains from the south end of Utah Lake to the north end of the Great Salt Lake was 10.0 linear miles (16.1 km). The closest eyries to each other were about 2 miles (3.2 km) apart and the

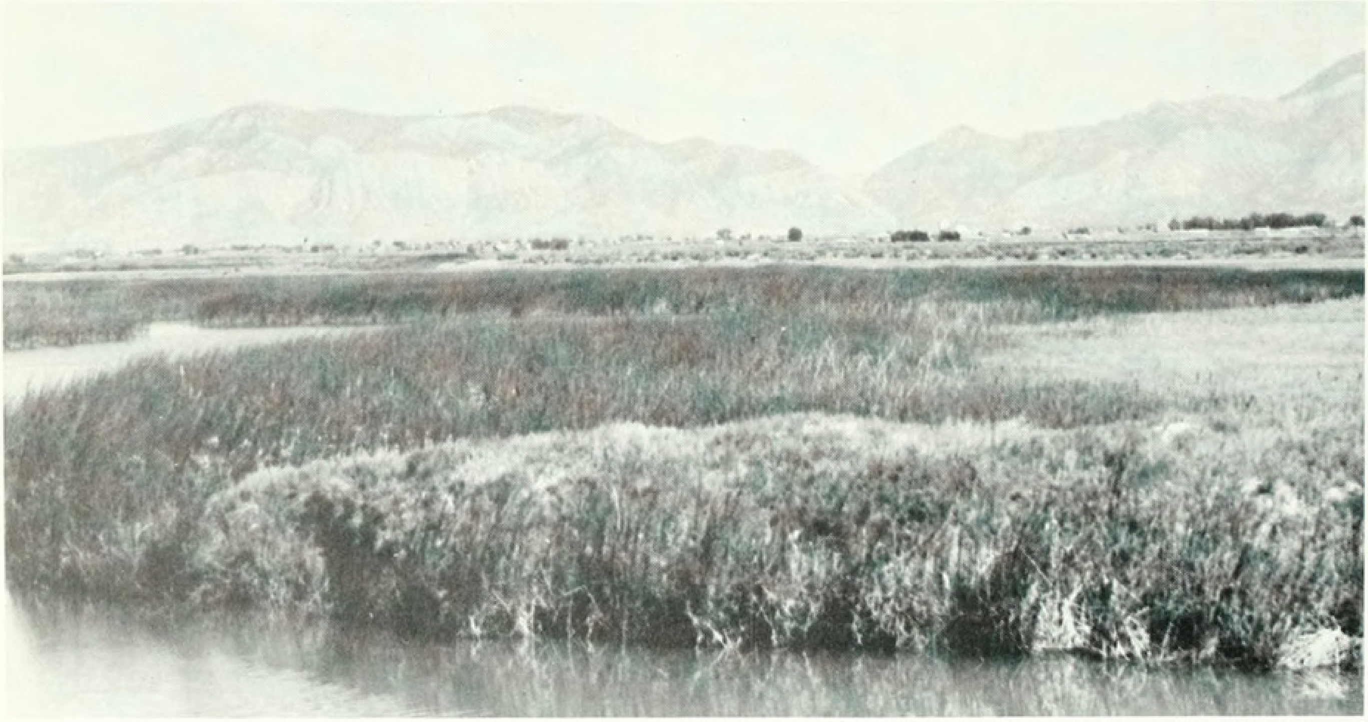

Fig. 12. Looking east from the peregrine's hunting habitat at a large Utah marsh toward its nesting habitat along the escarpment of the Wasatch Mountains. Two pairs of peregrines and three pairs of Prairie Falcons nested on the portion of the cliffs seen in the distance and both species utilized the marshes. Photo by R. J. Erwin, August 1971.

farthest were 20 miles (32.2 km) apart. However, since cliffs make up only about 25 miles (40 km) of the 130 linear miles, including side canyons (estimated from U. S. Geological Survey topographic maps), peregrine eyries, on the average, were only about two miles (3 km) apart on the cliff sections of the mountain. Several additional eyries near the western edge of Utah Lake and the eastern and southern edges of the Great Salt Lake were not included because they did not fall in a direct line with the 13 eyries mentioned above.

It is possible that populations of the peregrine were substantially greater prior to arrival of the first white settlers than historically, considering the apparent abundance of food that was available in nearby marshes, the number of cliffs which appear to be suitable (but which have not been known to harbor peregrines), and the probable lack of human disturbance.

Population densities of the magnitude of those occurring around the Great Salt Lake seemingly did not differ greatly from some of those present in other regions of North America where the environment is considered more congenial to the peregrine. For instance, Herbert and Herbert (1965) recorded nine eyries along 55 miles (88.5 km) of the Hudson River (eight on the west side) for an average of 6.1 miles (9.8 km) per eyrie. Berger and Mueller (1969) found 14 eyries along a 198.4-mile (319 km) stretch of upper Mississippi River for an average of 14.2 miles (22.8 km) between eyries.

White and Cade (1971) recorded a peregrine density along the Colville River in 1967-1969 to be one pair per 8.3 miles (13.4 km) above Umiat Mountain and one pair per 3.7 miles (6.0 km) below Umiat Mountain, giving an overall average of 6.03 river miles (9.7 km) between eyries. The distance between active eyries ranged from 0.4 miles (0.64 km) to 27 miles (43.4 km). There were 32 nesting pairs of peregrines along 183 miles (294 km) of the Colville River in Alaska in 1952, 40 pairs in 1959, and 27 pairs in 1967, for an average distance in miles between eyries of 5.7, 4.6, and 6.8 (9.2, 7.4, and 10.9 km), respectively (Cade, 1960; White and Cade, 1971).

The average distance between 19 eyries along 172 miles (277 km) of the Yukon River in Alaska was 9.3 miles (15 km) (range, 2.75–31 mi; 4.4–49.9 km) in 1951 and 10.1 miles (16.3 km) (range, 2-31; 3.2-49.9 km) in 1966 (Cade, White, and Haugh, 1968). Cade, White, and Haugh (1968) believed that the peregrine probably was never more common along the Yukon than in 1966.

For the Aleutian Islands, White, Emison, and Williamson (1971) found the average distance between peregrines defending territories to be about 5.8 miles (9.3 km) (range, 0.81-21 mi; 1.3-34 km) for Amchitka Island, similar densities on Rat and Semisopochnoi islands, and equal or perhaps greater densities on Kiska Island (M. Nelson, pers. comm., 1971).

On the other hand, no locality in Utah had populations approaching the densities found in several other regions. Hickey (1942), for example, in a local area of the eastern United States, reported five pairs of peregrines on 7 miles (11.3 km) of escarpment. In Great Britain, Ratcliffe (1962) found three pairs residing along a linear distance of 1,000 yards (914 m) of sea cliff, and 15 pairs along a 17-mile (27.4 km) distance. The highest densities known are for the Queen Charlotte Islands, where five to eight pairs of falcons utilized a linear distance of a mile (1.61 km) of sea cliff (Beebe, 1960).

Hickey (1942) listed 19 pairs of peregrines in an area of about 10,000 sq miles (25,900 km^2) around New York City, for an average of one pair for every 526 sq miles (1,362 km^2). Cade (1960) estimated a probable density of 200 and 300 sq miles (518 and 777 km^2) per pair in the Colville and Yukon river systems, respectively, and one known pair per 2,000 sq miles (5,180 km^2) in the Yukon country. Bond (1946) considered the peregrine to be common along the western coast of the United States and Baja, Mexico, where there was an average of less than 2,000 sq miles (5,180 km^2) per known pair. Judging from the data presented above, the peregrine was relatively common in the area of the Great Salt Lake and uncommon elsewhere in Utah.

TOPOGRAPHY, CLIMATE, AND PLANT COVER IN UTAH

Utah is in a region of generally high inland plateaus and mountains which have been dissected by numerous canyons and dotted with many lakes and inland valleys. A chain of mountains and high plateaus beginning at the corner of Wyoming and extending southwestward approximately two-thirds of the length of Utah separate the major part of the state into the Colorado and Great Basin drainage areas (see Fig. 1). The elevation of this central mountain chain ranges from 9,000 to 12,000 feet (2,743-3,658 m). The Wasatch Mountains make up the northern third of the central chain (to the southern end of Utah Lake) and high plateaus the remainder.

Nearly all of Utah west of the central mountain chain lies in the Great Basin and contains the entire drainage of ancient Lake Bonneville, of which Utah, Sevier, and Great Salt lakes are remnants. The Great Salt Lake, which is about 83 miles (134 km) long by 51 miles (82 km) wide, has fluctuated in area from 2,400 sq miles (6,216 km^2) in 1870 to 950 sq miles (2,461 km^2) in 1961 (Nelson, 1969). It contains high concentrations of salts (about 25 percent) comprising principally sodium chloride and sodium sulfate. Utah Lake, which is about 23 miles (37 km) long and 15 miles (24 km) wide, is fresh water. Water comprises nearly three percent of Utah's area due mainly to these lakes. The lowlands on the floor of the basin range from 4,200 to 5,550 feet (1,280-1,692 m) in elevation. Just west of the Great Salt Lake lies the Great Salt Lake Desert, one of the most formidable deserts in North America. In its greatest length and width it exceeds 150 by 60 miles (240 by 97 km) (see Fig. 1).

The eastern half of the state is in part of the Colorado Plateau or Colorado River Basin. The Colorado River Basin is bordered on the north by the high Uinta Mountains, some peaks of which exceed 13,000 feet (3,962 m), and contains the Uinta Basin immediately south of the mountains and the canyonlands farther south. It is dissected from north to south by the Green and Colorado rivers. The basin floor ranges in elevation from about 4,300 feet to 6,000 feet (1,311-1,829 m). The Virgin River Basin, in southwestern Utah, is about 2,250 feet (686 m) in elevation.

Because Utah lies in the rain shadow of the high coastal ranges, it is one of the drier regions in North America, with an average of only 4 to 10 inches (10.2–25.4 cm) of annual precipitation in the desert lowlands. The precipitation generally increases with an increase in altitude and may reach 30 to 50 inches (76.2–127.0 cm) annually in the higher mountains. Daily and seasonal temperatures in Utah vary widely. The summer maximum may exceed 100°F. The relative humidity is extremely low and the evaporation rate is high.

The desert lowlands are dotted with salt desert shrubs consisting chiefly of greasewood (*Sarcobatus vermiculatus*) and shadscale (*Atriplex confertifolia*) in areas below 5,500 feet (1,676 m) in elevation, and sagebrush (*Artemisia tridentata*) in areas higher than 5,500 feet (1,676 m) throughout much of the Colorado Plateau and the Great Basin. This low scrubby vegetation ranges from several inches to several feet in height. Desert scrub, consisting predominantly of mesquite (*Prosopis glanduliflora*), creosote bush (*Larrea divaricata*), and black brush (*Coleogyne ramosissima*), occurs in the southern desert of southwestern Utah.

The more arid foothills in the Great Basin and Colorado Plateau, which receive 10 to 15 inches (25.4–38.1 cm) of rainfall annually, are covered with pinon-juniper forests (*Pinus* and *Juniperus*), 10 to 30 feet (3.0–9.1 m) in height. Foothills receiving 16 to 20 inches (40.6–50.8 cm) of rainfall are covered with a variety of scrubby trees and bushes called chaparral, consisting of oak (*Quercus*), maple (*Acer*), serviceberry (*Amelanchier*), mountain mahogany (*Cercocarpus*), mountain laurel (*Ceanothus*), and manzanita (*Arctostaphylos*). Above the foothills lie montane forests of spruce (*Picea*), fir (*Abies*), and aspen (*Populus tremuloides*). The aforementioned data on relationships between precipitation and vegetation are modified from Woodbury and Cottam (1962).

Utah's numerous mountain ranges, its extensive plateaus, and its high cliffs and mesas supply a plentitude of suitable nesting sites for birds of prey. The low scrubby vegetation of its foothills and desert lowlands provides the extensive hunting areas preferred by the larger falcons.

ECOLOGICAL DISTRIBUTION OF UTAH PEREGRINES

Climate

The peregrine, as represented by a cosmopolitan assortment of geographically variable races, has adapted to a wide variety of environmental conditions. This is true also for the *anatum* race, which ranges from the tree line of the North American Arctic south sparingly into northern Mexico and the southern tip of Baja California. In Utah, the peregrine has been known to nest in the Great Salt Lake Desert, one of the more arid regions known to be inhabited by this cosmopolitan species. At Wendover, for example, the monthly rainfall for the critical breeding period of March through July averaged only 0.44 inches (1.12 cm) over a 49-year period; the mean monthly temperature ranged from 42° F (6°C) in March to 79°F (26°C) in July (U. S. Dept. of Commerce, 1965). Bond (1946) tells of peregrines nesting in the hot, arid climates along the lower Colorado River in California, in northeastern California, and eastern Oregon.

Climate along the Wasatch Mountains of Utah, where the peregrine historically attained its maximum density in the state, is more moderate. Here (Salt Lake City) the monthly rainfall for March through July averaged 1.03 inches (2.62 cm) over a 32-year period; the monthly temperature ranged from 40°F (4.4°C) in March to 77°F (25°C) in July (U. S. Dept. of Commerce, 1965).

Figures 13–15 delineate some of the climatic extremes associated with nesting peregrines in Utah. The hythergraphs given in Figure 13 are composites of the mean monthly extremes of daily temperature (for record period) and the mean monthly precipitation for weather stations near 18 known peregrine eyries distributed throughout Utah. The breeding period, March through August, is indicated also. The composite hythergraphs are constructed the same as those given by Twomey (1936) and Linsdale (1937), except that these authors used mean monthly averages of daily temperature rather than extremes (data from U. S. Dept. of Commerce, 1965).

In Figure 14 we have plotted the monthly average of the daily minimum temperature against the monthly average of the daily maximum relative humidity (from readings taken at three-hour intervals, 1965 through 1969) and the monthly average of the daily maximum temperatures against the monthly average of the daily minimum relative humidity for Salt Lake City (U. S. Dept. of Commerce, Local Climatol. Data 1965-1969).

Figure 15 gives a composite of the mean number of days per month that the precipitation was equal to or exceeded 0.1 inch (0.25 cm) and the mean number of days per month in which the temperature was equal to or exceeded 90°F (32.2°C), averaged for the 18 stations utilized in Figure 13 (data from U. S. Dept. of Commerce, 1965, [for record period]).

We used the extremes of climate since they, more than means, are likely to influence the general distribution of a species. According to Odum (1959:116-117):

> . . . temperature exerts a more severe limiting effect on organisms when moisture conditions are extreme, that is, either very high or very low, than when such conditions are moderate. Likewise, moisture plays a more critical role in the extremes of temperature.

It is at the environmental extremes that the evolutionary processes for a species are most pronounced in regards to the development of new limits of tolerance. By comparing the climatic extremes at the periphery of the ecological range of a species, such as the peregrine in Utah, one may gain an insight into the climatic factors which may limit its range.

Altitude

For western North America, Bond's data (1946) indicate that the peregrine rarely nests above 5,000 feet (1,524 m) in elevation, with a few nesting up to 10,000 feet (3,048 m) in California. However, many of the 18 eyries cited by Enderson (1965) for Colorado were above 5,280 feet (1,610 m), while the majority of them were above 6,000 feet (1,829 m) (Enderson, pers. comm.), with one eyrie in a high mountain region of Colorado, situated at an elevation of 12,000 feet (3,658 m) (Thomas D. Ray, pers. comm.). It may be that the habitat requirements of the peregrine are best satisfied in Colorado at these higher elevations. The paucity of eyries known to Bond (1946) to be at the higher elevations may be due, in part, to the difficulties encountered in reaching and searching the cliffs.

Nelson (1969) reported that peregrines in Utah nest at elevations up to tree line, between 6,000 and 7,000 feet (1,829 and 2,134 m). The only eyrie in Utah exceeding 6,000 feet (1,829 m), that is known to us, is at an elevation of 6,700 feet (2,042 m) (Table 1, site 36), but two are at 6,000 feet (Fig. 1, Table 1, sites 22 and 37), and the elevations of four others approach 6,000 feet (Fig. 1, Table 1, sites 26, 28, 35, 38). One suspected eyrie site, however, is at an elevation of 8,500 feet (2,591 m) (Fig. 1, Table 1, site 29) and another is at 9,750 feet (2,972 m) (Fig. 1, Table 1, site 27), suggesting the possibility that if higher areas were searched, others would be found. The mean elevation of peregrine eyries in Utah is about 5,000 feet (1,524 m) (Table 2). They ranged from 3,360 to 6,750 feet (1,024–2,057 m), with a preponderance of eyries (89 percent) between 4,000 and 6,000 feet (1,219 and 1,829 m) in elevation, and with nearly 50 percent of them at elevations between 4,500 and 4,999 feet (1,372 and 1,524 m). A frequency distribution of the elevations of Utah eyries is given in Table 2.

Habitat Niche

The habitat niche of the peregrine may be divided into two parts: (1) the cliff or substrate upon which it lays its eggs and rears its young

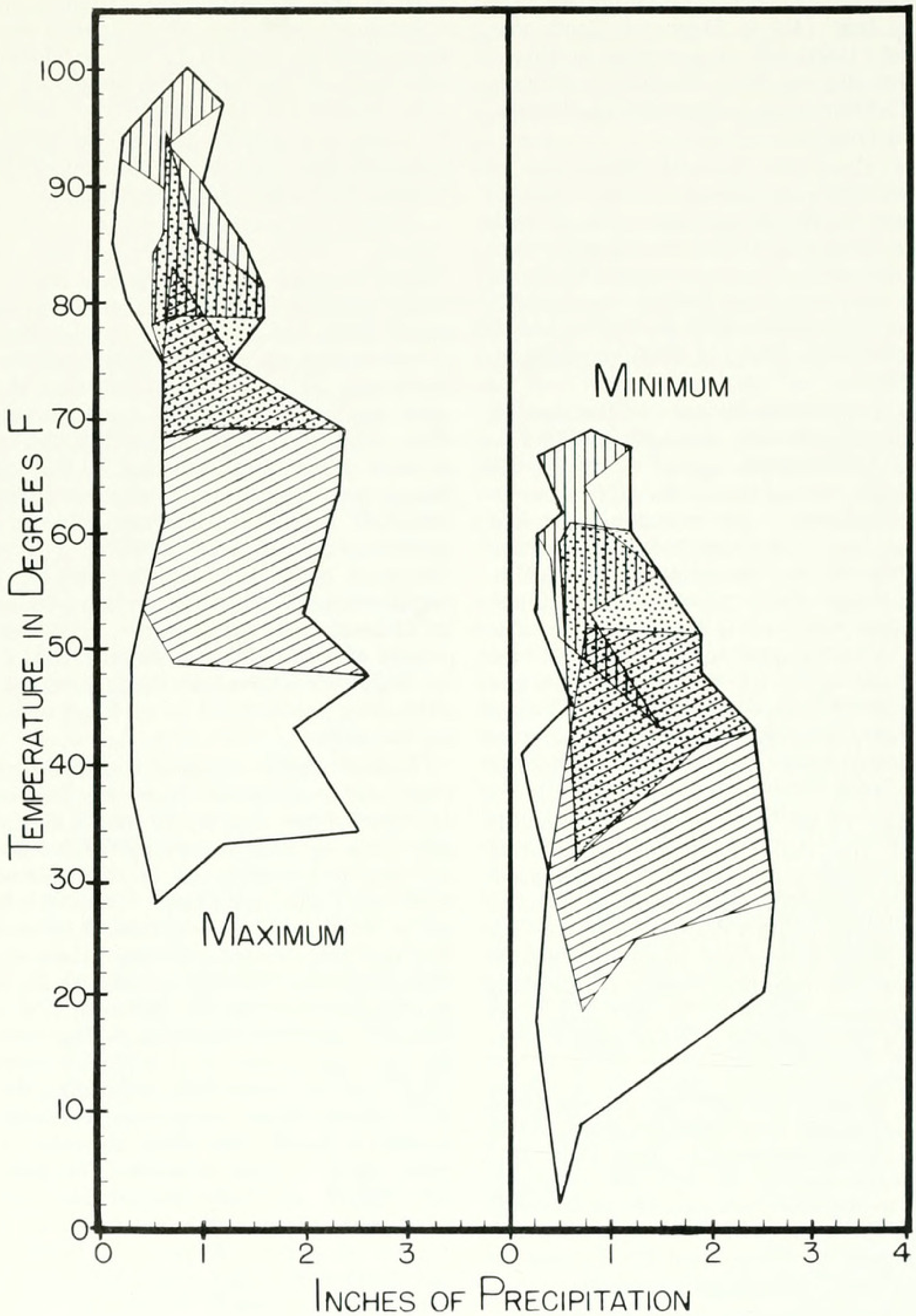

Fig. 13. Composite hythergraph for 18 stations situated near known peregrine eyries in Utah. Mean total monthly precipitation is represented in inches and mean monthly extremes of temperature (daily maximum and minimum, for record period) are represented in degrees F; they were constructed the same as those given by Twomey (1936) and Linsdale (1937), except that these authors used mean monthly temperatures (U.S. Dept. Commerce, 1965). The diagonally lined area depicts the climatic conditions for the egg-laying and incubation period (March-May); the stippled area represents the hatching and nestling period (May and June); the vertically lined area shows the fledging period (June-August).

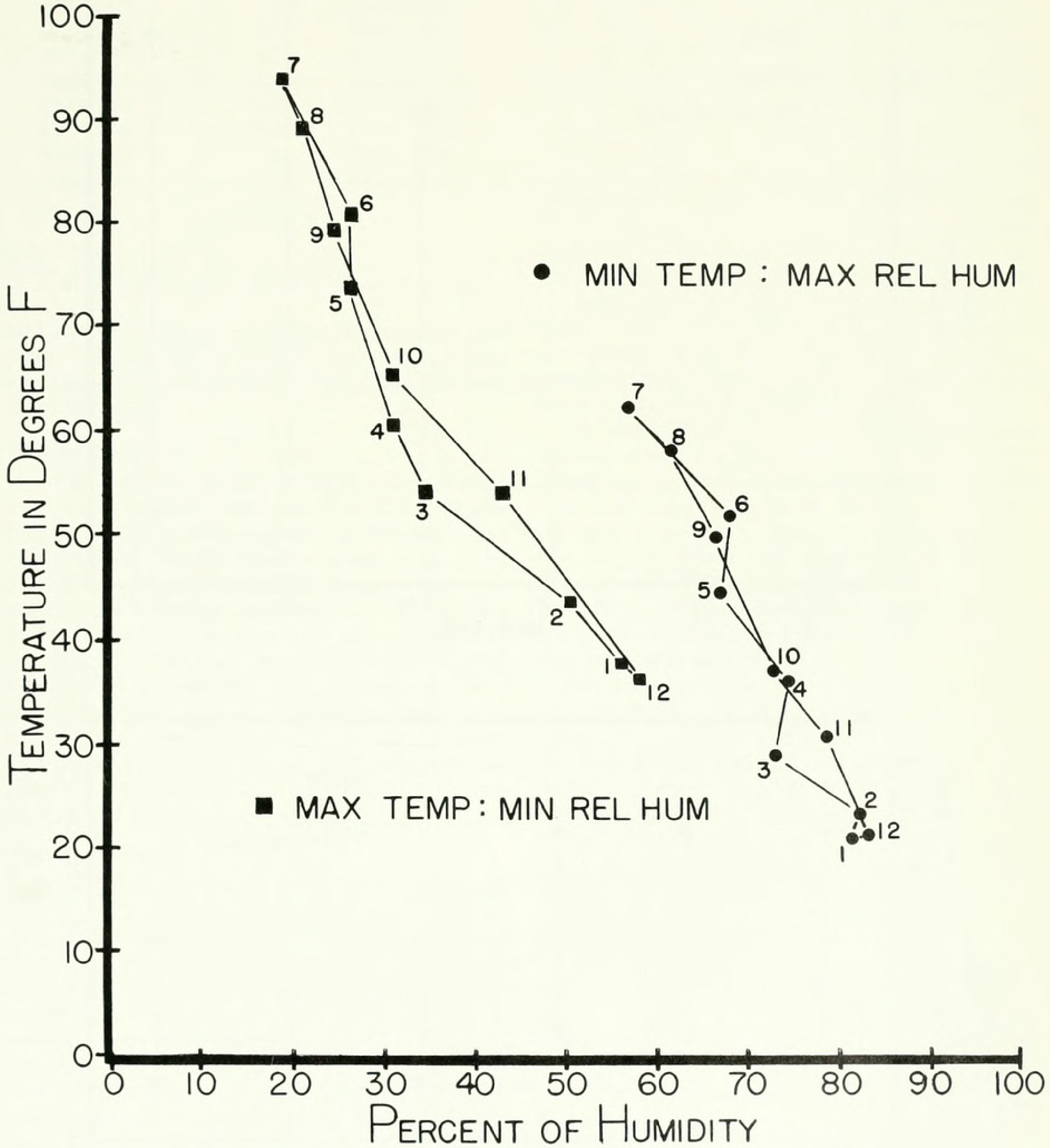

Fig. 14. Climographs for Salt Lake City, Utah. Daily maximum temperatures (averaged monthly for years 1965-1969), represented in degrees F are plotted against the mean daily minimum relative humidity for the same period; and the mean daily minimum temperatures for the same period are plotted against the mean daily maximum relative humidity. Humidity values were average from the maximum and minimum readings, taken at 3-hour intervals for 1965 through 1969 (U.S. Dept. Commerce, Local Climatological Data). Numbers beside points designate months of the year.

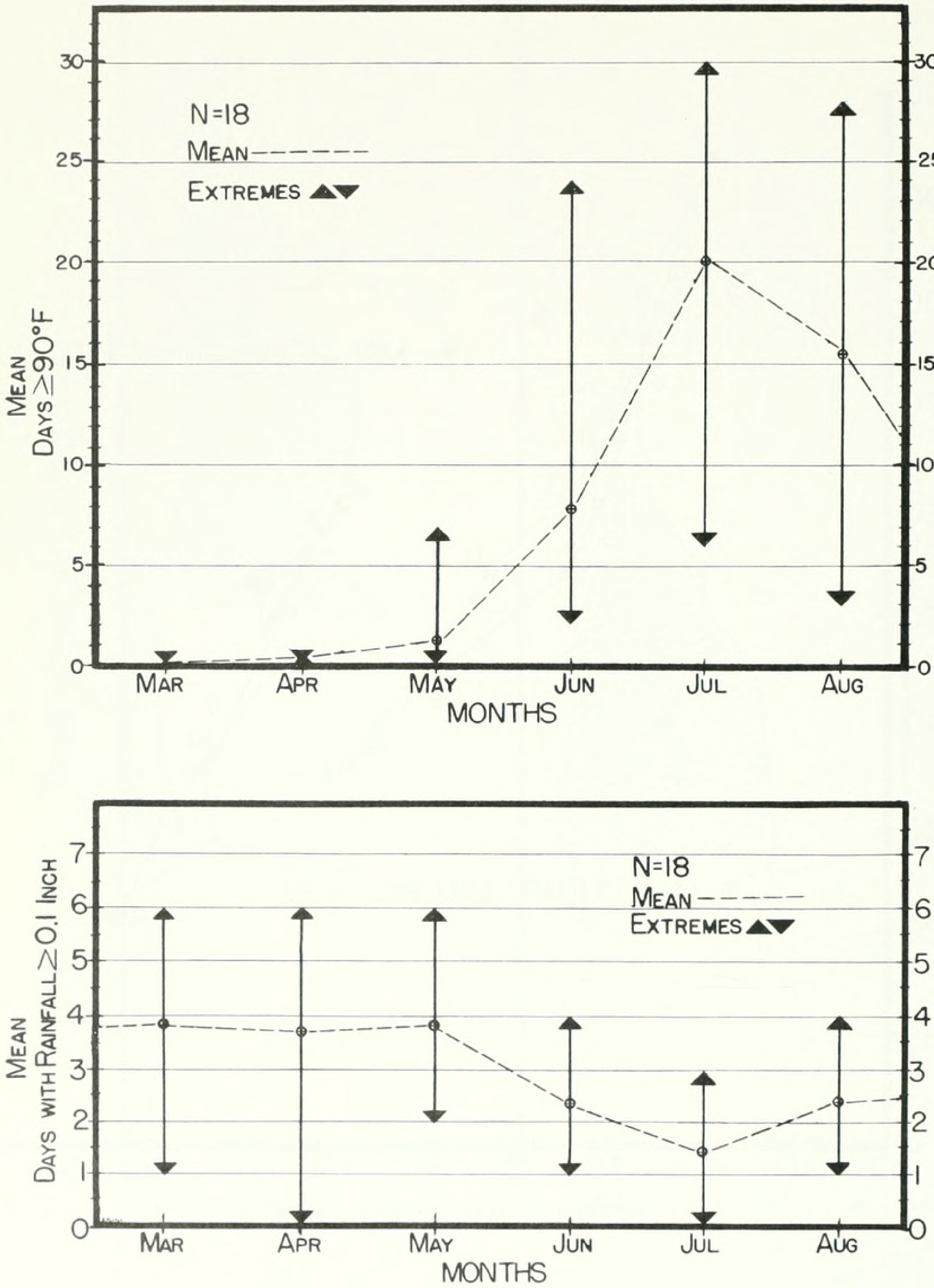

Fig. 15. Composite graph for 18 stations near peregrine eyries in Utah depicting the mean number of days per month in which precipitation was 0.1 inch (0.25 cm) or more and the average number of days per month in which the temperature was 90°F (32.2°C) or higher. (For record period, U.S. Dept. of Commerce, 1965.) Values were averaged (dashed lines) for the same 18 eyrie sites used in Fig. 13; extreme values are represented by solid triangles.

Table 2. Frequency distribution of peregrine eyrie site elevations in Utah.

Elevation (500-ft. intervals)	*n*	Percent	Elevation (intervals in meters)
3000–3499	1	3.2	914.4–1066.7
3500–3999	0	0.0	1066.8–1219.1
4000–4499	3	9.7	1219.2–1371.5
4500–4999	15	48.4	1371.6–1523.9
5000–5499	6	19.4	1524.0–1676.3
5500–5999	4	12.9	1676.4–1828.7
6000–6499	1	3.2	1828.8–1981.1
6500–6999	1	3.2	1981.2–2133.3
Totals:	31	100.0	

$\bar{x}$ elev. 4987 ft (1520 m)
Range 3360–6750 ft (1024–2057 m)

and around which its reproductive activities take place (nesting sites), and (2) the surrounding environs or territory where it obtains its food (hunting sites).

Nesting Sites

Most peregrine eyries in Utah were situated on a high ledge on the face of a cliff, but one female peregrine was reported to have laid her eggs in 1946 (Boyd Shaeffer, pers. comm.) on one of the dikes (elevated roadways) that separated two impoundment lakes at Ogden Bay State Waterfowl Management Area (Table 1, site 20). Additionally, an ornithologist (verbal report, to J. H. Enderson at AOU meeting, 1964) reported seeing an adult peregrine carry food to a young, nonflying falcon on the Mormon Temple in Salt Lake City in 1962, although we can find no corroborative evidence that falcons ever nested there.

Cliff Orientation

The ledges on which most Utah peregrines nest are in extensive mountain ranges which lie in a north-south direction. The escarpments of these mountains provide east- and west-facing cliffs, while their side canyons provide both north- and south-facing cliffs (Fig. 12). As illustrated in Figure 16, most peregrine eyries in the state were found in east- and north-facing cliffs. Although the escarpment along the Wasatch Mountains provided cliffs which faced all directions (Fig. 12), 10 of 12 eyries, for which data are available, were at sites facing northward (five eyries) and eastward (five eyries); three of the 12 faced slightly westward (NNW and NW), four faced southward (ESE and SE), one faced directly west, and one faced directly south. This suggests a directional orientation by the peregrine to the sun's exposure. Cliffs facing north or east should provide the eyrie better protection from the hot afternoon sun than would those facing south or west.

These findings tend to corroborate those of Nelson (1969), who has documented the death of nestling Golden Eagles (*Aquila chrysaetos*) due to direct exposure to the hot rays of the sun. He considers the peregrine to be more sensitive to the extremes of temperature and to the direct rays of the sun than the Prairie Falcon. He has pointed out that the later nesting of the peregrine, compared to that of the Golden Eagle and Prairie Falcon makes the peregrine's young more vulnerable to heat and sun than are the young of either of the other two species. McGahan (1968) found a preference by the Golden Eagle in Montana for southern exposures. He suggested that nest site preference was influenced by the direction of the sun and noted that exposure should be important when temperatures are below freezing as well as during the warmer months of June and July.

In Alaska, Cade (1960) found that peregrines nesting along the Yukon River preferred cliffs facing an easterly direction and that this orientation had some relation to the sun. He noted no such correlation, however, for eyries along the Colville River and hypothesized that the Yukon eyries faced eastward because of strong prevailing summer winds, whereas the lack of special orientation along the Colville was due to the absence of such winds.

On the other hand, in Great Britain, where the climate is more moderate, Ratcliffe (1962) found that suitable cliffs faced all directions and that British peregrines are indifferent to directional facing. He argues further that more intensive ice action on shaded north and east slopes have resulted in more extensive development of cliffs or crag ranges on these slopes. Hence, he concludes that cliff exposure is unlikely to influence the deliberate choice of a nesting cliff or site.

Our data and those of Cade's (1960) suggest that sun and wind exposure in the harsh extremes of climate such as those in the desert and in the Arctic may, indeed, elicit a deliberate choice of nesting sites. In Great Britain peregrine eyries probably are not subjected to such harsh extremes of climate, and thus, peregrines have less need for making deliberate choices there.

Rock Type, Cliff Size, and Eyrie Height

The physical characteristics of the cliff play an important role in their use by the peregrine as a nesting site. The geological formation, involving type of rock and height of cliff, contributes to the suitability of the cliff as a nesting site. Thirty peregrine eyries in Utah were

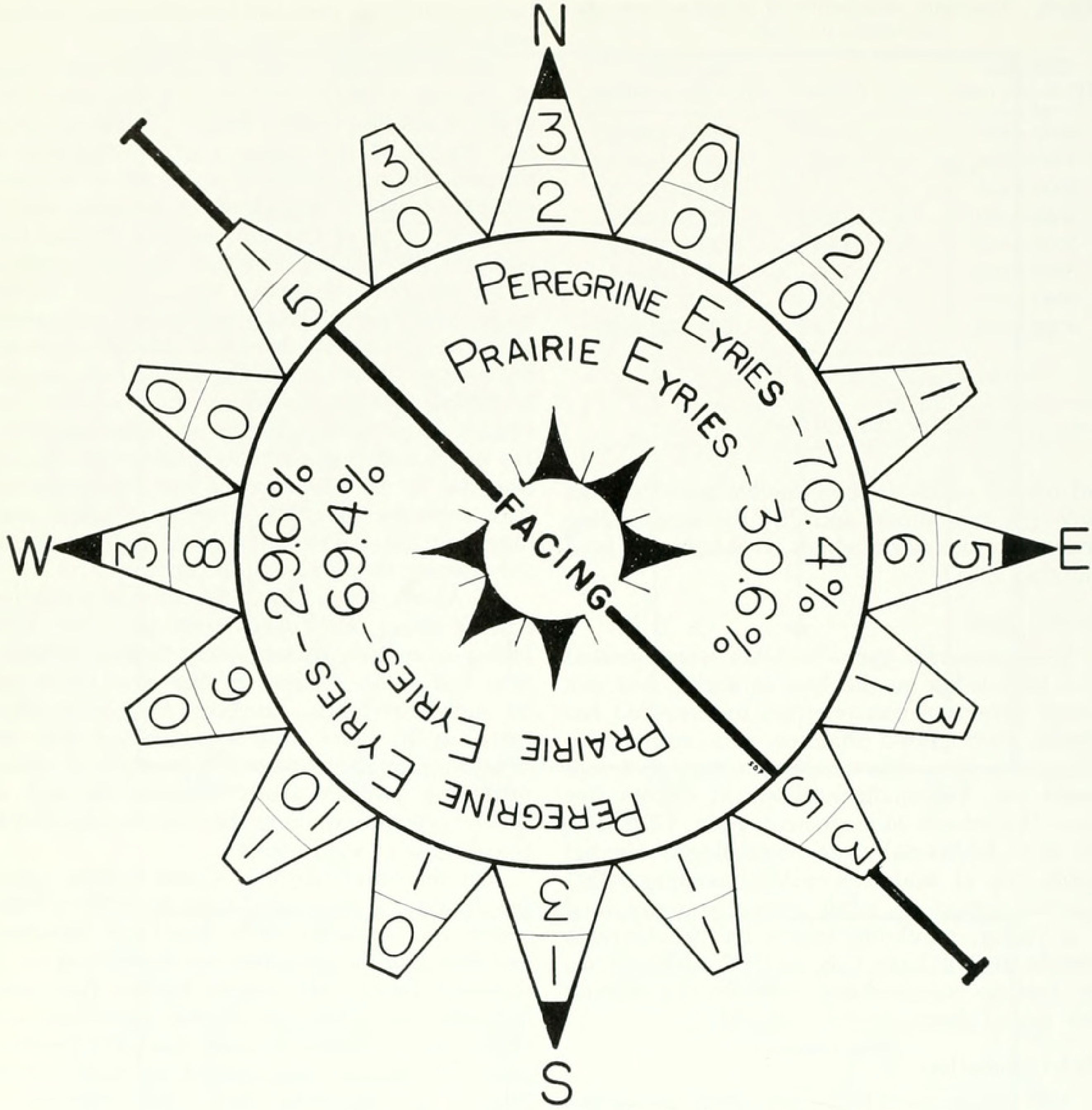

Fig. 16. Directional facings of Peregrine Falcon and Prairie Falcon eyries in Utah, both in areas of sympatry and in areas of allopatry. The values in the outer ring are for the peregrine; those in the inner ring are for the Prairie Falcon. The directional relationships shown here were statistically significant at $p < 0.01$ (X^2 test; calculated X^2 value, 7.37, 1 df) for the Prairie Falcon and $p < 0.05$ (X^2 test; calculated X^2 value, 4.48, 1 df) for the Peregrine Falcon.

situated on cliffs composed principally of four types of rocks: limestone, nine eyries; sandstone, nine eyries; quartzite, six eyries; and volcanic rock, three eyries. One additional eyrie each was located on volcanic agglomerate, granite, and metamorphic gneiss.

According to Hickey (1942), the height of the cliff is involved in the species' fidelity at the eyrie site over many generations of occupancy, and this concept is supported by Ratcliffe (1962, 1969) in Great Britain; Fischer (1967) has discussed the concept for eyries elsewhere in Europe. Hickey (1942), on the basis of height and continuity of use, classified cliffs in the eastern United States into three classes. Bond (1946) believes Hickey's (op. cit.) classification to be an oversimplification in the western United States.

Peregrines in Utah selected a wide variety of eyrie sites. Although the history of occupancy of individual eyries in Utah is largely unknown, there is some evidence to support Hickey's (op. cit.) hypothesis, at least in regards to height. Eyrie sites on the low, marginal cliffs were the first to be abandoned in Utah, whereas several that were situated high up, on massive cliffs that were difficult to climb, have the longest histories of occupancy.

A frequency distribution of heights of cliffs which supported nesting peregrines in Utah are given in Table 3. These cliffs ranged from 40 to 400 feet (12.2–122 m) in height. The mean height of 21 such cliffs in Utah was 178 feet (54.3 m). An additional cliff, first noted by Treganza early in this century and reported by Woodbury et al., (unpubl. ms), was in excess of 1,000 feet (304.8 m) in height (Figs. 1 and 7; Table 1, site 8). We excluded it from our calculations so as to not disturb unduly the more normal range of heights (see footnote, Table 3).

For 14 eyries the distance from the base of the cliff to the eyrie site averaged 105.5 feet (32.2 m) and ranged from 28 to 330 feet (8.5–100.6 m). These measurements do not include the talus slope and mountain side. If these distances were included, the values given above would be considerably higher for most sites, especially those on the escarpment of the Wasatch Mountains. Ratcliffe (1962) has discussed the importance of the steep slopes as a relevant factor in attracting peregrines to the cliff.

From the brink of the cliff to the eyrie sites below, the distance averaged 68.6 feet (20.9 m) and ranged from 12 to 250 feet (3.7–76.2 m) for 13 eyries.

The values given here for cliff heights average somewhat higher than those reported by Cade (1960) for the Yukon River in Alaska, and by White and Cade (1971) for the Colville River. Distances from the base of cliffs to the nest sites in Utah, however, averaged nearly twice those reported by Cade (1960) in the Arctic.

Hunting Sites

Marshes apparently play an important role in the breeding ecology of the peregrine in Utah (Figs. 12, 17, and 18), because nearly all peregrine eyries are situated near them. We measured the distances from each of 20 known eyrie sites in the Great Salt Lake and Utah Lake valleys to the closest nonflowing surface water, to the closest marsh 320 acres (130 ha) or larger, and to the closest marsh with no regard to size. The surface areas of the closest nonflowing water and the size of the closest marsh were also determined. Measurements were taken from U.S. Geological Survey topographic maps which were constructed from aerial photographs taken between 1945 and 1956; they are summarized in Table 4.

Of the 4,500 sq miles (11,655 km^2) surrounding and including these two lakes, marshes covered about 100 sq miles (259 km^2), while open water comprised about 1,443 sq miles (3,737 km^2). With exclusion of the Utah and Great Salt lakes, with their surface areas of about 138 sq miles and 1,661 sq miles (358 km^2 and 4,302 km^2), respectively, the surface area of water would be 80 sq miles (207 km^2). If the three large impoundment lakes (surface area, about 55 mi^2; 142 km^2) at the Bear River

Table 3. Frequency distribution of heights of cliffs containing Peregrine Falcon and Prairie Falcon eyries in Utah and the vertical distances of eyrie sites above bases of the cliffs.

Distance in Feet	CLIFFS				EYRIES				Distance in meters
	Peregrine		Prairie		Peregrine		Prairie		
	n	Percent	*n*	Percent	*n*	Percent	*n*	Percent	
0–24	0	0.0	1	2.3	0	0.0	10	19.6	0.0–7.5
25–49	1	4.5	11	25.0	3	21.4	19	37.3	7.6–15.1
50–74	1	4.5	10	22.7	3	21.4	8	15.6	15.2–22.8
75–99	4	18.2	8	18.2	3	21.4	7	13.7	22.9–30.4
100–124	4	18.2	5	11.4	0	0.0	2	3.9	30.5–37.9
125–149	1	4.5	0	0.0	1	7.1	0	0.0	38.0–45.6
150–199	3	13.6	3	6.8	2	14.3	2	3.9	45.7–60.9
200–249	1	4.5	2	4.5	0	0.0	1	2.0	61.0–76.1
250–299	1	4.5	1	2.3	1	7.1	1	2.0	76.2–91.3
300–349	2	9.1	2	4.5	1	7.1	0	0.0	91.4–106.6
350–399	1	4.5	0	0.0	0	0.0	0	0.0	106.7–121.8
400–449	2	9.1	0	0.0	0	0.0	0	0.0	121.9–137.0
450–499	0	0.0	0	0.0	0	0.0	1	2.0	137.1–152.3
500 ≥	1	4.5	1	2.3	0	0.0	0	0.0	152.4≥
Totals:	22	99.7	44	100.0	14	99.8	51	100.0	
x̄	178.0 ft* (54.3 m)		101.7 ft (31.0 m)		105.5 ft (32.2 m)		64.2 ft (19.6 m)		
Range:	40–400 ft (12.2–121.9)		7–500 ft (2.1–152.4 m)		28–330 ft (8.5–100.6 m)		2.5–450 ft (0.76–137.2 m)		

*Excludes one ground nester and one eyrie on a 1,000 ft (305 m) cliff.

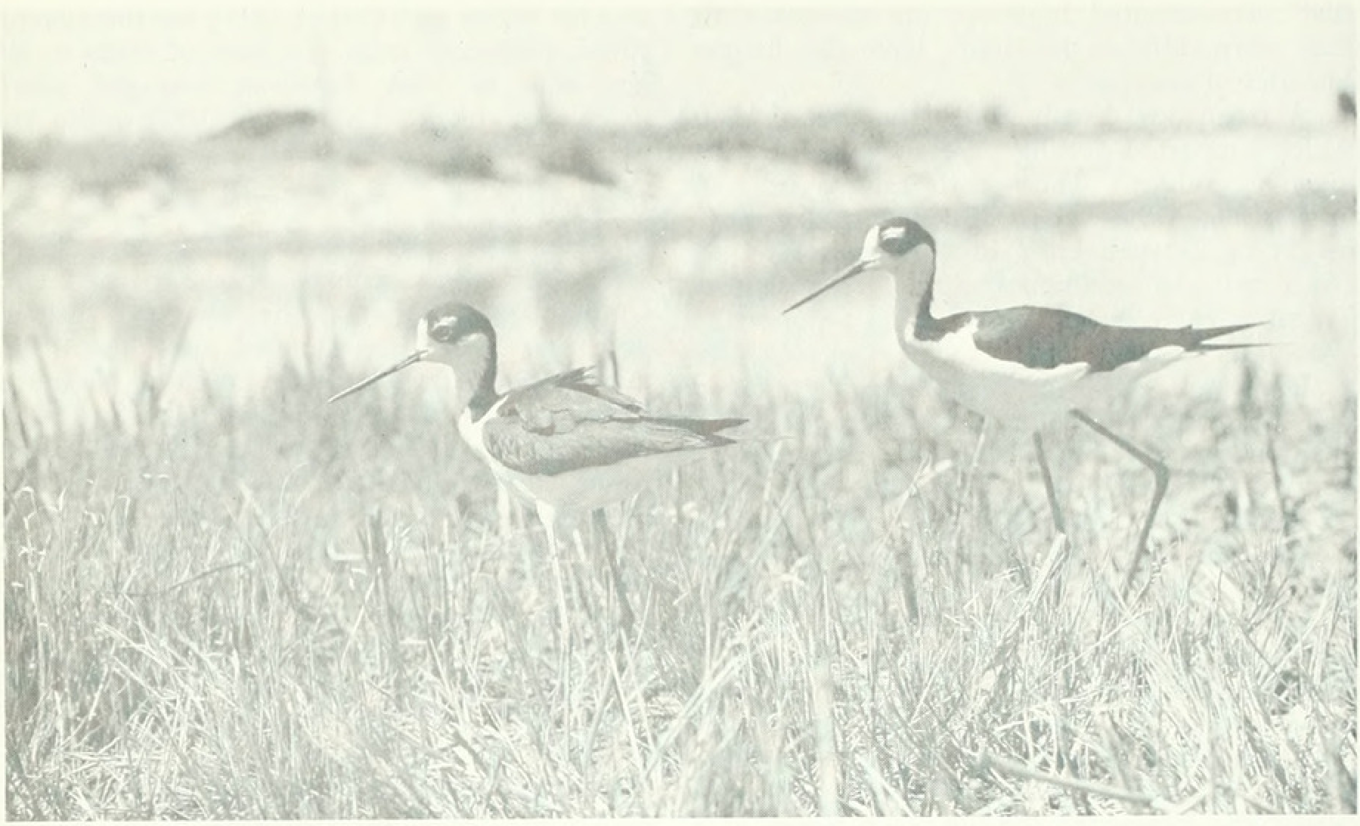

Fig. 17. Saltgrass (*Distichlis stricta*) marsh at Ogden Bay Refuge, Black-necked stilts (*Himantopus mexicanus*), a prey species of the peregrine, in the foreground. Photo by R. D. Porter, 1953.

Fig. 18. View to the west toward Promontory Mountains from Ogden Bay Waterfowl Management Area. Marshes in foreground are typical of those adjacent to Great Salt Lake from which peregrines and prairies nesting along the Wasatch escarpment and adjacent mountains obtained their major food source. Photo by R. J. Erwin, August 1972.

Table 4. Distances from peregrine eyrie sites in the Great Salt Lake Valley and Great Basin Desert to open, nonflowing water and marsh hunting areas and the size of these areas in relation to distance (measured from U.S. Geological Survey topographic maps which were constructed from aerial photographs taken between 1946 and 1956). Values in parentheses represent metric equivalence in kilometers or hectares.

	MARSHES			SURFACE WATER[1]		
Area & Statistic	Mi. to closest marsh (km)	Mi. to closest marsh ≥ 320 acres (130 ha)	Acres in closest marsh (ha)	Mi. to closest water (km)	Mi. to closest water ≥ 320 acres (130 ha)	Number of acres in closest water (ha)
Wasatch Mountains (Utah & Great Salt Lake valleys)						
n	19	19	17[2]	19	19	14[3]
$\bar{x} \pm SD$	3.3±2.6 (5.3±4.2)	7.6±5.1 (12.2±8.2)	17.5±20.6 (7.1±8.3)	2.5±2.0 (4.0±3.2)	5.2±4.3 (8.4±6.9)	59.6±34.4 (24.1±13.9)
Range	0.19–9.7 (0.31–15.6)	0.19–18.6 (0.31–29.9)	3.7–82.6 (1.5–33.4)	0.10–6.7 (0.16–10.8)	0.10–13.6 (0.16–21.9)	1.2–188.8 (0.49–76.4)
Desert, Great Basin						
n	3	3	3	3	2[4]	3
$\bar{x} \pm SD$	1.3±1.3 (2.1±2.1)	1.3±1.3 (2.1±2.1)	7,302±10,396 (2,955±4,207)	1.7±2.0 (2.7±3.2)	4.0 (6.4)	406±701 (164±284)
Range	0.19–2.8 (0.31–4.5)	0.19–2.8 (0.31–4.5)	640–19,281[5] (259–7,803)	0.19–4.0 (0.31–6.4)	4.0–4.0 (6.4–6.4)	1.0–1,216 (0.40–492)

[1]nonflowing waters; lakes and ponds. [2]excludes two large marshes; one 5,598 acres (2,266 ha), the other 1,114 acres (451 ha). [3]closest water to five eyries was either Utah Lake or Great Salt Lake; hence, they were excluded. [4]data for one desert eyrie, which was nearly 100 miles (161 km) from large body of water, was excluded. [5]Nelson (1966) gives 4,700 acres (1,900 ha) for Clear Lake Waterfowl Management Area, but topographic maps show an additional 14,581 acres (5,901 ha), contiguous with the management area, and a total of 53,000 acres (21,449 ha) are shown within about 20 miles radius of the Clear Lake eyrie.

Refuge were also excluded, the amount of surface water would be reduced to 25 sq miles (65 km^2). If both surface waters, exclusive of the Utah and Great Salt lakes, and marshes were divided equally by the 20 known peregrine eyries for the area, each pair of birds at these eyries would use prey species from 4.0 sq miles (10.4 km^2) of water, 5.0 sq miles (13.0 km^2) of marsh, and 9.0 sq miles (23.3 km^2) of the two combined. Nelson (1966), on the other hand, reports that there are 234 sq miles (606 km^2) of managed marshlands surrounding the Great Salt Lake (see Fig. 19), to which may be added several sq miles of unmanaged marshes controlled by duck clubs. The disparity between Nelson's measurements and ours probably is due to the fact that we used only marsh areas as shown on topographic maps and excluded mud flats and water, whereas Nelson's measurements probably include all lands and water within the Waterfowl Management Areas.

Marshes were the dominant features near three eyries in the Great Basin desert (Figs. 1 and 20, Table 1, sites 4, 23, and 25), and Twomey (1942) reported the use of the Ashley Creek marshes by peregrines nesting in Uintah County. The desert eyrie in the Colorado Plateau reported by White and Lloyd (1962) was by a river (Fig. 9). Figure 21 gives an aerial view of a river site in the desert of northern Arizona, typical of those in parts of Utah, and Figures 22 and 23 show marshes near eyrie sites in the Great Salt Lake Desert.

Peregrines nesting along the Wasatch escarpment traveled long distances to obtain shore and marsh birds, which made up the bulk of the food items found in their nests (Table 4), and the marshes where they hunted were rather extensive. In general, the Great Basin desert eyries were closer to marshes and to open water than were the Wasatch escarpment eyries (Table 4). One marsh supporting an eyrie in the Great Salt Lake Desert is only about a square mile (2.6 km^2) in extent, and is only about a mile (1.6 km) from the eyrie (Fig. 20). It is about the same size as the Ashley Creek marsh (Stewart Lake Waterfowl Management Area, Nelson, 1966) near the eyrie found by Twomey (1942). The marsh at one other eyrie in the Great Salt Lake Desert covers about 2¼ square miles (5.8 km^2) and is less than a mile from the eyrie site. An additional eyrie site (Woodbury et al., unpubl. ms) was 2.8 miles (4.5 km) from a marsh that covered over 30 square miles (78 km^2) (Table 4). The surface area of fresh water at two of the desert sites is only a few acres in extent (Fig. 23), whereas that at the additional site was about 2 square miles (5.2 km^2) in extent.

Of the 40 eyries and suspected eyries in Utah for which we have data, three were along rivers with marshes, streams, or lakes; five were

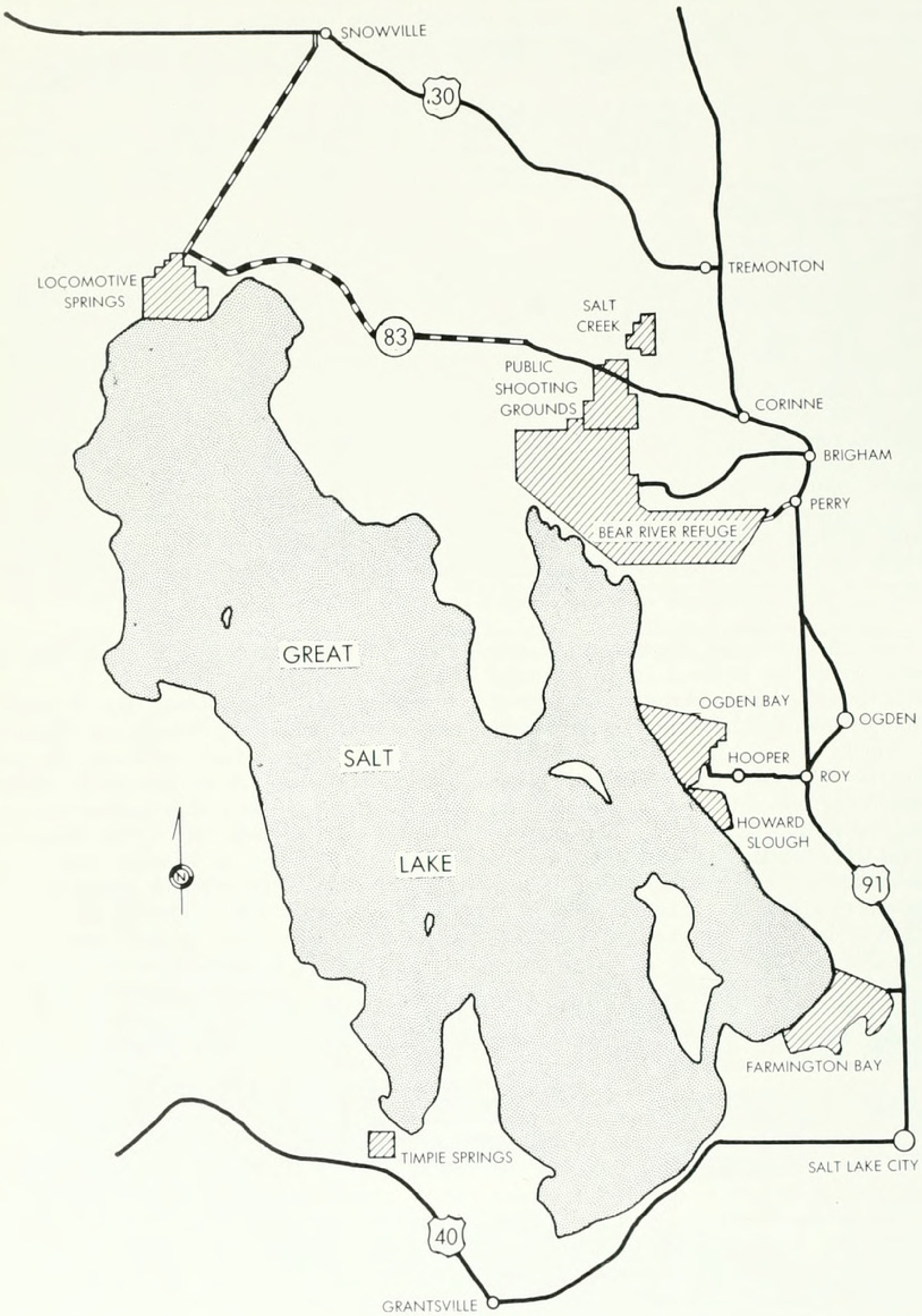

Fig. 19. Distribution of managed marshlands concentrated around the Great Salt Lake region. Photo by permission of Utah Division of Wildlife Resources, *in* Nelson, 1966.

Fig. 20. View across a marshy area adjacent to an eyrie in the Great Basin at the edge of the Great Salt Lake Desert. R. D. Porter is standing in foreground and is about 1 mile (1.6 km) east of the eyrie shown in Figure 44. Photo by R. J. Erwin, August 1972.

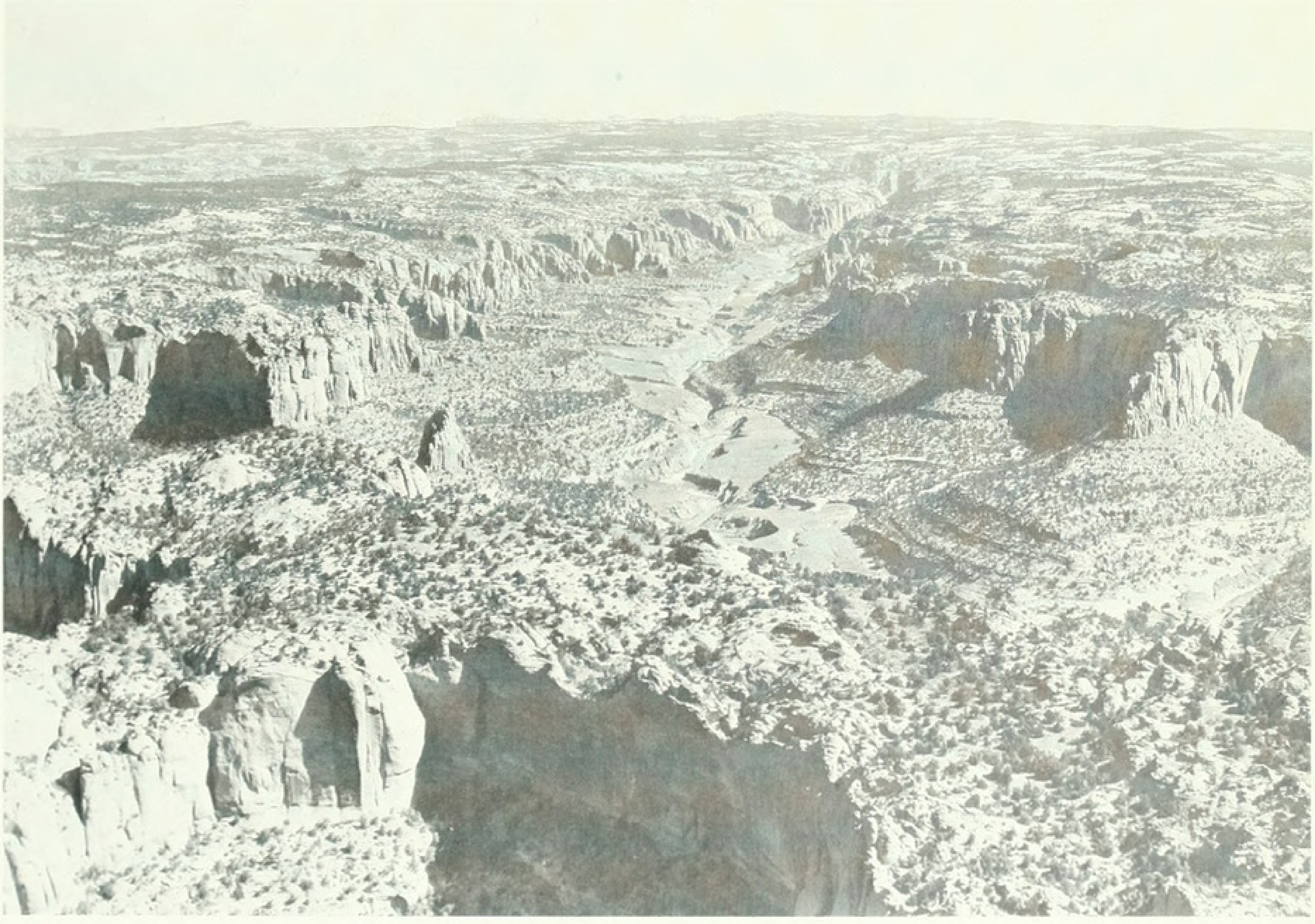

Fig. 21. Aerial view of a river eyrie site in the desert of northern Arizona typical of those in southeastern Utah. View looking NNE. Peregrines nested on the canyon wall on the right hand side of the photo. Photo by G. D. Lloyd, 1960.

along major rivers; 25 were near marshes with lakes and streams; five were along streams only; and there was one each near a marsh and a lake only. All but two of the 21 eyries near the Great Salt Lake were adjacent to a stream, which usually comprised the closest source of water. The smaller passerine birds associated with the streamside vegetation provided the peregrines with a source of food which frequently was within the immediate area of the eyrie.

The marshes originate from desert springs, from the overflow of rivers and creeks, from deltas at the junctions of rivers and lakes, and in more recent times, from artificial damming of streams or from the formation of ponds resulting from the drilling of wells. Bulrush (*Scirpus* sp.), saltgrass (*Distichlis stricta*) (Figs. 17 and 18), and cattail (*Typha* sp.) (Fig. 12) are the principal plants in these marshes.

The marshes supply food for peregrines during all seasons of the year, but are especially important during nesting season. The presence of an abundant food supply in the marshes at Ogden Bay undoubtedly was the major ecological factor responsible for the groundnesting of a peregrine there. Several easily accessible eyries that were mentioned by Beebe (1960) in the Queen Charlotte Islands may have been due to an abundant source of prey and to the absence of mammalian predators.

The combination of marshes adjacent to suitable cliffs for nesting may be considered an "ecological magnet" (Hickey, 1941) for the peregrine in Utah, especially along the Wasatch escarpment, where extensive marshes border the Utah and the Great Salt lakes. Here, marshes are formed at the deltas of three major rivers that flow into the lake (Fig. 19). Typical of

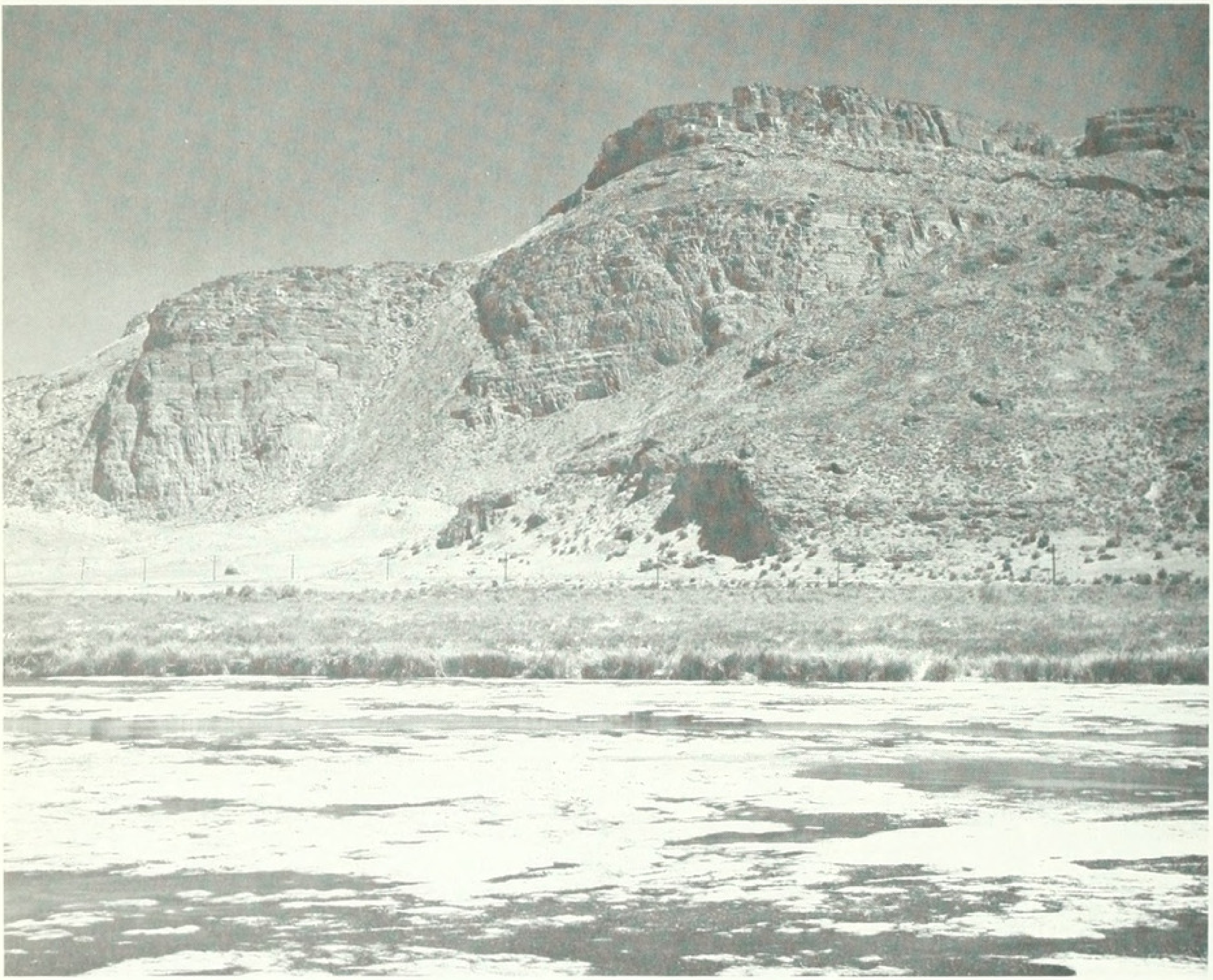

Fig. 22. Eyrie site near the eastern limits of the Great Salt Lake Desert. The eyrie, when first located by Porter in the early 1950s, was on a small cliff in the left foreground which does not show in this photo because it was removed to make a road bed. The peregrines were last seen using the cliffs near the top right of the photo. Prairie Falcons also used the same eyrie that was last used by the peregrines at least three years after the peregrines were last seen there. Photo by R. J. Erwin, August 1971.

their vegetation is that at the delta of the Weber River (Ogden Bay), which, from salt flats to river channels, consists mainly of glasswort (*Salicornia* sp.), saltgrass, alkali bulrush (*S. paludosus*), hardstem bulrush (*S. acutus*), cattail (*T. latifolia* and *T. angustifolia*), and sago pondweed (*Potamogeton pectinatus*) (Nelson, 1954). For a more comprehensive description of plant ecology in Utah marshes, see Nelson's (1954) studies of a marsh near the Great Salt Lake (Ogden Bay) and Bolen's (1964) discussion of a spring fed marsh in the Great Salt Lake Desert (Fish Springs).

Numerous remains of nine species of waterbirds, including grebes, ducks, rails, avocet, gulls, and terns, from anthropological sites at the northwest side of the Great Salt Lake, some dating back at least 8,350 years (Harper and Alder, in press), suggest that marshes were present in the Great Salt Lake valley long before the arrival of the white man. Some of the early hunters and explorers to enter the valley reported the presence of numerous waterfowl and shorebirds. Father Escalante, who visited Utah Lake in 1776, wrote that the lake "abounds in many kinds of fish and in geese and waterfowl" (Harris, 1909). Osborne Russell, a trapper, saw "miriads of Swans, Geese Brants, and Ducks which kept up a continuous hum day and night . . ." at Bear River marshes on 2 April 1842 (Haines, 1955). Fremont (1845), who visited the Bear River Delta on 3 September 1843, mentioned the thunderous noise made by multitudes of waterfowl in the marshes and described the area as being covered with rushes and canes. Captain Stansbury (1852) made similar observations on 22 October 1849 from a vantage point on the east side of Promontory Point. He recorded that ". . . thousands of acres, as far as the eye could reach, were covered with them [waterfowl]. . . ." Fremont (1845) reported that "the stillness of the night [8 September 1843] was enlivened by millions of waterfowl," this time at the mouth of the Weber River near Little Mountain; and on 9 September he reported that the shallow delta of the river was "absolutely covered with flocks of screaming plover." Stansbury (1852) noted innumerable flocks of ducks, geese, white swan, and long-legged plover around the shallows at the mouth of the Jordan River on 4 April 1850. It is probable that the "plover" were mostly American Avocet (*Recurvirostra americana*), Black-necked Stilt (*Himantopus mexicanus*), and Willet (*Catoptrophorus semipalmatus*).

Vegetation at the river sites was comprised mostly of cottonwoods (*Populus fremontii* in the Lower Sonoran desert areas; *P. angustifolia* in the Upper Sonoran areas) and willows (*Salix exigua* was most frequently present, with *S. lutea*, *S. gooddingi*, and *S. caudata* occasionally present also). Other plant species known to oc-

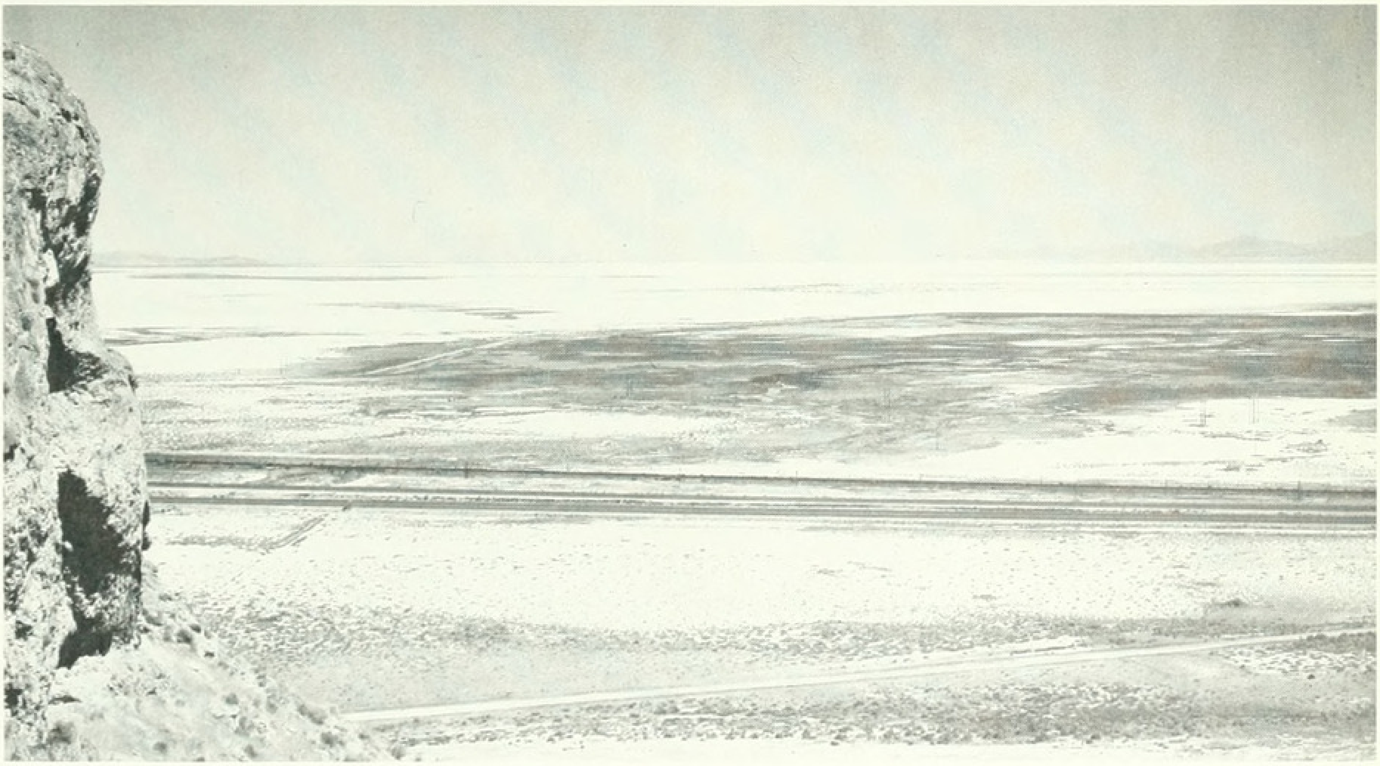

Fig. 23. View from hillside below eyrie in Figure 22. Brackish marsh can be seen in the midground, and salt flats from the Great Salt Lake can be seen in the background. Photo by R. J. Erwin, August 1971.

cur with the cottonwoods and willows include: squawbush (*Rhus trilobata*), wildrose (*Rosa* sp.), tamarix (*Tamarix ramosissima*), Joshua tree (*Clistoyucca brevifolia*), box elder (*Acer negundo*), ash (*Fraxinus* sp.), baccharis (*Baccharis emoryi*), hackberry (*Celtis douglasii*), and even scrub oak (*Quercus gambelii*). The presence or absence of the latter species is dependent upon altitude, latitude, and local ecological conditions.

Food Niche

Little has been published on the diet of the peregrine in the intermountain region. Wetmore's (1933:49–50) account of the hunting tactics of the peregrine on the Bear River marshes has been quoted elsewhere (Bent, 1938). It is repeated here because it gives a remarkedly vivid picture of the peregrine in its native haunts along marshes of the Great Salt Lake earlier in the present century.

> The birds [falcons] at rest perched in low willows, or on logs or bits of drift, where they had clear view of the teeming bird life about them. When hungry, they dashed across the open flats at high speed, striking ruthlessly at any birds that appeared, from small sandpipers to large ducks.
>
> Their appearance in the air was always the signal for chattering cries of alarm from blackbirds and avocets that put all their bird neighbors on the watch. These warnings had little effect, however, as the duck hawk, killing practically at will, was truly despot of this realm.
>
> I have seen this falcon dash through closely massed flocks of flying sandpipers, striking out two or three with as many thrusts of the claws, allowing each bird to drop and then wheeling swiftly to seize the falling prey in mid-air before it reached the ground. Again, I have seen one in a stoop, swift almost as light, knock a redhead duck to the ground, where it landed with a broken wing and other injuries.
>
> On one occasion a pair of duck hawks harried a helpless nighthawk, stooping at it playfully until one in passing gave it a quick squeeze with one foot. It then allowed the nighthawk to fall, when it was seized by the other duck hawk. Then the pair flew away, and the one with the booty at intervals dropped it, so that it could be seized in air by its mate.

Food items found in several Utah eyries are summarized in Tables 5 and 6. We collected 107 individual prey items representing 20 species of birds and at least one species of mammal from two eyries along the escarpment of the Wasatch Mountains between 1943 and 1957. The American Avocet was represented in the greatest numbers (Fig. 24). It, the Mourning Dove (*Zenai-*

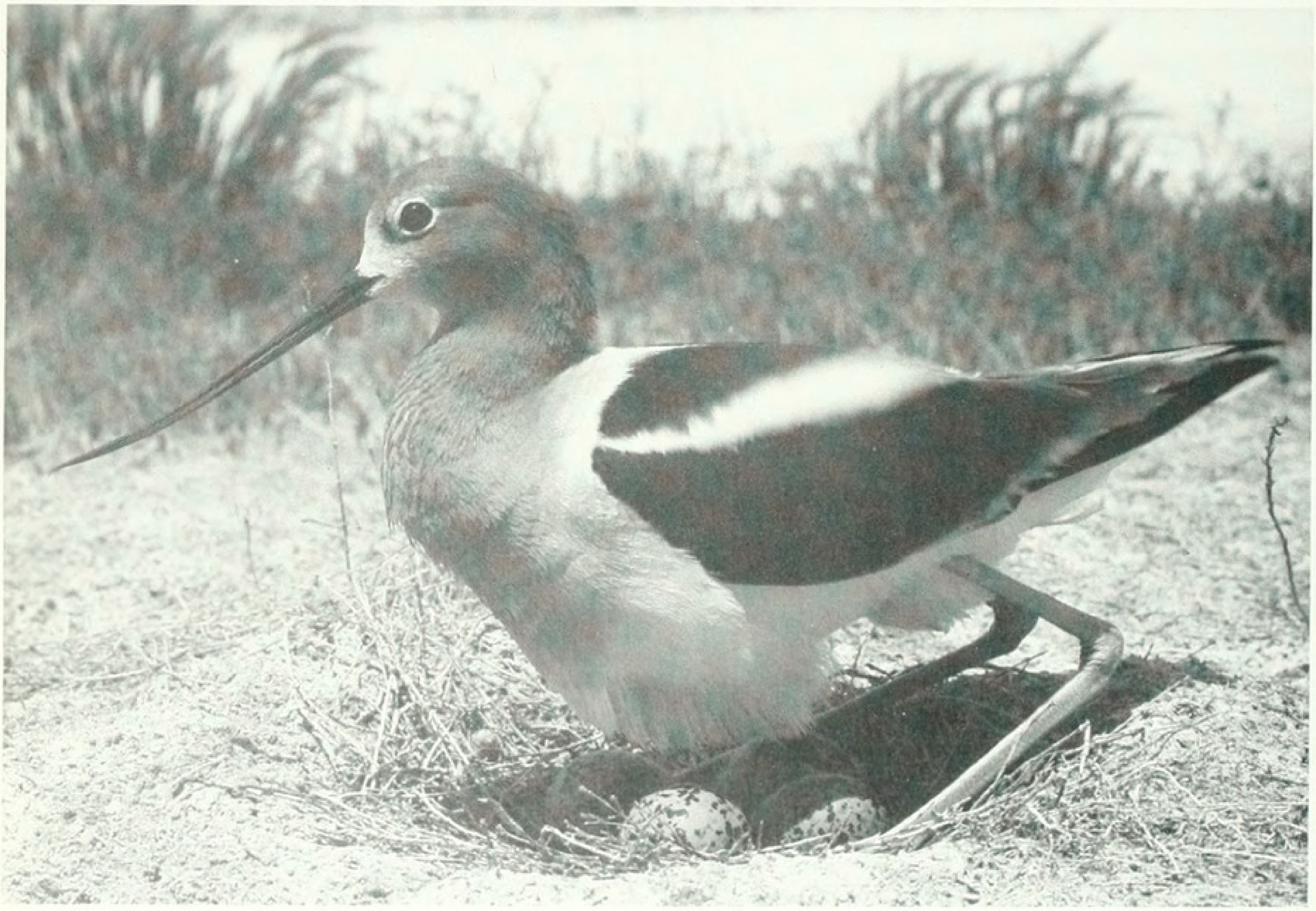

Fig. 24. Avocet at nest. This species was the most important food species found in the eyries of the peregrine in the valley of the Great Salt Lake and also the most frequent shorebird species in the eyries of the Prairie Falcon in the same locality. Photo by R. J. Erwin, 8 June 1959.

Table 5. Prey species in Peregrine Falcon and Prairie Falcon eyries in areas of sympatry along the escarpment of Utah's Wasatch Mountains[1], facing the marshes of the Great Salt Lake.

Prey species	Weight class in grams[2]	Peregrine Falcon n	Peregrine Falcon Percent of total	Peregrine Falcon Percent of biomass	Prairie Falcon n	Prairie Falcon Percent of total	Prairie Falcon Percent of biomass
Duck sp. (yng.)[3]	150	3	2.80	2.75	2	2.63	2.60
Killdeer (*Charadrius vociferous*)	106	2	1.87	1.29	9	11.84	8.26
Willet (*Catotrophorus semipalmatus*)	203	10	9.35	12.38	5	6.58	8.79
Greater Yellow-legs (*Totanus melanoleucus*)	165	3	2.80	3.02	–	–	–
Long-billed Dowitcher (*Limnodromus scolopaceus*)	86	2	1.87	1.05	–	–	–
Sanderling (*Crocethia alba*)	63	–	–	–	1	1.32	0.55
American Avocet (*Recurvirostra americana*)	281	22	20.56	37.10	6	7.89	14.60
Black-necked Stilt (*Himantopus mexicanus*)	152	1	0.93	0.93	–	–	–
Wilson's Phalarope (*Steganopus tricolor*)	58	6	5.61	2.12	–	–	–
Franklin's Gull (*Larus pipixcan*)	295	1	0.93	1.80	–	–	–
Shorebird and Gull Subtotal		50	43.92	59.69	21	27.63	32.20
California Quail (*Lophortyx californicus*)	198	–	–	–	1	1.32	1.71
Ring-necked Pheasant (*Phasianus colchicus*)	807	–	–	–	2	2.63	13.97
Gallinaceous Bird Subtotal		–	–	–	3	3.95	15.68
Mourning Dove (*Zenaidura macroura*)	115	13	12.15	9.12	2	2.63	1.99
Rock Dove (*Columba livia*)	318	5	4.67	9.70	1	1.32	2.75
Dove Subtotal		18	16.82	18.82	3	3.95	4.74
Red-shafted Flicker (*Colaptes cafer*)	137	8	7.48	6.69	1	1.32	1.19
Western Kingbird (*Tyrannus verticalis*)	42	–	–	–	1	1.32	0.36
Horned Lark (*Eremophila alpestris*)	29	–	–	–	1	1.32	0.25
Scrub Jay (*Aphelocoma coerulescens*)	77	1	0.93	0.47	–	–	–
Robin (*Turdus migratorius*)	82	2	1.87	0.99	7	9.21	4.97
Bohemian Waxwing (*Bombycilla garrula*)	56	2	1.87	0.68	–	–	–
House sparrow (*Passer domesticus*)	26	–	–	–	9	11.84	2.03
Western Meadowlark (*Sturnella neglecta*)	89	9	8.41	4.89	18	23.67	13.87
Redwinged Blackbird (*Agelaius phoeniceus*)	54	4	3.74	1.32	–	–	–
Brewer's Blackbird (*Euphagus cyanocephalus*)	68	3	2.80	1.24	1	1.32	0.59
Unidentified blackbird	61	5	4.67	1.86	1	1.32	0.53
Green-tailed Towhee (*Chlorura chlorura*)	30	2	1.87	0.37	–	–	–
Rufous-side Towhee (*Pipilo erythrophthalmus*)	37	–	–	–	2	2.63	0.64
Passerine Subtotal		28	26.16	11.82	40	52.63	23.24
Big brown bat (*Eptesicus fuscus*)	18	1	0.93	0.11	–	–	–
Unidentified bat	10	2	1.87	0.12	–	–	–

Table 5 (Continued)

Uintah ground squirrel (*Citellus armatus*)	250	–	–	–	2	2.63	4.33
Rock squirrel (*Citellus variegatus*)	696	–	–	–	2	2.63	12.04
Unidentified ground squirrel (*Citellus* sp)	400	–	–	–	1	1.32	3.46
Meadow mouse (*Microtus* sp)	60	–	–	–	1	1.32	0.52
Mammal Subtotal		3	2.80	0.23	6	7.90	20.35
Totals		107	99.98 20 species	100.00	76	100.01 21 species	100.00

[1]Most prey items for both species originated from the Peregrine Falcon and Prairie Falcon eyries at site 7 (Table 1, Fig. 1); hence, for the most part, they represent prey species from a common resource.

[2]Weights of all avian species, with exception of the common pigeon, were obtained from Porter, Bushman, and Behle (unpubl. ms); the value for the common pigeon was obtained from Roxie Laybourne, of the U. S. Bureau of Sport Fisheries and Wildlife; weights of mammalian species were estimated from those given by Hall (1946). Those of unidentified bats, ground squirrels, and young ducks were estimated by the authors.

[3]Weight of the young ducks is estimated; young pintails (*Anas acuta*) not yet feathered were in the peregrine eyrie on 13 and 14 June 1947.

dura macroura), Willet (Fig. 25), Western Meadowlark (*Sturnella neglecta*), Red-shafted Flicker (*Colaptes cafer*), Wilson's Phalarope (*Steganopus tricolor*), Rock Dove (*Columba livia*), and two species of blackbirds (*Agelaius phoeniceus* and *Euphagus cyanocephalus*) made up nearly 79 percent of the food items at the eyries. However, in both total biomass (59.7 percent) and in numbers (43.9 percent), the shorebirds comprised the largest segment of the diet, of which the avocet (37.5 percent biomass) (also see White, 1963) and Willet (12.4 percent biomass) were by far the most frequent. This is probably a reflection of the availability of shorebirds in the Great Salt Lake marshes.

Aside from being common, both avocet and Willet may have some conspicuous behavior that makes them easy to capture and that accounts for the numbers taken by the falcons. Tinbergen (1940) has shown that various behavioral peculiarities of certain passerine birds enhance their vulnerability to predation, and F. and J. Craighead (1956), based on the study of the food remains at 20 peregrine eyries, have suggested that the flash patterns of meadowlarks, redwings, and the Blue Jay (*Cyanocitta cristata*) and the conspicuous flight of flickers may increase the vulnerability of these species to predation by the peregrine. This hypothesis may be applicable to the Willet and avocet, both of which have conspicuous flash patterns.

Mourning Doves and Rock Doves were important columbiforme items (18.8 percent of biomass and 16.8 percent of total items). Passerines, woodpeckers, and bats were represented in smaller numbers and biomass (Table 5).

The use of bats for food by peregrines has been reported from Texas by Stager (1941), and desert nesting Shaheen Falcons (*Falco pelegrinoides babylonicus*) of the Middle East, which are either peregrines or are very closely related to them (Vaurie, 1961; White, 1968b; Brown and Amadon, 1968), reportedly hunt bats at dusk (Dementiev, 1951 and 1957). In Indonesia, Mees (1949) reports that wintering tundra falcons seem to be specialized for feeding on bats. He saw one falcon kill seven bats one after another. Fischer (1968) reports that the subspecies of peregrine (*F. p. ernesti*) indigenous to Indonesia also hunts bats.

Fig. 25. Willet (*Catoptrophorus semipalmatus*) on nest. The Willet was an important prey species in peregrine eyries of the Great Salt Lake Valley. This species is inconspicuous while on nest but in flight it, like the stilt and avocet, shows a striking flash pattern. Photo by R. J. Erwin 1959.

Table 6. Prey species in two Peregrine Falcon eyries in Utah's desert (sites 4 and 28, Table 1, Figs. 1, 9, and 22).* C=Colorado Plateau, GB=Great Basin.

	Weight class in grams	No.	Percent of total	Percent of biomass
Chukar (*Alectoris graeca*) (C)**	520	1	5.26	26.52
American Coot (*Fulica americana*) (GB)**	365	1	5.26	18.60
Mourning Dove (*Zenaidura macroura*) (C, GB)	115	2	10.53	11.73
Common Nighthawk (*Chordeiles minor*) (GB)**	62	1	5.26	3.16
Ash-throated Flycatcher (*Myiarchus cinerascens*) (C)**	29	2	10.53	2.96
Say's Phoebe (*Sayrnis saya*) (C)**	21	1	5.26	1.07
Horned Lark (*Eremophila alpestris*) (C, GB)**	29	3	15.79	4.44
Pinon Jay (*Gymnorhinus cyanocephala*) (C)**	116	1	5.26	5.92
Western Meadowlark (*Sturnella neglecta*) (GB)	89	1	5.26	4.54
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) (C)**	92	3	15.79	14.07
Redwinged Blackbird (*Agelaius phoeniceus*) (C, GB)	54	2	10.53	5.51
Lark Sparrow (*Chondestes grammacus*) (GB)**	29	1	5.26	1.48
Unidentified Passerines (C)				
Passerine Subtotal		14	73.68	39.99
Desert Totals		19	99.99	100.00
			12 species	

*See footnote for Table 5.
**Not recorded in Wasatch Mountain eyries (see Table 5).

Eyries adjacent to the Great Salt Lake contained no full-grown waterfowl despite the abundance of waterfowl in the adjacent marshes, although the peregrine has been observed eating or pursuing full-grown ducks of several species during the breeding season. These include the Gadwall (*Anas strepera*) (observed 5 May 1938, field notes of R. G. Bee), a teal (H. Austin, pers. comm.), a teal on 10 April 1948 at Ogden Bay (Porter), and the Redhead (*Aythya americana*) (Wetmore, 1933). Calvin Wilson (pers. comm.) has watched peregrines from an eyrie in the Wasatch Mountains eating Ruddy Duck (*Oxyura jamaicensis*), Cinnamon Teal (*Anas cyanoptera*), Pintail (*Anas acuta*), and American Coot (*Fulica americana*) on dikes of a nearby marsh. R. J. Erwin (unpubl. data) flushed a peregrine from the side of a highway in Grand County in April 1958, where it had just captured an adult Mallard (*Anas playtrhynchos*).

Cade, White, and Haugh (1968), on the other hand, found that waterfowl constituted nearly 50 percent (biomass) of the food items in the eyries of the Alaskan taiga peregrine (*F. p. anatum, sensu lato*). Utah peregrines are smaller, however, than those of interior Alaska. The absence of ducks in the Wasatch Mountain eyries may possibly be explained on the basis of the weight of the prey item in relation to the distance that peregrines must carry it to their eyries. A full-grown duck may be too heavy for peregrines to carry the several miles from the Great Salt Lake marshes to eyries along the Wasatch escarpment.

Shorebirds were not present in two desert eyries. One eyrie was located near a marsh in the Great Basin and the other near a river in the desert of the Colorado Plateau. The availability of a variety of marsh and shorebirds to the peregrines at the desert eyries in the Great Basin (Table 6) accounts for the presence of the coot. The coot in the Great Basin desert eyrie probably came from a pond (desert spring) which was only about 1,200 yards (1,097 m) from the eyrie site. Since its weight (400 g) is about the same as that of a duck, it is possible that its absence from the Wasatch Mountain eyries may have been for the same reason that ducks were missing from these eyries. The small sample-size of food items probably accounts for the absence of shorebirds in this desert eyrie.

At a Wasatch Mountain eyrie, observed by R. D. Porter (site 7, Table 1) for the first two weeks after hatching, only one, and at most, two, prey items were found each day in the nest; these usually consisted of Redwinged Blackbirds, Mourning Doves, Willets, and meadowlarks. But as the nesting season progressed, a greater number of species and items were brought to the nest. On 28 June 1952, for example, about three weeks after hatching of the young falcons, the female returned with a young Willet at 11:00, a robin-sized bird at 11:50, and an unidentified item at 17:20. The male returned with a young avocet at 15:20 and a leg of a young avocet at 15:45. The next day the male brought a Wilson's Phalarope to the nest and the female an avocet. Other items found in the nest on 29 June were Scrub Jay (*Aphelocoma coerulescens*), unidentified blackbird, big brown bat (*Eptesicus fuscus*) and one adult and one immature Wilson's Phalarope. Of the shorebirds brought to the young at this eyrie (site 7, Table 1) during the years it was observed, 33 percent were partially fledged young of the season. Peregrines nesting along the face of the Wasatch Mountains traveled several miles to obtain the marsh and shorebirds (Table 4); other species were obtainable much closer to the eyries.

Despite the peregrine's reported antipathy to capturing food on or near the ground (Bond, 1936a), mammalian prey species such as the brush rabbit (*Sylvilagus bachmani*) (Bond, 1936c), rats (*Rattus* sp.) (White, et al., 1973), and certain gallinaceous birds (ptarmigan, *Lagopus* sp.) (Cade, 1960; White and Cade, 1971) also are taken for food occasionally. Bond (1946) reported that peregrines commonly brought Horned Larks to their small young. The Horned Lark, which is essentially a ground-dwelling species, is one of the most abundant birds in Utah's salt desert scrub vegetation. It was present in peregrine eyries in both the Colorado Basin and Great Basin deserts of Utah (Table 6).

Much of the desert lowlands and foothills of Utah are vegetated with desert scrub and with pigmy conifer forests, respectively, yet the peregrine was not known to nest far from water in those areas where the Horned Lark of necessity would have been an important item in its diet. Jays (*Aphelocoma* and *Gymnorhinus*), kingbirds (*Tyrannus*), Ash-throated Flycatcher (*Myiarchus cinerascens*), Lesser Nighthawks, Red-shafted Flickers, Robins, Mourning Doves, and Black-throated Gray Warbler (*Dendroica nigrescens*), some of which are known to be used as prey by the peregrine, are available in the pigmy forests, yet the peregrine nests in these areas only when water or marshes are nearby.

A more intensive study of the peregrine's food habits in Utah during nesting season undoubtedly would have revealed a much wider variety of prey species, especially the smaller passerines. In terms of biomass, however, the smaller species of birds probably would not have altered appreciably the percentages of each category of birds.

The abundance of doves in Utah eyries is not surprising, despite the availability of marsh and shorebirds, since the domestic pigeon has been found to be a favorite prey species of the peregrine, not only in the eastern United States, but also in many other areas of the peregrine's cosmopolitan distribution (Hickey and Anderson, 1969).

The Utah peregrines utilize a wide variety of prey species (at least 29 species, see Tables 5 and 6) during the nesting season, and in this respect their diet is more comparable to that of populations elsewhere in North America than to that of populations in the Queen Charlotte Islands, where Beebe (1960) found them limited mostly to one and not more than four prey species during the nesting season. On Amchitka in the Aleutian Islands, White, Emison, and Williamson (1973, in press) list 32 species in the peregrine's diet, most of which were found in the nests, and comprised principally marine birds, waterfowl, gulls, and shorebirds. Shorebirds were represented frequently in the eyries of peregrines along the Colville River of Alaska (White and Cade, 1971). Cade, White, and Haugh (1968) reported 49 prey species in eyries located in the taiga zone of the Arctic, and Cade (1960) found 21 species in nests located in the tundra zone.

NESTING BEHAVIOR IN UTAH

History of Nesting at a Wasatch Mountain Eyrie

Eyrie sites of the Peregrine and Prairie Falcon at a cliff on the escarpment of the Wasatch Mountains (Table 1, site 7; Fig. 26) were observed by R. D. Porter, R. J. Erwin, and others from 1943 through 1952, exclusive of two war years, 1944 and 1945. We obtained data at this cliff on interspecific competition between the two species and on productivity, incubation periods, and reproductive failure for the peregrine, all of which will be discussed under separate headings.

The cliffs were composed of quartzite and faced westerly along the west-facing escarpment of the mountains and southerly along a south-facing edge of a side canyon. Peregrines were first noted there on 3 April 1943, the year the cliff was first under our observations, by R. J. Erwin and J. F. Poorman, and again that year by J. F. Poorman and R. L. Porter on 15 April. A nest containing three eggs was found on 26 April. Prairie Falcons were also first noted at this cliff in 1943. A summary of the reproductive history of the peregrines at this site is given in Table 7. The physical characteristics of the various peregrine and Prairie Falcon sites utilized during the period of study are given in Table 8. The photographs represented by Figures 27–39 were taken in 1947, 1948, and 1952.

In 1949 the peregrines defended a nesting

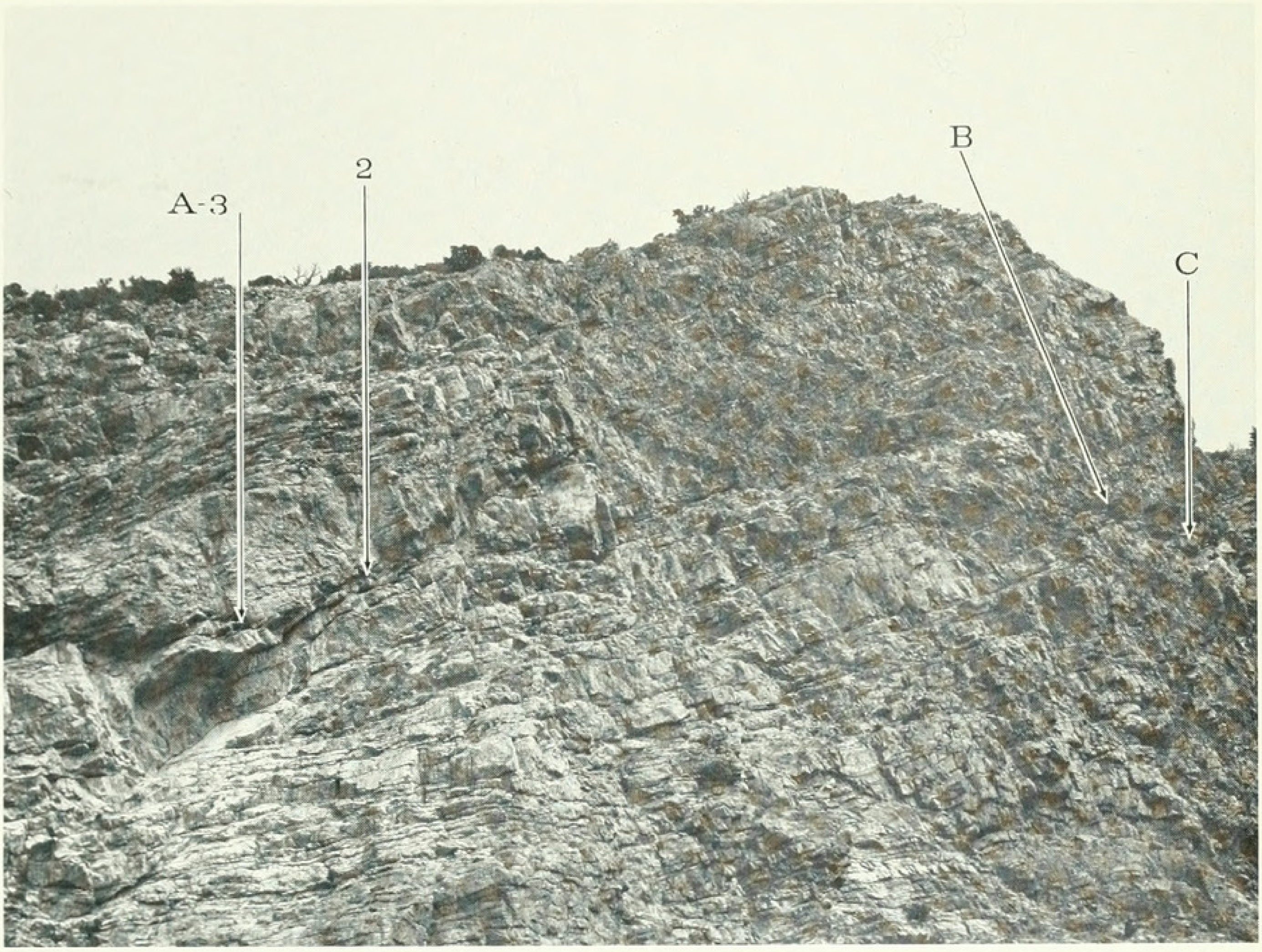

Fig. 26. A cliff along the escarpment of the Wasatch Mountains which contained eyries of both the Peregrine Falcon and the Prairie Falcon (Table 1, site 7). The Peregrine Falcons used site A-3 in 1943, 1952, and 1953; site B in 1946 and 1947; and site C in 1948 and 1951. The Prairie Falcons used site 2 in 1948; site A-3, 1949; and site 1, to the north (not shown in photograph) of site A-3, in 1943 and 1950. Sites B and C faced south, sites 1, 2, and A-3 faced west. Photo by R. J. Erwin, 1972.

ledge, which contained two nest scrapes, but apparently laid no eggs. They defended several sites on the cliff in 1950 but with less tenacity than usual. Although they made 20 to 25 scrapes along several hundred feet of ledge, no eggs were found. Between 4 March and early June the cliffs were searched for an eyrie 10 times without success. The behavior of the birds suggested the presence of a nest at numerous places along the cliff. However, each new section of cliff was defended with nearly equal spirit.

In 1952, the two young at site A (Fig. 26 and Tables 7 and 8) were measured and weighed from date of hatching until 13 August. They were removed from the nest on 5 July. R. J. Erwin banded three young peregrines at the 1943 site in 1953. He obtained no information on egg number or occurrence of Prairie Falcons.

A new female peregrine nested at alternate site A in 1952. She still had some immature

Fig. 27. Five-egg clutch of Peregrine Falcon (eyrie site 7-B, Table 1, 1947). Note the wood rat (*Neotoma* sp.) scat on ledge and about the eggs. Photo by R. D. Porter.

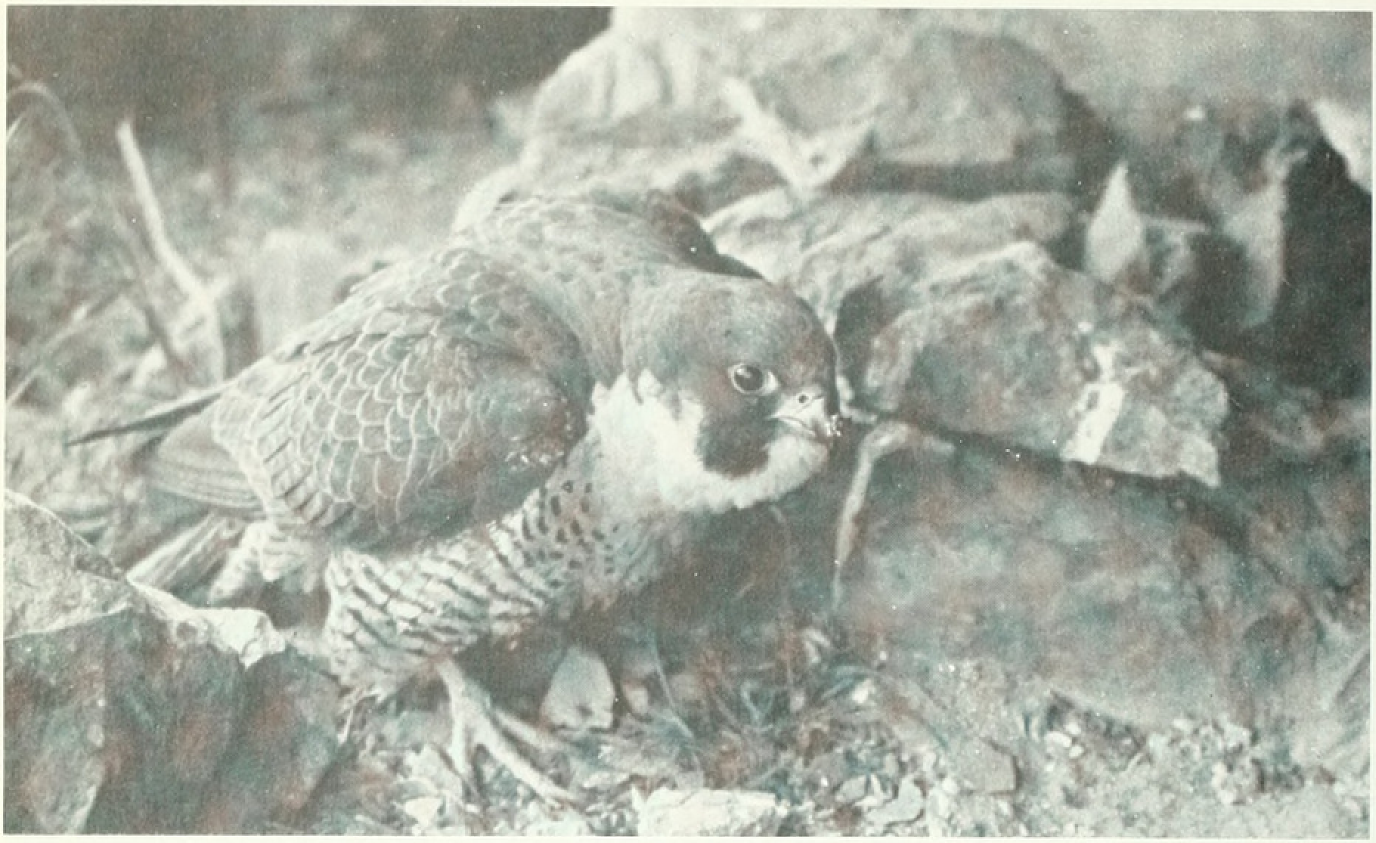

Fig. 28. Female peregrine entering eyrie. Photo by R. D. Porter and R. J. Erwin, 1948.

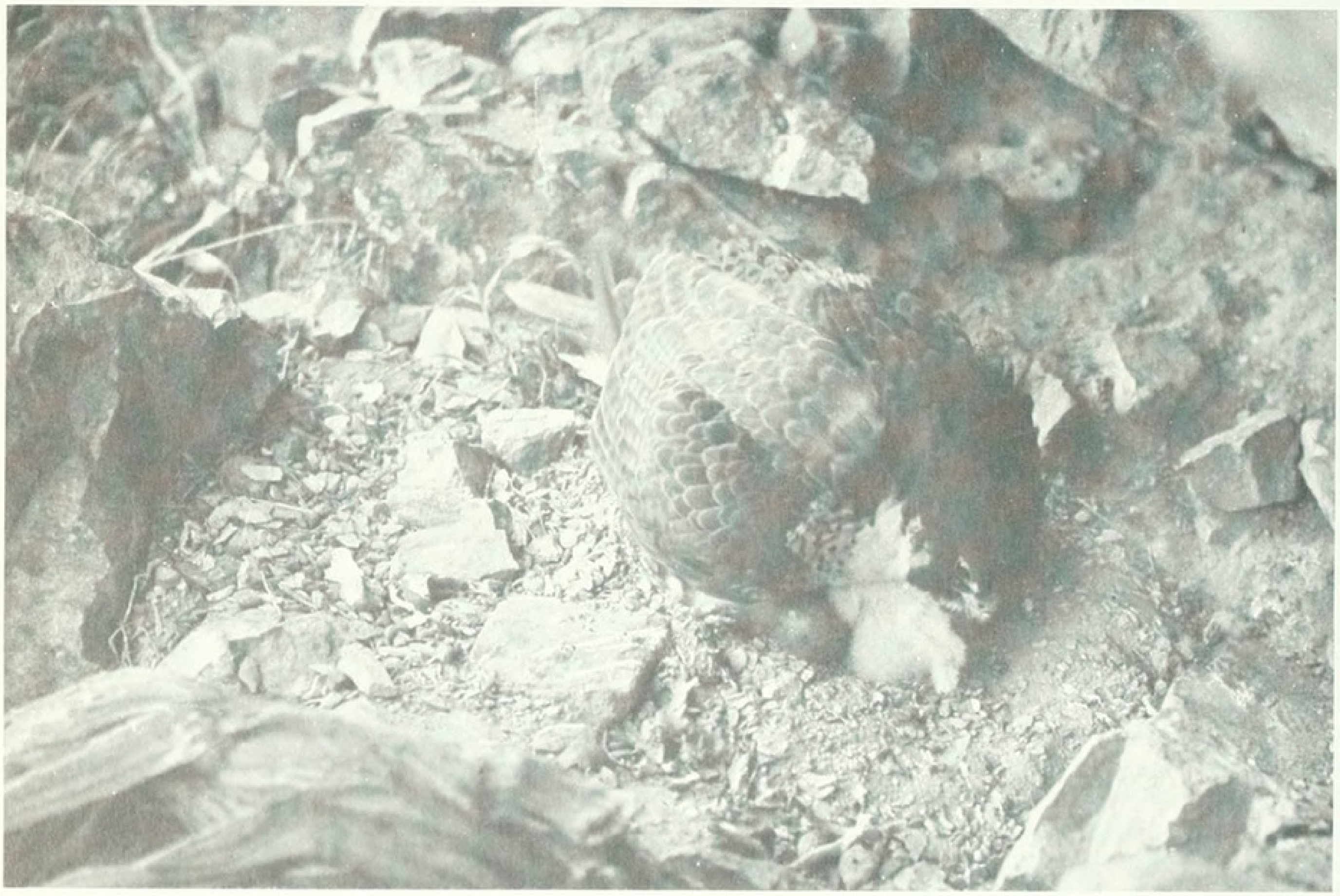

Fig. 29. Female peregrine settling down over nestlings which are only a few days old (Table 1, site 7, alt. site C). Photo by R. D. Porter and R. J. Erwin, 1948.

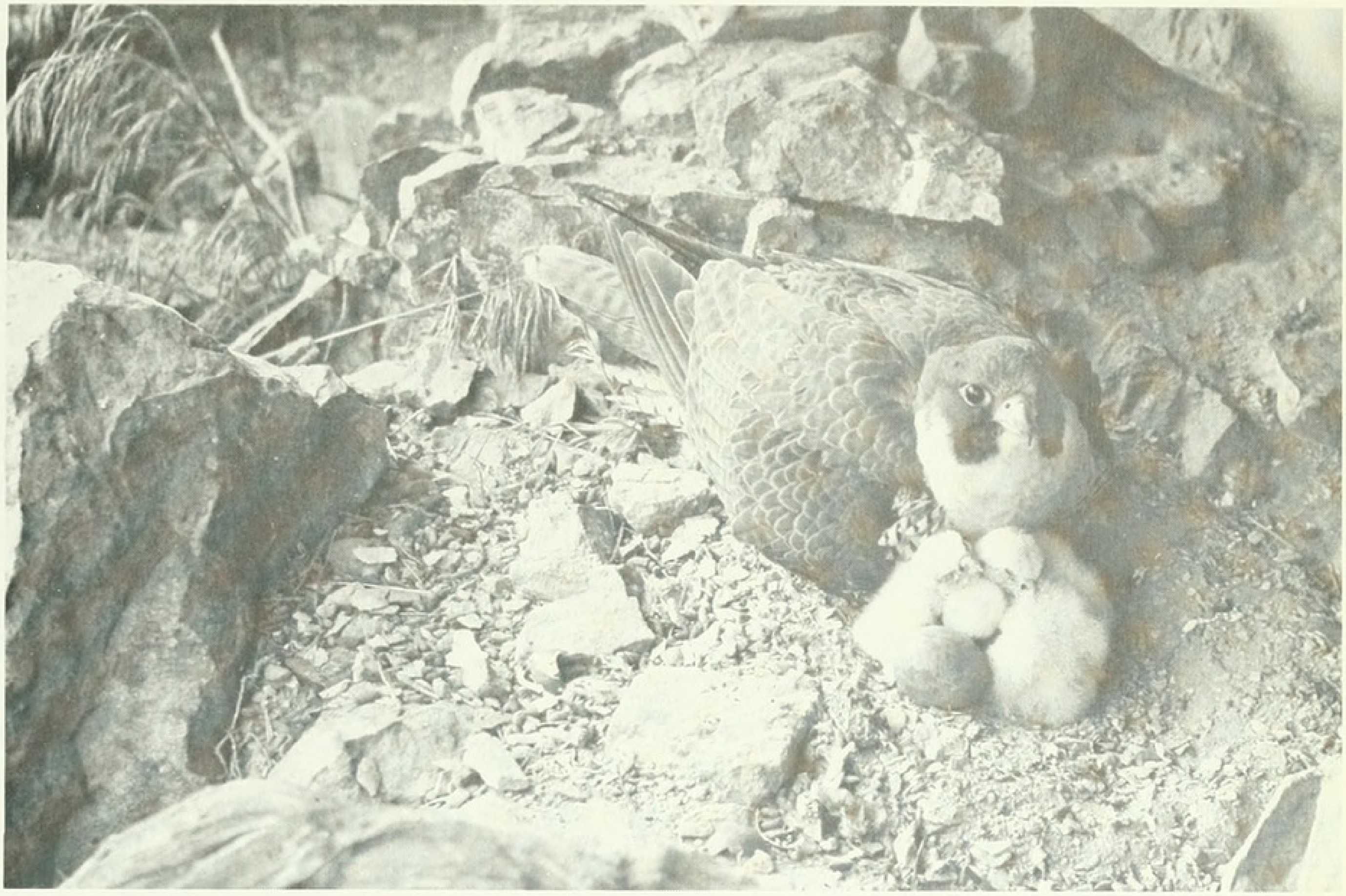

Fig. 30. Female peregrine brooding young. Note addled egg. Photo by R. D. Porter and R. J. Erwin, 1948.

Fig. 31. Female peregrine with young, in defensive attitude. Photo by R. D. Porter and R. J. Erwin, 1948.

Fig. 32. Female peregrine feeding young. Photo by R. D. Porter and R. J. Erwin, 1948.

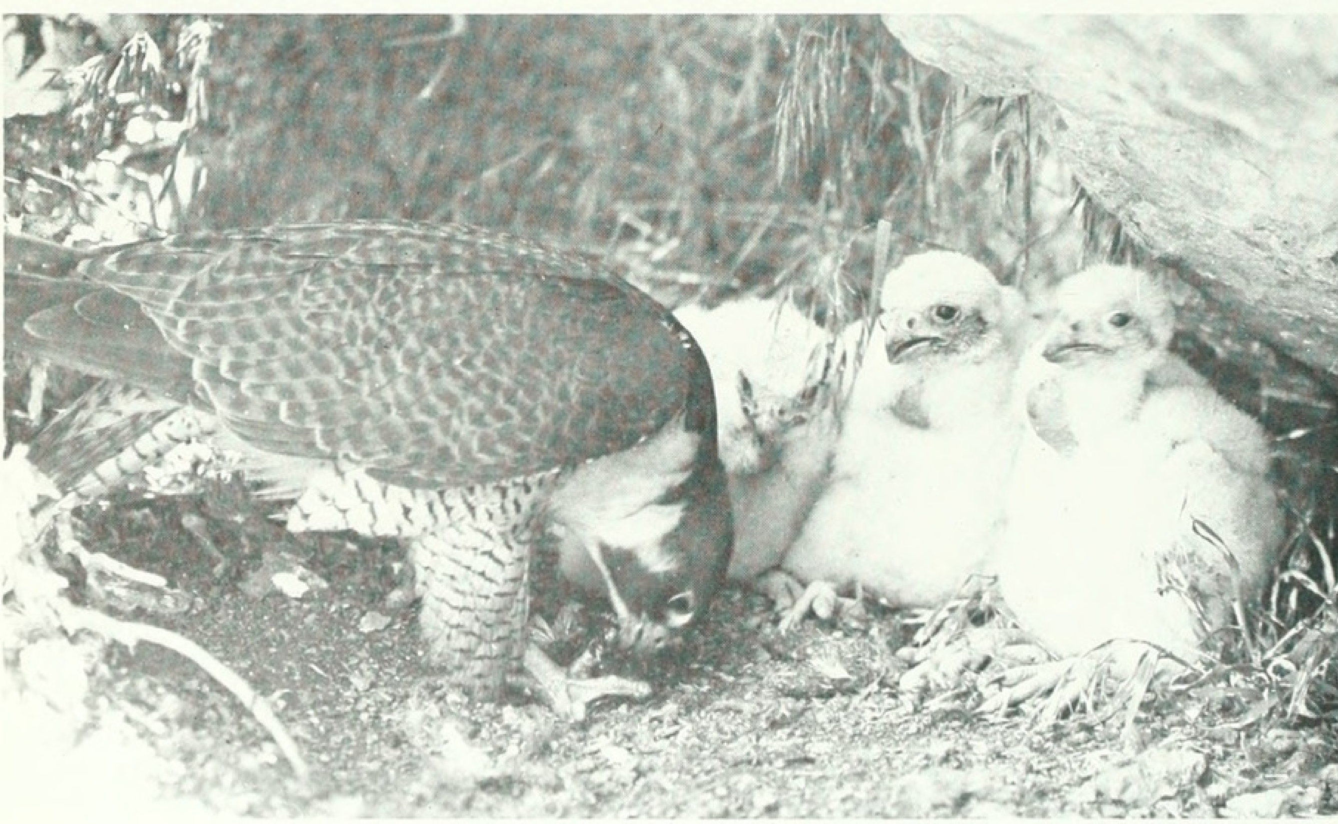

Fig. 33. Female peregrine feeding young which were nearly 3 weeks old (eyrie site 7, alt. site B, Table 1). Photo by R. D. Porter, 1947.

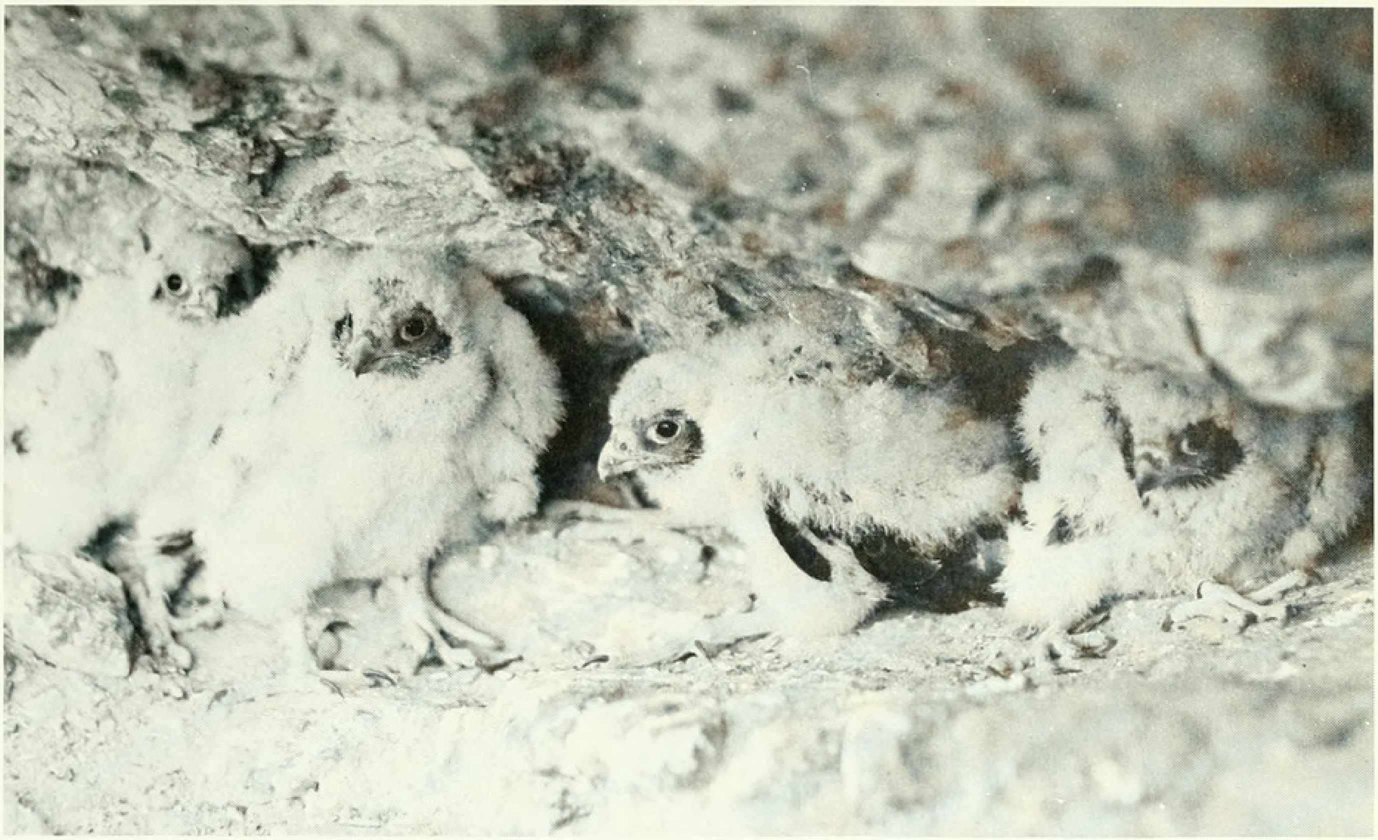

Fig. 34. Young peregrines at approximately 4 weeks of age (eyrie site 7, alt. site C). Photo by R. D. Porter and R. J. Erwin, 1948.

Fig. 35. Young peregrines about 6 weeks of age, nearly old enough to fledge (eyrie site 7, alt. site C). Photo by R. D. Porter, 1947.

Table 7. Reproductive history of the peregrines at a Wasatch Mountain eyrie (site 7, see Tables 1 and 8, and Figs. 26–29).

		EGGS				NESTLINGS			
Year	Alternate site location	Dates recorded	No.	Probable date of 1st egg	Incubation period (in days)	No.	Dates hatched	Other dates of record	Misc. Data
1943	A	26 April	3	–	≤37 (3rd egg)	3[1]	unknown	31 May	
1946	B	–	–	–	–	unknown	4	unknown	26 June	Young nearly fledged, two taken
1947	B	26 April	3	21-22 April	35-37 (3rd egg)	3	unknown	31 May	Downy young
		17 May	5?						
1948	C	16 April	3	11-12 April	42-44 (3rd egg)	4	28-29 May	29 May	
		19 April	4		39-41 (4th egg)				5 eggs, 1 pipped 27 May; 4 young + 1 addled egg, 29 May
		27 May	5						
								29 June	4 young, 2 taken[2]
								5 July	young fledged[2]
								17 July	young full grown[2]
1951	C	2 May	3		unknown	0	–		
		3 May	3						
		13 May	2						
		19 May	0						
1952	A	29 April	1[3]	29 April	37 (egg 1)	0[4]	–	4 June	2 eggs pipping
		1 May	1[3]			2	5 June, 07:00	5 June	1 hatched, 1[5] nearly hatched
		27 May	3						
		31 May	3	–		2		7 June	both hatched
		1 June	3	–					
1953	A	–	–	–	unknown	3	–	–	

[1]Three young were about ready for flight when two were taken for falconry sometime in early July. [2]29 June: 4 young, 2 males, 2 females; females taken for falconry; oldest male, tail half grown, flew from nest. 5 July: 1 young male, still on nest ledge, flew at approach of observer, first male to leave nest on rock above nest. 17 July: females taken from nest about full grown. [3]Marked with a numeral 1 in India ink. [4]Two eggs pipping, one with small hole (egg 1), other barely dented, young peeping inside both eggs, loudest in egg marked with numeral 1; marked egg weighed 47 g, other pipped egg, 50 g, and unpipped egg, 48 g. [5]Shell around abdomen and legs; it probably hatched on 6 June; third egg addled.

feathers (see Figs. 36-38), and was undergoing a molt as evidenced by the fact that on 28 June the upper surface of the wings had just begun to molt into the adult plumage. The molt on the back (capital and spinal feather tracts) and the lower breast (ventral tracts) was nearly complete, while that of the primaries and rectrices had only begun. The capital tracts of the head were only partially molted. While the female was in flight, it was noted that at least one primary was missing on each wing as well as at least one retrix on each side of the tail.

The plumage condition of this bird indicates that she probably was no more than three years of age. Records of breeding peregrines while still in their immature plumage are not common. Beebe (1960) noted no instances of mated pairs in immature plumage, or even in plumage showing traces of immaturity, in a rather large sample of pairs along the northwest Pacific Coast. However, Herbert and Herbert (1965) pointed out two instances of immature-plumaged females occupying an eyrie, neither of which was found to lay eggs. Hickey (1942) reported on three immature, one-year-old females that failed to lay eggs and a fourth that brooded a clutch of two eggs, making a total of only one first-year female out of 34 falcons over a two-year-period in New York. A report by Herbert of two females believed by him to be two-year-old birds, both of which laid only two eggs in different years, also was mentioned by Hickey (1942). White and J. R. Haugh (pers. obser.) found one female, out of 17 pairs breeding on the Yukon River in 1966, that was essentially still in the streaked brown immature plumage. Therefore, it was thought to be but one year old. She laid two fertile eggs, one of which hatched.

Egg Laying

At the alternate site A eyrie (Table 1, site 7) egg laying began between 12 and 29 April (1943-1952) as estimated by counting back from known dates certain eggs were laid (Table 7). Published records for the state range from about 22 March (counting back from 30 March as given by Johnson, 1899) to the second or third week in May (counting back from 20 May given by Bee and Hutchings, 1942). The first egg of a three-egg clutch found by White and Lloyd (Table 1, site 28) was probably laid around 6 May, as indicated by the date of hatching. At the aforementioned eyrie in the Wasatch Mountains (Table 1, site 7), 3.8 eggs (range 3–5) on the average were laid per year during the five

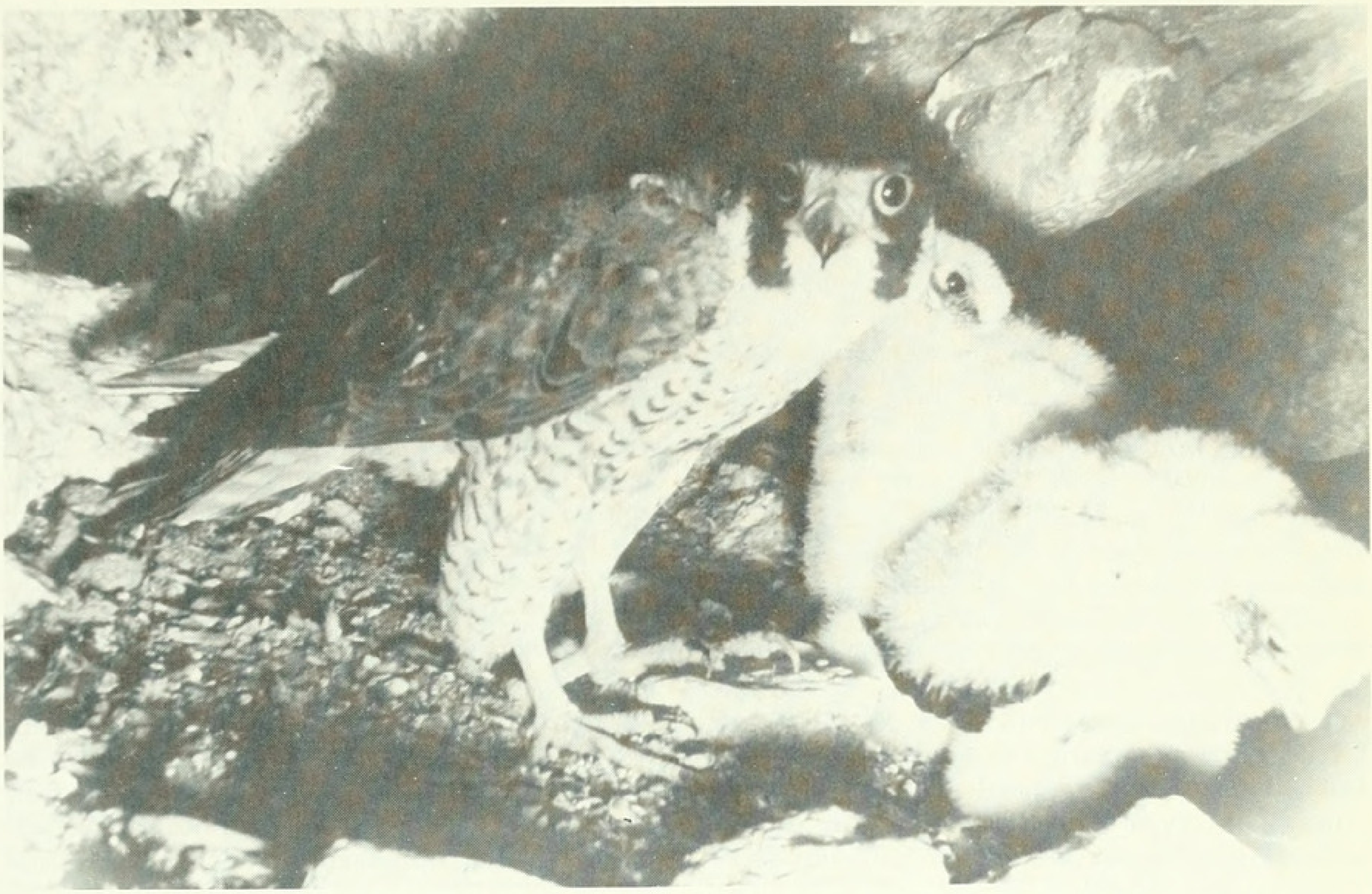

Fig. 36. A view of female peregrine with unmolted immature plumage. Her two young are about 3 weeks old (eyrie site 7, alt. site A). Photo by R. D. Porter, 1952.

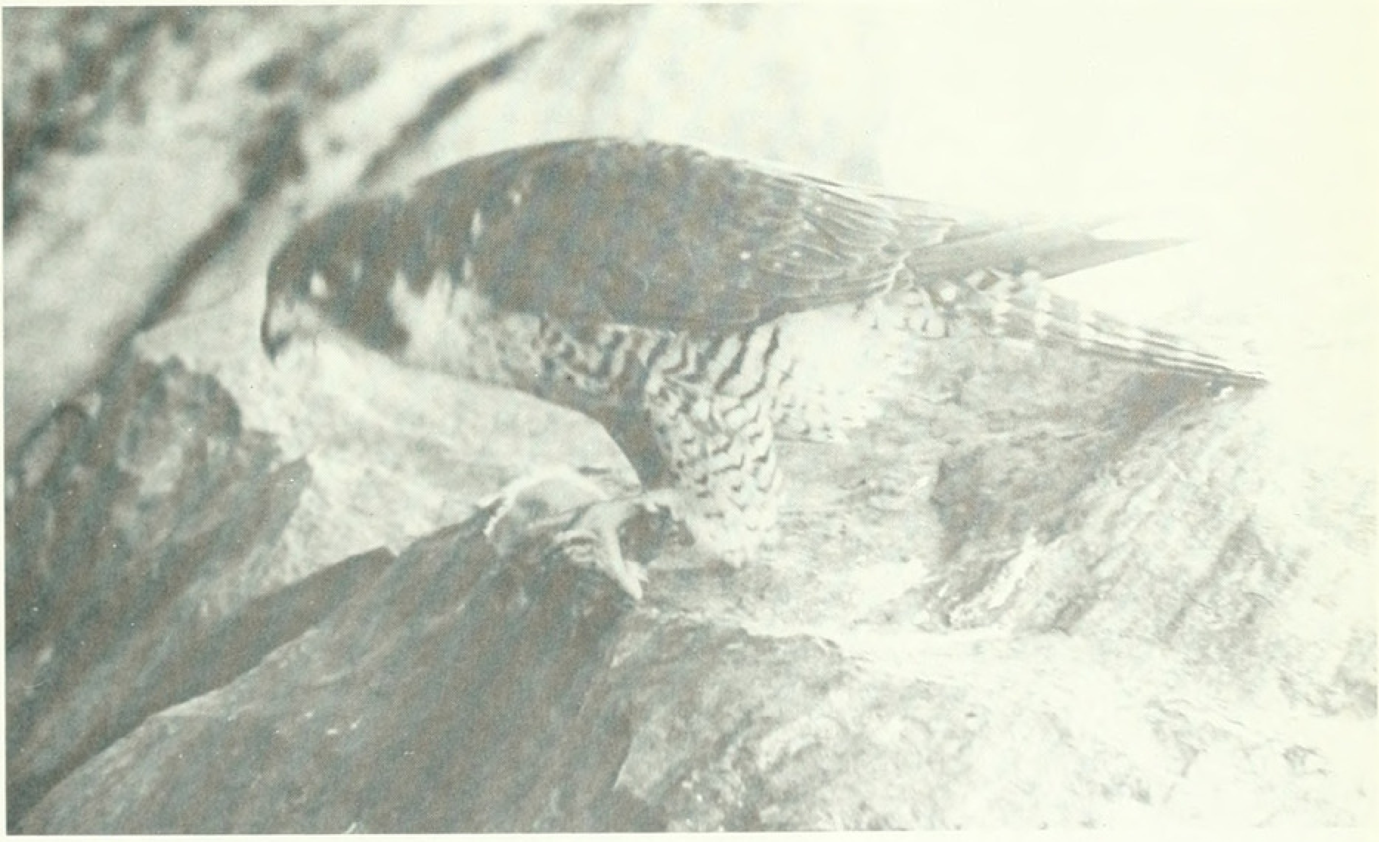

Fig. 37. Same female as in Fig. 36. This bird is certainly not more than three years old because of the amount of immature plumage retained. Note that most of the tail, secondary wing feathers, and greater wing coverts are immature feathers. Photo by R. D. Porter, 1952.

Table 8. Physical characteristics of eyrie sites at a cliff in the Wasatch Mountains (Table 1, site 7, see Figs. 26-39) used by both peregrines (Pe) and Prairie Falcons (Pr). Values in parentheses represent metric equivalents.

Alt. site	Approx. dist. in ft (m) from site A to site	Species[1] and year used	Cliff height, ft (m)	Eyrie height, ft (m)	Direct facing	Ledge length, inches (m)	Ledge width, inches (m)	Dist. Eyrie below overhang, inches (m)	Nest area ft² (m²)	Dia. nest scrape, inches (m)	Depth soil, inches (m)
A-3[2]	0	Pe 1943	110	85	W	72	62	20	7.42	6.9	2
		1952	(34)	(26)		(1.8)	(1.6)	(0.51)	(0.69)	(0.18)	(0.051)
		1953									
		Pr 1949									
B	320	Pe 1946	135	90	S	120	60	18	6.45	–	–
	(98)	1947	(41)	(27)		(3.0)	(1.5)	(0.46)	(0.60)		
C	350	Pe 1948	135	90	S	156	48	35	6.55	6.4	
	(107)	1951	(41)	(27)		(4.0)	(1.2)	(0.89)	(0.61)	(0.16)	–
1[3]	300	Pr 1943	110								
	(91)	1950	(34)	–	W	–	–	–	–		–
2[2]	55	Pr 1948	110	95	W	61	90	21	21.8	–	2
	(17)		(34)	(29)		(1.5)	(2.3)	(0.53)	(2.0)	–	(0.051)

[1]Prairie Falcons were not recorded in 1947, 1952, and 1953; were seen, but no nest was found in 1951.
[2]All values were obtained by direct measurements at eyrie sites; all other values given in the table, except cliff and eyrie heights, distances between eyrie sites, are approximations from photographs, using a peregrine's egg or the adult peregrine as a unit of measurement.
[3]Exact eyrie site was not reached.

years that eggs were found (see Fig. 27), and 2.4 of the eggs (range 0–4) on the average hatched. The eyrie produced a total of 19 young during the seven years it was known to have been active, for an average of 2.7 young per year. Although the number of fledged young was not ascertained, no young were known to have died in the nest. Eight young, however, were removed for falconry when nearly fledged.

These values approach those for the peregrine

Fig. 38. A close-up of same female as in Fig. 36. Photo by R. D. Porter, 1952.

in eastern North America, where Hickey (1942) found the average clutch size to be 3.72 and the average number of downy young to be 3.0. For western North America, Bond (1946) reported an average clutch size of 3.7 and Cade (1960) recorded an average of 2.7 eggs per clutch in northern Alaska and 3.1 eggs per clutch in other locations in the Arctic.

Incubation

The eggs are laid usually at two-day intervals, and occasionally at three (Cade, 1960; Herbert and Herbert, 1965; Demandt *in* Fischer, 1967). On the Hudson River, incubation generally began on the fifth day with the laying of the third egg and averaged 32–33 days from time of commencement until the hatching of the last egg (Herbert and Herbert, op. cit.). The incubation period is determined best by checking the time between the last egg laid and the last young hatched (Nice, 1954), providing that all eggs hatch. Although the incubation period in the peregrine is said to be 28–29 days (Witherby, et al., 1939; Dementiev, 1951; Herbert and Herbert, 1965), there is still some uncertainty regarding its exact length, as suggested also by Nelson (1972), who believes it to be closer to 32 to 34 days in *F. p. pealei*. If the incubation period for the fifth egg is 28 to 29 days, and not more than two days elapse between the laying of each egg, the period between laying of the fourth egg and the hatching of the fifth egg would be 30 to 31 days; between the laying of the third egg and the hatching of the fifth, 32 to 33 days; between the second and the fifth, 34 to 35 days; and between the first and the fifth egg, 36 to 37 days. In four-egg clutches, the intervals between the laying and hatching of the third and fourth egg would be 30 to 31 days; between the second and the fourth egg, 32 to 33 days; and between the first and fourth egg, 34 to 35 days. For three-egg clutches, the intervals between the laying of the second and third eggs would be 30 to 31 days; and between first and third eggs, 32 to 33 days. If, as reported by Nelson (ibid.), the incubation period is 32 to 34 days, 4 to 6 additional days must be added to each of the above values.

At the Wasatch Mountain eyrie (Tables 1 and 7, site 7), the incubation period in 1947 and 1952 was close to that given by Nelson (op. cit.) for *pealei*. In 1948, however, it seemed to have lasted abnormally long. The period from laying to hatching was about 40 days (39 to 41) for the fourth egg and at least 42 days (42 to 44) for the third egg, which is about 10 days longer than that expected using the 28 to 29 day period. This could be explained if the first clutch was destroyed within a day or so after the fifth egg was laid and if the first egg of a new clutch was laid a day or two later. This would increase the observed incubation period by about 10 days. This phenomenon has been reported in captive American Kestrels (*Falco sparverius*) (Porter and Wiemeyer, 1972).

In 1952, the period between the laying and hatching of marked egg number one was about 37 days. It likely was laid the day it was first found or the day before. Unfortunately, the period of 36 to 37 days corresponds closely to the expected incubation period for the first egg of a five-egg clutch, if the incubation period is 28 to 29 days, as well as that expected for the first egg of a three-egg clutch if the incubation period is 32 to 34 days.

The 32- to 34-day period seems to fit our data better than does the 28- to 29-day period. Additional observations are needed to resolve this problem.

Two days elapsed between the pipping of the first egg to hatch and the fourth egg to hatch (a fifth egg did not hatch) in 1948. Only one day elapsed between pipping and hatching of egg number one in 1952 and the same was probably true of the second egg as well. This appears to agree with Hall's (1955) observation in 1943 on the Sun Life peregrines, which hatched two eggs on each of two successive days. Porter and Wiemeyer (1972) reported a two-day interval between the hatching of the first and the last egg of five-egg clutches of captive kestrels. The kestrels frequently began incubation with the laying of the fourth egg. Unlike the peregrines of the lower latitudes, those in the Arctic reportedly initiate incubation with the laying of the first egg (Cade, 1960; Dementiev, 1951). Cade (1960) reported as much as a week's difference between the ages of the youngest and oldest nestlings in four-egg clutches in the Arctic.

PEREGRINE DECLINE IN UTAH

The peregrine in Utah, as elsewhere in the United States and in Europe (Hickey, 1969), declined precipitously in the past two decades. To our knowledge, only two or three of the 29 eyries known to occur in Utah over the past several decades are still active. Nelson (1969) reported that before 1942, 50 percent of the "9 or 10" (9, Nelson, pers. comm. 1969, see Table 1) eyries located by him between 1939 and 1942 around the Great Salt Lake were taken over by Prairie Falcons, and by 1948 only three or four of them were left. White (1963), however, noted that five of these eyries (Table 1, sites 4, 7, 8, 10, and 13) were still active as late as 1952, and two additional eyries (sites 17 and 18) are known to have been active in 1952 (C. Ward, pers. comm.), indicating that some of them were overlooked by Nelson (1969) or else previously unoccupied eyries were reactivated later. However, White's (1969b) report of the occupancy by peregrines in 1954 of an eyrie which earlier in the century (1927) was used by Prairie Falcons (Wolfe, 1929) suggests that the reverse situation also may have taken place.

The usurpation of peregrine eyries by Prairie Falcons may not have been permanent, as suggested by our observations of the two species utilizing one another's eyries in Utah. Nelson (1969) indicates that he was unaware of the utilization of alternate nesting sites by the peregrine between 1939 and 1942, which increases the possibility that some of the peregrine locations believed to have been taken over by Prairie Falcons at that time were still being utilized by peregrines nesting at alternate eyries.

By 1956, only four of the 20 known eyries along the Wasatch Front were active. No young have been known to fledge from any of these eyries since then (White, 1963), although one adult was seen at each of two eyries in 1969 (Table 1, sites 8 and 18), and a third is reportedly still active. Only two or three eyries were believed to have been active by 1969 in the entire state, which represents only about 10 percent of the total known to occur earlier. On the other hand, there are vast areas in Utah with seemingly appropriate ecological conditions that have remained virtually unexplored for falcons. It is possible that 10 or more eyries exist in these areas. It is interesting to note that the eyries in the more remote parts of Utah remained active nearly a decade longer than did those in the more populous and more intensively cultivated areas.

Climatic Change Hypothesis for Peregrine Decline

Nelson (1969) has hypothesized that the reduction in numbers of active eyries in Utah was caused by a combination of rising average temperature and drastically reduced precipitation, starting about 1870. He suggested that these changes resulted in the drying up of small lakes and ponds and the lowering of the surface water areas of larger lakes, causing a critical reduction in the habitat for the prey species of the peregrine in Utah and in other areas of the northwestern United States. According to Nelson (ibid.) by 1961 the drought gave way to more moderate conditions resulting in habitat changes more suitable to the peregrine.

Besides the drought conditions reported by Nelson (1969), river waters were diverted for irrigation and the vegetation adjacent to the marshes was overgrazed by livestock (Behle, 1958). By 1910, thousands of once productive acres of heavily vegetated marshlands along the shores of the Great Salt Lake, with their smaller lakes, ponds, and channels of fresh water, became mud flats with stagnant pools of alkaline water. Ultimately these changes caused the death of thousands of ducks, shorebirds, and marshbirds due to botulism (Wetmore, 1915, 1918; Behle, 1958). It was not until after the completion of the Bear River Migratory Waterfowl Refuge between 1932 and 1935 and the Ogden Bay and Farmington Bay refuges in about 1941 that these marshes regained much of their former vitality and productivity.

Some changes took place as late as the early 1950s in the marshes further removed from the lake. Weller, Wingfield, and Low (1958), for example, recorded a drastic change in the size of the Knudson Marsh, four miles west of Brigham City, Utah, between 1950 and 1955. They attributed the changes to a deepening of the water channel entering Bear River Refuge, an increased demand for irrigation waters, a below average rainfall between 1952 and 1954, and overgrazing by cattle. The change in size of the Knudson Marsh resulted in a decline of one-third in the number of species and two-thirds in the number of birds nesting there.

By 1960, the total acreage of marshland in Utah was reduced by nearly 50 percent (Smith, 1961) of the 1,174,400 acres (475,279 ha) known to exist originally (Low, 1966). Smith (1961) reported the existence in 1960 of 600,000 acres (242,820 ha) of wetland habitat in Utah of variable value to wildlife. Of this acreage, 83,000 (33,590 ha) were owned by the U.S. Fish and Wildlife Service and 60,000 (24,282 ha) were owned and operated by the State Fish and Game Department. The remaining acreage was in private ownership, either as managed clubs or as unmanaged natural wetlands. Unfortunately, the effects of these environmental changes on the peregrine were never documented adequately.

Morlan Nelson (Hickey, 1969: 96) has suggested that in 1965 there was only enough habitat left in the Bear River marshes to support one pair of peregrines. This would seem to be an underestimation, since we know of several eyrie sites in the western United States where peregrines have bred successfully adjacent to marshes much smaller and much less productive than are the Bear River marshes.

In discussing the decline of the peregrine in Utah, Nelson (1969) indicated that the peregrines nesting in 1939 at the U1 site (site 11, Table 1) adjacent to the Bear River Migratory Bird Refuge did not return to nest by 1941 because the drought dried up their hunting sites. So that we might critically assess Nelson's implication, we measured the extent of the marshes and open waters within a five-mile (18 km) radius of the U1 eyrie, using U. S. Geological Survey topographic maps (aerially photographed, 1953-1956). The resulting measurements tend to weaken Nelson's argument, since there were still 16.6 sq miles (43 km^2) of marsh and 5.8 sq miles (15 km^2) of open water within the five-mile radius. Moreover, the Bear River Refuge, with its extensive marshes, was only seven miles away. However, this is based on the assumption that these marshes did not increase appreciably in size between 1941 and 1956. We cannot comment on the latter premise because we have no information on the extent of these marshes for the early 1940s.

Since we consider the cliff at the U1 site to be marginal in terms of accessibility to humans and predators, we believe that human disturbance may have been the major factor causing the abandonment of this eyrie, although habitat change and competition with the Prairie Falcon probably played a subordinate role.

Further evidence which tends to weaken Nelson's climatic change hypothesis was obtained from Noland F. Nelson, manager of the Ogden Bay State Waterfowl Management Area. Nelson spent many hours at the Bear River and Ogden Bay marshes prior to the completion of the refuges. He noted that there was not a dearth of shorebirds and marshbirds at these marshes before the dikes were constructed (N. F. Nelson, pers. comm., 1971) and that the development of the Ogden Bay area increased the numbers of nesting and migrant shorebirds (Nelson, 1954). Nevertheless, he does believe that the shorebird populations at Ogden Bay have declined in the past several years (N. F. Nelson, pers. comm., 1971).

Furthermore, it is of interest to note that Noland Nelson observed fewer peregrines at Ogden Bay in the 1950s than in the 1940s. He saw them there occasionally in the 1940s (Nelson, 1954), but rarely after the early 1950s (N. F. Nelson, pers. com., 1971). The occasional observation of peregrines at Ogden Bay during the 1940s is about all one would expect, considering that these marshes were supporting at most only three pairs of active eyries during these years. These observations correspond with the reduction of breeding pairs along the Wasatch escarpment between 1940 and the 1950s.

The Great Salt Lake has been subject to major cyclic fluctuations in size twice historically, and perhaps many times in the past several thousand years. Early historical evidence indicates that in 1850, when the Great Salt Lake was first surveyed by Captain Howard Stansbury, it was much reduced in size compared to earlier and later reports. James Clyman, who with a party of trappers first circumnavigated the Great Salt Lake in a bullboat in 1826, wrote the following in his journal on 1 June as he passed through the Great Salt Lake Valley in 1846 on a trip east from California.

> proceeded nearly east to the point of a high mountain [Oquirrh Mountains] that Bounds the Southern part of the greate salt lake I observed that this lake like all the rest of this wide spread Sterility has nearly wasted away one half of its surface since 1825 [1826] when I floated around it in my Bull Boate and we crossed a large Bay of this lake with our horses which is now dry . . . (Korns, 1951:36).

Four years later when the lake was surveyed by Stansbury (1852), it covered 1,750 sq miles (4,433 km^2) (Powell, 1879). By 1869, the lake had increased in size to 2,166 sq miles (5,610 km^2) (ibid.), and by 1870 to 2,400 sq miles (6,216 km^2) (Bue, 1963 *in* Nelson, 1969). By 1961, the Great Salt Lake had receded to an unprecedented low (950 mi^2; 2,461 km^2) following several decades of drought (ibid.), and by 1971 it had risen about seven feet (2.1 m) above its historic low, with a surface area of 1,461 sq miles (3,784 km^2) (U.S. Geol. Survey, 1971). Powell (1879) considered the lake to be at its highest level in 1869, which exceeded a level to which it had long been subjected, and that its old mean area was 1,820 sq miles (4,714 km^2). A drawing of the lake in 1850 by Stansbury (Powell, 1879) is a near duplicate of the size and shape of the lake shown on U.S. Geological Survey topographic maps constructed from photographs taken in 1953. Anthropological studies in Utah by Antevs (1948) and Harper and Alder (in press) and the studies of Blackwelder (1948) suggest that the lake probably was subjected to fluctuations in size many times prior to written history; this will be taken up in more detail under a separate heading.

Despite these periods of drought and their corresponding changes in aquatic habitat, the peregrine persisted until the late 1950s. Although the relationship between the changes in climate and concomitant fluctuations in the size of the lake and the effects of these changes on peregrine populations of the area may never be fully understood, it is clear that never before had these populations been so adversely influenced by the activities of man as in the past century.

Data from Utah Lake also do not seem to fully support Nelson's (1969) hypothesis. Data on the fluctuations of water surface and compromise levels have been plotted for the period 1883 to 1960 (from several sources, including Bureau of Reclamation and Utah State Fish and Game). The lake oscillated around the compromise level (4,488.95 ft; 1,368.23 m) between a plus and minus five feet (1.5 m) through 1925. Between 1925 and 1930, the lake remained around the minus five-foot (1.5 m) level, and starting in 1930 the lake level gradually lowered to its lowest level, slightly below minus 10 feet (3.0 m), in 1934 and 1935. There was a slow regain, remaining near the minus five-foot (1.5 m) level through the mid-1940s, until it reached above the compromise level in 1952. However, the lake has remained below the compromise level since then. At its lowest level (1934–35) about 37 percent of the surface area was lost (data through D.A. White from the Utah Lake Research Station). Presumably many marshes around the edge of the lake dried up during this low period, thereby reducing shorebird and water bird habitat. However, this may not be a totally satisfactory index to the availability of marshes. Many areas formerly covered by water but apparently dry during the low water years, such as Provo Bay, were fed by springs and doubtless maintained some habitat for the prime avian prey species. Some of these areas were situated opposite active peregrine eyries. Thus, the impact of the drought years on peregrines is difficult to evaluate. Even so, it is clear that it was not until well after the drought years and after the 1950s that some of the eyries around Utah Lake became inactive (Table 1, sites 17 and 18, for example).

As mentioned earlier, the number of peregrines wintering in the marshes adjacent to the Great Salt Lake declined steadily from 1939 ($p<0.01$, linear regression analysis), the year Nelson (1969) located his first eyries in Utah, until the early 1960s when the species disappeared as a resident in the marshes (Fig. 11). The decline correlated closely in time with the abandonment of local eyries. The desertion of some eyries during the early 1940s and perhaps earlier in the century is explainable on the basis of Nelson's (ibid.) climatic change hypothesis. However, the magnitude of the decline which followed later in the decade and on into the late 1950s is not, since management methods by then had brought about stability to the marshes and a concomitant increased population of prey species. If climate had been the sole cause of the decline in Utah, one should have expected the reactivation of eyries by the early 1950s following the development of the migratory waterfowl refuges in Utah, yet this did not happen.

(Additionally, a reported increase in nesting peregrines since 1939 in Arizona at the expense of the Prairie Falcon is still unexplained [Phillips, Marshall and Monson, 1964].)

We do not question the validity of Nelson's (op. cit.) climatic change hypothesis for Idaho and elsewhere in the Northwest, where peregrine food producing marshes and waters disappeared. We do believe, however, that the more permanent nature of the Great Salt Lake marshes greatly lessened the impact of these climatic changes in Utah, resulting in the abandonment of a few marginal eyries (Table 1, sites 11 and 25) that were situated near smaller and less permanent marshes or that were located on small, relatively accessible cliffs. However, the number of eyries, if any, that disappeared prior to Nelson's (1969) 1939–1948 observations in Utah is not known. Furthermore, a 10-year reversal of the prolonged drought of the preceding half century which purportedly caused the peregrine decline has not yet resulted in an appreciable recolonization of old eyrie sites or the establishment of new sites.

Nelson (op. cit.) also suggested that Utah's peregrines may have made altitudinal adjustments during periods of drought to compensate for the changes in climate. Our data show no indication whatever of shifts in the species nesting populations from lower to higher elevations (see Table 2). Only one known eyrie (site 36, Table 1) and two suspected eyries (sites 27 and 29, Table 1) in Utah were above 6,000 feet (1,829 m) in elevation. Two of these were known earlier in the century (early 1900s and middle 1930s), whereas the third is of more recent observation in an area that was not investigated biologically earlier in the century.

Pesticide Hypothesis for Peregrine Decline

Pesticide Syndrome in Utah Peregrines

Because climatic change did not appear to be the complete answer to the peregrine decline in Utah, we have investigated the possibility that pesticides may have been involved during the later stages of the decline.

Abnormal behavior and increased reproductive failure were recorded at several Utah eyries during the period following World War II (Table 1).

As mentioned earlier, the birds at site 7 in the Wasatch Mountains either failed to lay in 1949 and 1950 or if they laid, their eggs were destroyed and the adults showed little inclination to defend their nests during these years. In 1951 the eyrie contained three eggs, but they disappeared one by one over a 17-day period, and in 1952 the nesting female at the eyrie was a new one (see Table 7).

A pair of peregrines at an eyrie which was located several miles away (Table 1, site 13), reacted similarly when they were first observed on 20 May 1951. An adult male and immature female dived at us only halfheartedly once or twice, otherwise they circled, screamed, or just perched. A third falcon which flew by at this time elicited no response from either bird. A pair was seen there again on 1 June 1952 by R. J. Erwin. Although they apparently had no eggs, they responded more normally to human intrusion than they had the previous year.

The occurrence of immature females at these two eyries suggests the possibility of a breakdown in the normal ratios of adult to immature peregrines during the early 1950s. The two aforementioned eyries were visited again by us in 1961, but no falcons were seen.

One of the four eggs in a Great Basin desert eyrie (Table 1, site 4) was partially caved in on one side and contained a small hole about one-fourth inch (0.64 cm) in diameter when the nest was first located on 13 May 1954. The male was not seen at this time, but the female displayed little if any of the expected aggressiveness toward our intrusion (Porter, et al., unpubl. ms). When the eyrie was next visited on 24 June, only one youngster was present, and both adults screamed incessantly at the observer. The eyrie was still active in 1954 (White). It was last observed to be active in 1957 or 1958 by a local falconer, who trapped the adults after a complete clutch of eggs was said to have disappeared.

White and Lloyd (1962) found two freshly killed peregrines, about 28 days old, at an eyrie in the desert of the Colorado Plateau (Table 1, site 28, Figs. 9 and 10). The two young were located near their nest, 70 feet (21 m) from the top of a 400-foot (122 m) vertical cliff composed of smooth Navajo sandstone on 7 July 1961. The back, portions of the thoracic organs, and parts of the neck and wings of each had been eaten. They attributed the death of the two young to predation by a Ringtail (*Bassariscus astutus*), because of the presence of fresh Ringtail scats along the ledge and because of the nature of the wounds on the young.

When next visited on 6 July 1962, the adults screamed, using the "wailing" call described by Hagar (*in* Bent, 1938). The female then left the area, while the male flew back and forth but remained silent. The following year both adults were present, but they remained perched and made no noise. Only one adult was seen in May 1964 and none in May of 1965.

Later, White re-examined the young peregrines, which had been preserved (Univ. Utah collection) and could find no chewed off feathers so characteristic of fox-killed peregrines and other mammalian predation observed subsequently by him in the Arctic. Furthermore, the feathers appear to have been plucked from the young as though by a bird, suggesting that their death may have been the result of predation by the parent birds or an avian predator rather than a mammalian predator. As suggested by Morlan Nelson (pers. comm., 1971), the deaths of these two young could have been caused by Great Horned Owls (*Bubo virginianus*), or some raptor other than the adult peregrines. (See Fischer 1967, for a more complete assessment of owl and other avian predation on peregrines.)

The phenomenon of egg breakage and egg disappearance may not be restricted to the peregrine. A Prairie Falcon eyrie north of the Bear River marshes observed by R. D. Porter, R. L. Porter, and Jack Hagan on 6 May 1951 contained a single egg which was slightly cracked on the small end. The female was not seen on the nest, nor did she react defensively towards her nest. The egg was absent on our next visit to the nest on 13 May. Moreover, many of the Prairie Falcon eyries that were present around the Great Salt Lake were abandoned during the past two decades, while those farther removed from the marshes, occupied by pairs living mostly on rodent diets, have persisted.

The pattern of reproductive failure described here is similar to, and synchronous with, that associated with the drastic declines which afflicted the peregrine elsewhere in the United States, in Great Britain, and in northern Europe (Hickey, 1969) beginning early in the 1950s.

The pattern of reproductive failure in Great Britain, where the documentation is the most complete, was characterized by a marked increase in the number of eggs that were broken in the nests, in the number of eggs that disappeared, and in the number of eggs eaten by the parent birds. This pattern was followed by the disappearance of one or both of the adult birds and finally by the complete abandonment of the eyries (Ratcliffe, 1958, 1963, 1965, 1967b, 1969). It was determined later that the eggshells of the peregrine in both Great Britain (Ratcliffe, 1967a, 1970), and in the United States (Hickey and Anderson, 1968) had experienced a marked decrease in thickness starting about 1947. Ratcliffe (1967a, 1970), who was the first to recognize and document this phenomenon, attributed eggshell thinning to the chlorinated hydrocarbons.

These reproductive abnormalities have been duplicated experimentally in the American Kestrel (Porter and Wiemeyer, 1969), the Mallard (Heath, Spann, and Kreitzer, 1969), and Black Duck (*Anas rubripes*) (Longcore, Samson, and Whittendale, 1971) by giving them low dietary levels of organochlorine pesticides. The mode of action of these chemicals on avian reproduction has been investigated (Peakall, 1969, 1970, 1971; Bitman, Cecil, and Fries, 1970), and the effects of DDT on the structure and chemistry of the eggshell are now being studied (McFarland, Garrett, and Nowell, 1971; Longcore et al., 1971).

Experimental studies which indicate that DDT delays ovulation in the Bengalese Finch (*Lonchura striata*) (Jefferies, 1967) and also in American Kestrels (Porter and Wiemeyer, unpubl. data), suggest that this phenomenon may have occurred in wild peregrines as well. The laying date of the first egg in 1952 at eyrie number 7 (Tables 1 and 7) (29 April) was two and one-half weeks later than in 1948 (approximately 11-12 April), and a week later than in 1947 (about 21-22 April). However, this may be a reflection of the change in females that was known to have taken place at the eyrie in 1952, or of an adjustment to a change in weather, rather than to a pesticide-induced delay in ovulation.

Direct mortality of adult birds due to DDE-poisoning cannot be discounted as a factor in the decline of the peregrine, since Porter and Wiemeyer (1972) have demonstrated that dietary levels of only 2.8 ppm (wet weight basis) *p,p'*-DDE were lethal to 8 percent of male captive American Kestrels after one year on dosage. The effects were most pronounced during molt and immediately following nesting season—a period when the fat cycle of the kestrel was at its lowest point. They have also shown (Porter and Wiemeyer, in preparation) that kestrels dosed at both low (0.28 ppm dieldrin; 1.4 ppm DDT) and high (0.84 ppm dieldrin; 4.7 ppm DDT) (wet weight basis) dosage levels of DDT and dieldrin in combination are more susceptible to death following stress of weather than are non-dosed kestrels.

Residues of Pesticides in Peregrine Prey Species

We will now consider the quantity of organochlorine pesticides in the tissues of some of the peregrine's prey species in Utah, since many of the principal prey of the peregrine are known to contain high levels of these chemicals. Cade, White, and Haugh (1968), and Enderson and Berger (1968), for instance, determined that DDT, DDD, DDE, and dieldrin were present in greater quantities in the tissues of migrant sandpipers than in any other of the peregrine's prey species in the Arctic. Some contained DDE in their tissues in quantities of sufficient magnitude to be cause for concern (see Porter and Wiemeyer, 1969, and Wiemeyer and Porter, 1970).

DDE is considered to be the most inimical to avian reproduction of the metabolites of DDT. Relatively high DDE residues were present in the eggs and in tissues of Short-billed Dowitchers (*Limnodromus griseus*), Killdeer (*Charadrius vociferus*), American Avocets and Black-necked Stilts in California (Keith and Hunt, 1966). Surprisingly high residues of *p,p'*-DDE (expressed in average and extreme ppm, wet weight basis) were found in the eggs of Black-necked Stilts (4.92, range 1.0–13.7), American Avocets (4.43, 1.5–12.0), and Franklin's Gulls (0.92, 0.5–2.2) collected at the Bear River marshes in 1968 (unpubl. data, Denver Wildlife Research Center). The whole body tissues of two Lesser Yellowlegs (*Totanus flavipes*) contained on the average 10.95 (range 5.1–16.8) ppm *p,p'*-DDE (wet weight basis); four Long-billed Dowitchers (*Limnodromus scolopaceus*), 13.25 (0.7–49.20); one avocet, 3.4; nine White-faced Ibis (*Plegadis chihi*), 2.55 (0.1–6.5); and three Marbled Godwits (*Limosa fedoa*), 6.04 (0.15–17.8). Dieldrin in the tissues of these birds ranged from 0.1–0.86 ppm in the ibis, 0.2 ppm in the Lesser Yellowlegs, 0.05–0.50 ppm in the godwits, and 0.68 ppm in the avocet. Many of the DDE values are greater than the 2.8 ppm (wet basis) of DDE that caused eggshell thinning (Wiemeyer and Porter, 1970) and adult mortality (Porter and Wiemeyer, 1972) in American Kestrels. Residues of PCB's were found in four of the dowitchers and two of the yellowlegs. They averaged 3.75 ppm (1.5–10.0) and 4.5 ppm (3.0–6.0), respectively.

Mosquitocide Usage in Utah

The chemical DDT was used as a mosquitocide in the marshes along the Great Salt Lake as early as 1947 in Weber (Ogden Bay State Waterfowl Management Area) (Benge and Fronk, 1970) and Box Elder counties (K. L. Josephson, pers. comm., 1971) and on an experimental basis in Salt Lake County (Salt Lake City Mosquito Abatement District) in 1945 (Graham and Rees, 1958). This chemical was used at Ogden Bay until 1961, at which time the use of parathion was initiated (Benge and Fronk, op. cit.). Davis County probably began the use of DDT in 1951 or 1952, since mosquito control was initiated there in 1951 (Stewart, 1954; Nielson, 1962). The quantities of DDT used in the early years probably were not great, since it was applied by means of foggers and hand-operated sprayers. However, beginning in 1949, DDT was applied to the extensive marshes bordering the Great Salt Lake by means of aircraft (for additional history of mosquitocide usage in Utah, see Appendix. The utilization of DDT increased with the use of airplanes as a vehicle for application. It is interesting to note that reproductive failure in the peregrine was most pronounced in the years coincident with, and immediately following, the initiation of aerial spraying, although this may be an unrelated coincidence.

Between 1947 and 1961 many thousands of pounds of DDT were deposited on agricultural crops, and more importantly, directly on the marshes and waters in the Great Salt Lake Valley where nesting peregrines obtained much of their food. The quantities applied by mosquito abatement districts were greatest along the marshes of the Great Salt Lake, where no peregrine eyries are known to have been active after 1957, and least in Utah County, where several peregrine eyries apparently remained active until the late 1960s.

Data on the quantities of organochlorine insecticides used for agricultural purposes in the area surrounding the Utah and Great Salt lakes were unavailable to us, but chlorinated hydrocarbon pesticides probably were used in large quantities, judging from a recent survey of pesticides in Utah (Warnick, 1971). However, they were applied to farm crops, farm animals, and buildings, and not directly on the marshes where the peregrine obtained its food. Unfortunately, little is known regarding the movements of these chemicals from agricultural lands to the marshes.

We have no direct evidence linking these chemicals with the sharp reduction in active peregrine eyries along the Wasatch Mountains during the critical years between 1945, when the chemicals were first used, and 1957, when the species was last known to breed in the area. Nor do we know the extent of the environmental contamination at that time by other chemicals such as the polychlorinated biphenyls (PCBs). We do not know the effects of PCBs on raptor reproduction, although some PCBs (1245) in small dietary concentrations do not seem to affect reproduction in Mallards, Pheasants (*Phasianus colchicus*) (Heath et al., 1972), and Ring Doves (*Streptopelia risoria*) (Peakall, 1971) in the same way as does DDE.

We can only speculate regarding the residues of chlorinated hydrocarbons present in the tissues of either the peregrine or its prey species during the period of its decline in Utah. Most of the peregrine's prey species were migratory in nature. Thus, part of the insecticide residues acquired by them were from areas other than Utah and the Great Salt Lake valleys. We are unable, therefore, to establish an absolute cause and effect relationship between the quantities of chlorinated hydrocarbons used and the decline of the peregrine in Utah, although one is suggested by the experimental, ecological, and behavioral evidence which we have presented.

Disease Hypothesis for Peregrine Decline

White (1963) referred to 27 cases of botulism (*Clostridium botulinum*) in peregrines that were found in the Great Salt Lake marshes between 1943 and 1958. Ralph B. Williams (pers. comm., 1972) also found several affected peregrines on marshes around Utah Lake in the mid-1940s. The disease was most prevalent between late July and early October, and it appeared to affect adults more than young, and females more than males. Botulism undoubtedly has taken its toll of peregrines during the past several decades and perhaps, sporadically, for many hundreds of years. Its effects, historically, on the local peregrine population cannot be assessed because the fluctuations in numbers of active peregrine eyries in Utah are not known. We cannot evaluate the effects of botulism toxins combined with those of pesticides, since knowledge of the effects of pesticides on the susceptibility of birds to various diseases and the interactions of botulism toxins with the chlorinated hydrocarbons are poorly understood. However, any mortality of adult birds due to disease during periods of reproductive failure would tend to accelerate the decline.

Human Activity Factors in the Decline of the Peregrine

A number of human activities, besides the agricultural practices already mentioned, may have adversely affected the peregrine in Utah, particularly in combination with the inimical effects of organochlorine pesticides, botulism poisoning, and changes in the climate. (See an earlier analysis by White (1969b) of the effect of human pressures.)

The impact of nest robbing, which started earlier in the century with egg collecting and later in the century, starting about 1939, with the utilization of the nestlings for falconry, are difficult to evaluate, although there is no evidence that these activities per se were responsible for the sharp increase in abandoned eyries in the state. Some peregrine eyries in Europe were robbed of their young for many hundreds of years without apparent harmful effects (Fischer, 1967; Ratcliffe, 1969).

Photography at eyrie sites also may have caused some birds to abandon their eyries, although to our knowledge only one nest in Utah (Table 1, site 7) was harassed in this way and the eyrie site was known to have been active subsequently.

The reported collection of an adult falcon from the Pelican Point eyrie (Table 1, site 3) in 1935 (Bee and Hutchings, 1942) apparently had little impact on this eyrie, since it was still occupied as late as 1939 (notes of R. G. Bee). The removal of the adults from eyrie site 4 (Table 1) in 1957 or 1958 by a falconer probably hastened the abandonment of that eyrie by only a few years, since what seems to us to have been the pesticide syndrome was already in strong evidence there.

The cliff at Pelican Point (site 3, Table 1, Fig. 6) became a limestone quarry in recent years and the eyrie site was destroyed, as was an eyrie site in southwestern Utah (site 37, Table 1). Lower portions of the cliff near one of the most inaccessible peregrine eyries in the state (Table 1, site 8) were blasted away during the 1960s. Some of the earlier observations of peregrines in Utah were near this site. A bird was noted there in 1969 (C. M. White), but not in 1971 (R. J. Erwin).

A recreation area, established after 1968, is situated below one eyrie in east-central Utah (Table 1, site 28). When the eyrie was visited in May 1971, several motorcycle clubs were using the area as a point of rendezvous and all day and night the roar of motorcycles echoed through the canyon. Although fresh excreta was seen along a ledge running adjacent to the old eyrie site, no falcons were seen in two days of observations. This eyrie had shown evidence of the pesticide syndrome as early as 1961, however. The extent of the damage to the above site is not known.

Depredation of the species by hunters is a mortality factor which is frequently overlooked. Utah's marshes, which in the past were frequented by peregrines in the fall and winter, have been used by increasingly greater numbers of waterfowl hunters in recent years. This is especially true of areas around the Great Salt Lake since the establishment of state and federal waterfowl refuges between 1930 and the early 1940s. Often hunters kill raptors and other birds indiscriminately. This could be a contributory factor to the peregrine decline, since peregrines frequenting the marshes during hunting season probably were from local eyries. However, the significance of depredation by hunters is difficult to assess since the peregrine is noted for its ability to withstand this type of persecution and destructive treatment by man (Ferguson-Lees, 1957; Cade, White, and Haugh, 1968; Ratcliffe, 1962, 1969).

In the past two decades, the construction of human dwellings on the high foothills of the Wasatch Mountains below certain eyrie sites may have had an adverse affect on these eyries (see White, 1969b), and the effects of the activities at a nearby rifle range on one such eyrie also are unknown. One can only speculate what the construction of homes near eyrie sites will do to these sites, since there is already a precedent set for peregrines nesting above railroad tracks, on bridges, and in heavily populated urban centers (Hickey, 1942; Olivier, 1953). The extent to which some individuals of the species persist, despite the presence of human populations near their eyries, is illustrated by the peregrines at one eyrie that tolerated for over a century the activities of a village of two hundred people at the base of the cliff that housed the falcon eyrie (Hickey, 1942).

To sum up, pollution, shooting, nest site and habitat destruction, human disturbance, and climatic changes have contributed singly and jointly to the near demise of the peregrine in Utah. Of these, pollution and climatic change appear to have played the dominant roles.

FACTORS INFLUENCING PEREGRINE DISTRIBUTION AND ABUNDANCE IN UTAH

To more fully understand the various factors involved in the distribution of the peregrine in Utah prior to its catastrophic decline, we have attempted to examine the impact on the species of various ecological factors, both past and present.

Water, Food, and Nesting Sites as Limiting Factors

Bond (1946) has reported that in the western United States the peregrine seldom nested more than one half mile (0.8 km) from water in which to bathe. Exceptions to Bond's (ibid.) observations are few. Gabrielson and Jewett (1940), for example, tell of a pair that nested in Oregon on an isolated rock far from water (11 mi.; 17.7 km., Bond, 1946), and Thomas Ray (pers. comm.) located an active eyrie far from water in arid western New Mexico.

The peregrine's affinity for free water probably is associated more with its needs to bathe and to obtain food than with its needs to drink. Bartholomew and Cade (1963) point out that the larger predatory birds obtain adequate quantities of water from their food under most circumstances. They cited instances of several falcons, including the peregrine, maintaining weight for many months without free water.

Beebe (1960) concluded that because 11 of 13 young peregrines taken from nests in the Pacific Northwest and raised in Denver died of dehydration, humidity rather than nearness of free water was perhaps a critical factor in brood success in areas of the West other than the Northwest Pacific coast. Since these nestlings died despite having been supplied with drinking water, Beebe (ibid.) hypothesized that peregrines were more or less restricted to nesting sites near water because of high humidity rather than the presence of free water.

An important question appears to be whether or not the young mentioned by Beebe were acclimatized to the cool, humid climate of the Northwest before being transferred to the arid intermountain area. Nelson (pers. comm., 1971) has suggested that these birds may have died of malnutrition rather than dehydration. He raised and trained one of them and encountered no difficulty with dehydration. Other nestling peregrines from British Columbia and the Aleutian Islands, similarly transferred to Utah, have not been affected in this manner. Nestlings taken from Utah eyries have not appeared to suffer greatly from dehydration nor has there been any evidence of moisture loss among young peregrines cared for in the nest by their parents.

This affinity for high humidity, if it exists, may be an inherited physiological characteristic of the *pealei* race, which is less pronounced in the peregrine populations of the arid Intermountain West (see also, White, 1968b, for further documentation of this problem). Furthermore, other populations of falcons, such as those of the Shaheen, exist and breed in the deserts of the Middle East under the harshest conditions known (Bartholomew and Cade, 1963).

Food availability appears to be a major criterion influencing the distribution and abundance of the peregrine in arid regions of the West. Density and distribution of peregrine populations in Utah appear to correlate best with the abundance of the food supply. Peregrine populations are most dense in the area surrounding the Utah and Great Salt lakes where the preferred prey species, particularly shorebirds and marshbirds, are most abundant. Here, the marshes have historically supplied food for 10 to 20 eyries during a single nesting period. Hunting areas for isolated pairs of peregrines elsewhere in the state were supplied by smaller, less extensive marshes or by narrow tongues of streamside vegetation. Usually, isolated pairs survived and reproduced where adequate food was available.

Food availability apparently is an important factor in the distribution and abundance of the peregrine in more humid and mesic regions as well as in arid regions. Beebe (1960) has attributed an unusually high breeding density of peregrines in British Columbia to the extremely high concentrations of four or five species of colonial seabirds occurring there. These small pelagic birds apparently were especially suited as prey species for the peregrine.

Ratcliffe (1962) considered the geographic variation of food supply as the most obvious factor associated with population density of the peregrine in Great Britain. He has correlated size of territory and density of peregrine populations in Britain with the nature of the food supply.

The same factor generally appeared to be operative in Utah, although peregrine density in the Great Salt Lake Valley of Utah probably was not limited by the size of the prey populations. However, the species may be limited by the distance (up to 17 mi, 27.4 km; Table 4) it must fly to reach the marshes where it obtains its preferred prey species.

Peregrines may select easily accessible nesting sites in areas containing an abundance of suitable prey species, as occurs in the Queen Charlotte Islands (Beebe, 1960). Such sites are seldom utilized in areas containing less favorable food supplies. This is illustrated in Utah by the occurrence of the ground-nesting peregrines at Ogden Bay.

Hickey (1942, 1969) considered the cliff on which peregrines nest as the dominant feature of their ecological niche. He considered extremely high cliffs as "ecological magnets" which attract peregrines regardless of nesting success.

Cade (1960), on the other hand, has argued that the ability of the pair to breed effectively is a result of a strong pair bond, and that the strength of the bond is a more important consideration than the size of the cliff. He argued that the pair bond would be dissolved and that the eyrie would become inactive indefinitely if both the male and female disappeared from the eyrie. Ratcliffe (Hickey, 1969), in support of Hickey (1942, 1969), has cited examples of several eyrie sites which were consistently reoccupied following the deaths of both adults. This also has been noted in the Arctic by White (unpubl. data). (See Fischer, 1967 for additional documentation.)

In Utah, selection of eyrie sites by peregrines is associated with the availability of suitable sites near a readily available supply of preferred prey species. The preferred prey species usually are closely associated with a marsh or stream. These two factors combined, then, constitute the most important aspect of the peregrine's nesting economy in the state.

Interspecific Competition During Nesting Season

Cade (1960) has discussed competition between the peregrine and the Gyrfalcon (*Falco rusticolus*). White and Cade (1971) have discussed competition among several species of raptorial birds in the Arctic, and White (1968b) has discussed this problem as concerns peregrine distribution and its relation to large congeners over broad distributional areas. These papers give a valuable basis for the evaluation of the competition between the peregrine and other raptors whose range and habitat in Utah are sympatric. In our discussion of interspecific competition, we prefer the more restricted definition of the term "interspecific competition" as given by Birch (1957) and as discussed by Cade (1960). That is, competition results when more than one species requires a resource that is in short supply.

Competition for food and/or nesting sites between the peregrine and other species of raptors, particularly the Prairie Falcon and the Golden Eagle, may be factors contributing to the relative paucity of peregrines in the arid Intermountain West.

Where relatively abundant, the Golden Eagle may be a competitive factor limiting the density of the peregrine in the more arid regions of Utah. Bond (1946) has watched the peregrine strike at Golden Eagles and R. J. Erwin and J. F. Poorman (unpubl. notes) have made a similar observation in Utah. Dixon (1937) tells of one instance when a pair of Golden Eagles in California usurped a cliff that had been occupied by peregrines for years. The eagles persistently outfought the peregrines, forcing them to leave. Cade (1960) found that the peregrine was quicker and more persistent in its attacks on Golden Eagles than on any other raptor discussed. Ratcliffe (1962, 1963) reported that in many districts in Scotland, where there is a surplus of suitable cliffs, the density of Golden Eagles is high while the densities of the peregrine and the Common Raven (*Corvus corax*) are low. In these situations apparently the eagle replaced the peregrine as the chief nesting predator in the Scottish Highlands.

In Utah, peregrines and eagles were found nesting concurrently on the same set of cliffs only once. The eagles nested one mile (1.6 km) (Morlan Nelson, pers. comm., 1971) from active peregrine and Prairie Falcon eyries (see Nelson, 1969), but on the opposite side of the mountain (north). The eagles apparently foraged northwardly, while the peregrines foraged southwardly. No aggression was noted between the eagles and the falcons (Nelson, pers. comm.). A cliff formerly occupied by peregrines in Utah (site 15, Table 1) contained an active Golden Eagle's nest in the spring of 1971, and the presence of two old eagle nests (R. J. Erwin) suggests a long period of occupancy by the eagles. The cliff also had been occupied by as many as three pairs of Prairie Falcons simultaneously during some of the intervening years (Nelson, pers. comm., 1971).

The food habits of the eagle and peregrine are sufficiently diverse in Utah so as to negate a strong competition for food. Additionally, the eagle seems to attain its greatest abundance in the more arid regions of the state, where it more likely would compete with the Prairie Falcon for nesting sites than with the peregrine, although the abundance of eagles in the deserts of Utah may be one of the reasons why the peregrine seldom occurs there. This latter postulation, however, appears unlikely because of an absence of the food niche preferred by the peregrine.

The Common Raven has been shown by White and Cade (1971) to compete rather extensively with Gyrfalcons for nest sites in the Arctic, though it seems to have only limited competitive effect on Arctic peregrines using the same cliffs. In Utah, where the raven is common, only three cliffs with peregrines were known to house ravens. Like the situation in the Arctic, ravens probably had "no" effect on Utah peregrines, although Porter observed peregrines at site number 4 pursuing ravens on 8 April 1954. Ravens may, however, have a considerable modifying effect on Prairie Falcons, as will be discussed in a later section. (See also Ratcliffe, 1962, for a consideration of raven-peregrine interaction in Great Britain.)

The Prairie Falcon (Fig. 39), on the other hand, is more closely related phylogenetically, is more similar in size, and is more equivalent in ecological function to the peregrine, than is either the eagle or raven. Hence, it likely would be a more serious competitor of the peregrine and it probably would be a more important factor limiting peregrine populations in areas of sympatry.

The Prairie Falcon is a true desert falcon. It undoubtedly evolved in the arid West, and therefore is probably better adapted than is the peregrine for Utah's arid environment. The Peregrine Falcon is separated from the Prairie Falcon and the Gyrfalcon at the subgeneric level. The two species are of similar size, although the peregrine is somewhat heavier than the Prairie Falcon (See Table 9 and Webster, *in* Beebe and Webster, 1964).

The peregrine, which is nearly cosmopolitan in its geographic distribution, has a breeding range which completely overlaps that of the Prairie Falcon geographically but not ecologically. The Prairie Falcon breeds from central British Columbia, southern Alberta, southern Saskatchewan, and North Dakota, south to Baja California, and northern Mexico (See AOU Checklist of N. Am. Birds, 1957). The peregrine is most abundant north of its zone of sympatry with the Prairie Falcon.

According to Bond (1946), the Prairie Falcon may be quite common up to 6,000 or 7,000 feet (1,829 or 2,134 m) in suitable localities and at elevations where trained Prairie Falcons, with their much greater surface to weight ratio, clearly outfly trained peregrines, which are their superiors at sea level. Morlan Nelson (pers. comm. 1971), who has tested Bond's (1946) hypothesis on several occasions with captive falcons, considers that it is more a matter of individual variation within both species than it is a factor of elevation.

Actual contact between the two species occurs where their ecological niches overlap. To our knowledge, there is no locality in Utah where peregrines nest which is not also inhabited by Prairie Falcons, but not the reverse. The peregrine's proclivity to nest near water or marshes where both its food and nesting requirements are met is not shared by the more euryecious Prairie Falcon which may fulfill these requirements both near water and in the desert many miles from water.

As discussed previously, the several peregrine eyries found in the deserts of Utah were situated within easy access of marshes, desert springs, ponds, streams, or rivers. Perhaps this reflects the differences in hunting methods and food habits of the two species, as well as the proclivity of the peregrine to bathe in water as discussed by Bond (1946) and Cade (1960). Both species can be dust bathers in captivity (Nelson, pers. comm.), although the Prairie Falcon is less dependent on water than is the Peregrine Falcon.

Some Factors Modifying Competition and Success

Before examining the kinds of competition that may affect Utah peregrines, a general discussion is in order. There are many ways that falcons can exploit their respective environments. Their success, that is, the total number of young that become breeding adults in the next generation, depends upon the effectiveness of this exploitation.

Frequently ecologists use the terms "generalist" and "specialist" to describe a species in terms of the manner in which it utilizes certain resources. Most frequently this pertains to the manner in which the food or habitat niche is exploited, or to the modes of hunting certain species of prey.

Although the specialist has a narrower habitat tolerance, it usually compensates by being more competitive (see, for example, Cade,

Table 9. Weights (in grams) of Peregrine Falcons and Prairie Falcons from various North American populations.

Species and Population	MALES			FEMALES		
	n	$\bar{x}$	range	n	$\bar{x}$	range
PEREGRINE FALCONS (White, 1968a & b)						
F. p. tundrius[1]	12	610.9	550–647	19	952.0	825–1,094
F. p. anatum[2]	5	678.0	675–682	5	1,038.0	870–1,201
PRAIRIE FALCONS[1] (Enderson, 1964)	15	554.0	500–635	31	863.0	760–975

[1]Weights are from adult birds.
[2]From population in western United States.

1960). When the optimal requirements for the specialist are present, it tends to capitalize on or "monopolize" the resources or conditions to receive maximum benefit, often to the exclusion of the generalist or other specialists. It is the existence of a specific or optimal set of conditions that allows the specialist to be successful. The generalist might also successfully exploit the precise conditions. However, because of competition with the specialist, it may alter the manner in which it uses the conditions by partitioning the resource, or it may be forced into suboptimal conditions because of the dominance of the specialist. In the absence of the specialist, the generalist obtains even greater benefit by the use of the specific combination of resources or conditions that the specialist would have used.

The generalist tends to be more widespread geographically and often more common than the specialist. Moreover, when two closely related species with similar ecological niches occupy the same geographic area, one tends to assume the role of the "specialist" and the other the role of the "generalist," depending upon their individual needs. Gyrfalcons, for instance, are specialists on the Arctic Slope of Alaska, where they have specific nesting requirements and where they specialize on ptarmigan for food, while the sympatric peregrine is the generalist, having rather broad requirements for nesting and feeding (White and Cade, 1971). The Gyrfalcon seemingly has the advantage and appears to outcompete the peregrine for certain resources. However, because the peregrine is a generalist, it has less precise requirements and therefore is able to occur over a much broader geographic range in Alaska, such as the taiga regions. Then, too, it is probably more numerous when considering its entire range.

Even though the peregrine is probably a generalist over much of its cosmopolitan range, it becomes a specialist in the Aleutian Islands, where it has a narrower food niche consisting mostly of marine birds of the family Alcididae and of the order Procellariiformes. Thus, the role of the species is modified by the conditions in a given locality.

Prairie Falcons have been thought of as specialists because they are able to exploit very arid climates where a limited number of food species are present. They often occur where other large falcons are unable to survive. Because they are able to concentrate on the prey species most available, Prairie Falcons may have a rather highly specialized food niche, especially in the more arid regions where a limited number of food species occur. Their ability to "specialize" on what is available enables them to live successfully in a wide variety of ecological situations.

If one considers the Prairie Falcon's entire geographic and ecological range, it is narrowly selective in its exploitation of the climatic conditions available to it (i.e. a near obligate of xeric conditions), but it is broadly selective in its exploitation of food and nesting sites. Additionally, where the geographic ranges of the two species overlap, Prairie Falcons are much more common than are peregrines. Because of the Prairie Falcon's seemingly narrow climatic tolerance during the breeding season, climate may be a major factor limiting its geographic distribution.

Peregrines, unlike prairies, are broadly selective in their exploitation of climatic conditions over their entire geographic range. However, they are narrowly selective in their exploitation of food and nesting sites in the arid West where they must compete with the sympatric Prairie Falcon. Moreover, they are much less common than are Prairie Falcons, where the ranges of the two species are sympatric. Their specialized food requirements (generally "water-type" birds) and restrictive methods of capturing prey (not prone to capture prey on the ground), are the major factors limiting the expansion of their geographic and ecological ranges in Utah and probably elsewhere in the arid West.

The presence of surface water in the arid West may dramatically alter the environment. For certain species it may even act as a limiting factor. Water creates a food niche which apparently is optimal for the peregrine, providing an abundance of aquatic birds in these localized areas. Hence, the peregrine does better in the presence of surface water. This is especially evident at the margin of the species' ecological range in the arid parts of Utah. With the presence of these "oases" of aquatic habitat in an otherwise unexploitable environment, the peregrine assumes the role of specialist; and, where the peregrine and prairie occur together in Utah, the prairie seemingly assumes the role of the "generalist." The broad spectrum of food, habitat, and nesting sites which the prairie selects overlaps and surpasses the requirements of the peregrine. The requirements of the peregrine are more limited and restrictive, yet it may do better competitively than its congener when the optimal conditions prevail.

Competition with the Prairie Falcon for Food

Where the two species occur together along the escarpment of the Wasatch Mountains and adjacent to the Great Salt Lake, their food appears to be quite similar (Table 5), although there are some marked differences. In this region of joint occupancy, the Prairie Falcon utilizes a much wider variety of vertebrate species than does the peregrine. As illustrated in Table 5, the Prairie Falcon is more prone to feed on rodents and on ground-dwelling birds, such as quail, pheasants, meadowlarks, and passerine birds in general, and is less inclined to feed on pigeons, doves, and flickers than is the peregrine (also see Bond, 1936a, b, and c).

Prairie Falcons also feed on reptiles. For instance, at one Prairie Falcon eyrie in the Great Basin, not far from a peregrine eyrie, adults were observed carrying large whiptail lizards (*Cnemidophorus* sp.) to the eyrie.

The Prairie Falcon exploits a different food resource in the allopatric parts of its geographic range than in those that are sympatric with the peregrine. A case in point is the high plateau country of Utah NNW of the Uinta Mountains (6,800 feet elevation; 2,073 m) where only the Prairie Falcon occurs, although one would expect peregrines also to occupy the habitat. Food items taken from several nests between 1961 and 1964 in this region of allopatry consisted of 61 percent mammals, about 90 percent of which was the Uintah Ground Squirrel (*Citellus armatus*), although another species of ground squirrel, a chipmunk (*Eutamias* sp.), and a vole (*Microtus* sp.) also occurred. Birds made up the remaining 39 percent, with Mourning Doves being the principal avian food, though the Brewer's Blackbird (*Euphagus cyanocephalus*), Flickers (*Colaptes* sp.), Horned Larks, Starling (*Sturnus vulgaris*), and the Mountain Bluebird (*Sialia currucoides*) also occurred. Thus, about 75 percent of the total food was made up of two species, one mammal and one bird. In this case, and those cited by Enderson (1964), with an absence of peregrines in both localities, the Prairie Falcon tended to fill the role of a "specialist" in food habits; and to a large extent the species was mammivorous (mammal-eating). (See Bond, 1936b). The avivorous (bird-eating) peregrine, on the other hand, consumes few mammals and fewer, if any, reptiles.

Ground-nesting birds and rodents are important items in the diet of the Prairie Falcon in areas other than Utah. For example, Enderson (1964) found remains of the ground-nesting Horned Lark and of the Richardson's ground squirrel (*Citellus richardsonii*) most often, and sometimes exclusively, in the nests of Prairie Falcons in eastern Wyoming and Colorado. Ogden (1971) considered the Townsend's ground squirrel (*Citellus townsendi*) to be the most important food species, followed by Horned Larks, Meadowlarks, and whiptail lizards in Prairie Falcon eyries along the Snake River of southwestern Idaho. The antelope ground squirrel (*Citellus leucurus*) was also present, but in smaller numbers.

The Horned Lark was also a staple item in the winter diet of Prairie Falcons in Utah and in the prairies of Wyoming, Colorado, and New Mexico, where it influences the falcon's seasonal movements and distribution (Enderson, 1964).

An overlap in the food niches of the peregrine and Prairie Falcon is evident in the area along the Wasatch Mountains (Table 5). In terms of biomass, aquatic birds comprised the largest category of prey species in the Wasatch Mountain eyries of both species, but they were much more predominant in the eyries of the peregrine than in those of the Prairie Falcon.

The avocet was the major aquatic species in the eyries of both falcons (see Frontispiece and Fig. 39). The importance of the avocet as a prey species of the Prairie Falcon was apparent also at two eyries in the Great Basin, northwest of Great Salt Lake, where the adult Prairie Falcons brought avocets and Antelope Ground Squirrels to their young almost exclusively in 1962 (C. M. White, unpubl. data) and commonly in 1969 (Platt, 1971). This, however, was in the apparent absence of competition with the peregrine.

The presence of the avocet in the diets of both species is probably a reflection of the local abundance of this shorebird and the ease with which it may be captured. The avocet likely did not represent a resource in short supply and undoubtedly was an important item in the diet of the peregrine long before the first white settlers arrived in the western United States. In 1871 Allen (1872) found it very abundant along the shores of Great Salt Lake, where he noted flocks containing several thousand individuals from 1 September to 8 October, and a quarter of a century earlier (4 April 1850), Stansbury (1852) observed innumerable flocks of long-legged plovers, many of which probably were avocets, Willets, and stilts. The avocet predated white man in the Great Salt Lake area by many thousands of years, as evidenced by its presence among the bird remains dating back nearly 8,500 years B.P. in the early strata of Hogup Cave, just north of the Great Salt Lake (Harper and Alder, in press).

The White-faced Ibis was an additional marshbird upon which both species of falcons apparently preyed. Weller et al. (1958) indicated that the peregrine killed White-faced Ibis in the Knudson marshes near Brigham City, and R. D. Porter (unpubl. data) observed a Prairie Falcon feeding on an ibis at the Bear River marshes on 5 June 1951. Since the ibis was not found in the eyries of either species, it was probably too heavy for the falcons to carry to their eyries. The weight of an adult female ibis as determined by Porter et al. (unpubl. ms) is 517 grams, whereas the weights of two adult female avocets average 281 grams.

In Prairie Falcon eyries along the Wasatch Mountains, shorebirds, passerines, rodents, and gallinaceous birds were nearly equally represented; whereas in the eyries of the peregrine, shorebirds predominated and gallinaceous birds and rodents were absent (Table 5). The ducks present in the eyries of the Prairie Falcon (Table 5) were about half grown and probably incapable of flight. Hence, they probably were either captured on the water or on the ground and were sufficiently light in weight that they could be carried by the falcons.

We have no data for comparison of the food habits of the peregrines nesting in the desert (Table 6) with those of desert-nesting Prairie Falcons in the same region. A comparison of this kind is needed to fully evaluate the competition for food by the two species. Cade (1960) found that the overlap in food species of the peregrine and Gyrfalcon were least in the areas of contact and greatest in areas where ranges were not sympatric. A comparison of this kind between the peregrine and Prairie Falcon would be difficult to make, since in Utah the Prairie Falcon occurs in the same geographic area as the peregrine. Nevertheless, one would expect

Fig. 39. Prairie Falcon feeding its young a downy avocet (peregrine site 7, alt. prairie site 2, see Fig. 26). Photo by R. J. Erwin and R. D. Porter, 1948.

less rather than more overlap in food habits in areas of allopatry than in areas of contact. The isolated peregrine's eyrie in Oregon, which was situated far from water (Gabrielson and Jewett, 1940), contained birds usually preyed upon by Prairie Falcons, and an adult peregrine at an eyrie in Zion Canyon was observed by Grater to carry a squirrel into a crag (Woodbury et al., unpubl. ms).

In Utah, then, the Prairie Falcon has a wider versatility in taking prey species than does the peregrine, which would seem to lessen the competition between the two species for food. Hence the role played by the Prairie Falcon in Utah is similar to that of the peregrine in the Arctic (Cade, 1960; White and Cade, 1971), and that played by the peregrine in Utah is similar to that of the Gyrfalcon in the Arctic.

According to White and Cade (1971), there is no evidence to suggest that density of breeding peregrines is influenced in any way by availability of food in the Colville valley of Alaska. This generally is not applicable to the peregrine in Utah, but in the region surrounding the Great Salt Lake it is difficult to surmise how the density of the peregrine could have been limited by availability of food, considering the superabundance of prey species in the Great Salt Lake marshes. Nevertheless, extensive distances from eyrie sites (Table 4) to hunting sites in the marsh may have limited their density.

Competition with the Prairie Falcon for Eyrie Sites

Directional Exposure Preferences

In Utah the peregrine's preference for cliffs with northerly or easterly exposures (Fig. 16) would tend to lessen the competition for nesting sites between it and the Prairie Falcon if the Prairie Falcon had a preference for south-facing cliffs similar to that reported for Colorado and Wyoming by Enderson (1964). We investigated this hypothesis by examining the directional facing of the 49 eyrie sites of the Prairie Falcon in Utah for which we had available data. As shown in Figure 16, 69.4 percent of these eyries faced south and west and 30.6 percent faced north and east. This relationship was statistically significant at $p<0.01$ (X^2 test; calculated X^2 value, 7.37, 1 df). Conversely, 70.4 percent of 27 peregrine eyries in Utah faced north and east and 29.6 percent faced south and west, and this relationship was significant at $p<0.05$ (X^2 test; calculated X^2 value, 4.48; 1 df).

When the two species nested in close juxtaposition on the same set of cliffs, as at site 7 in the Wasatch Mountains, the Prairie Falcon seemingly selected the sites more exposed to the afternoon sun (west-facing sites) than did the peregrine (see History of Nesting at a Wasatch Mountain Eyrie, Table 7 and Fig. 26). As a general rule, the Prairie Falcon eyries on the escarpment of the Wasatch Mountains were situated directly on the west face, whereas those of the peregrine, as discussed previously, usually were on cliffs in the side canyons with northerly or easterly exposures. For example, three of the Prairie Falcon eyries were situated on west-facing cliffs (see Figs. 26 and 39–42). At each of these sites, peregrines had been seen in the side canyons, although not always concurrently with the nesting of the Prairie Falcon (sites 7, 8, and 16, Table 1). In 1943, a Prairie Falcon nested in one of the canyons (near peregrine site 16, Table 1), but at a west-facing site in an easily accessible Red-tailed Hawk's nest.

Morlan Nelson (pers. comm., 1971) noted a similar orientation between the eyries of the two species at the U1 site in northern Utah (site 11, Table 1), where he observed the two species in aerial combat (Nelson, 1969). The peregrine eyrie was on a ledge facing east and the Prairie Falcon eyrie was in a pothole (cave-like recess) in the side of the west-facing cliff, less than half a mile away (1,320 ft; 402 m; Nelson, pers. comm., 1971). Potholes probably provide greater protection from the hot afternoon rays of the sun than do exposed ledges.

These data suggest that both species may select eyrie sites on the basis of directional exposure to the sun, and that such a preference by these two species tends to lessen competition between them for eyrie sites. Nevertheless, this phenomenon needs further investigation, both in Utah and elsewhere, since some studies suggest that the Prairie Falcon in some parts of its range selects eyrie sites on the basis of availability of suitable cliffs rather than directional facing. For example, Leedy (1972) investigated the directional facing of 49 Prairie Falcon eyries in Montana during 1970 and 1971 and compared them with the directional facing of the available cliffs. He found that 72 percent of the eyries faced south (33 percent) or east (39 percent), 8 percent faced north, and 20 percent faced west. Of the 45 available cliffs in Leedy's study area, 71 percent faced south (31 percent) or east (40 percent), 7 percent faced north, and 22 percent faced west—a near duplication of the directional facing of the eyrie sites. Similarly, Tyler (1923) reported that most Prairie Falcon eyries examined by him in southern California had northern exposures because in the region where he made his observations the north ends of the ridges broke off abruptly into cliffs that faced north. Nevertheless, a few of his eyries were on west-facing cliffs; one was on an east-facing cliff; and none were on south-facing cliffs.

Height Preference for Cliffs and Eyrie Sites

The Prairie Falcon in Utah may use nesting sites of a quality inferior to those normally used by the peregrine in Utah. Judging from Bond's (1946) observations, this may be typical of the behavior of the two species wherever their geographic ranges overlap.

Three of nine Prairie Falcon eyries found in Utah by Porter and Erwin between 1950 and 1952 were at locations that were easily accessible to both humans and mammalian predators. Two were situated in potholes, one of which was located only 30 inches (76.2 cm) from the base of a small sandstone cliff and the other was only 36 inches (91.4 cm) from the base and 48 inches (121.9 cm) from the top of an outcropping of limestone. A third eyrie was located in 1943 by R. L. Porter and J. F. Poorman in an old Red-tailed Hawk's nest that was situated on a small pinnacle of rock which required no climbing to reach. One found in 1958 by F. Welch and G. L. Richards was on a large rock about 15 feet (5 m) above the ground and 6 feet (2 m) below the top of the rock. It probably could have been reached by a good climber without the aid of a rope. In southwestern Utah the Prairie Falcon has nested in a stick nest in the top of a 20-foot (6 m) juniper tree (*Juniperus* sp.) (Williams and Matteson, 1948).

In Utah peregrine eyries were a greater distance from the base of the cliffs, on the average, than were those of the Prairie Falcon. They were on higher cliffs, on the average, and they were on relatively more inaccessible ledges than were the eyries of their congener (Table 3). Moreover, the peregrine eyries averaged a greater distance below the brink of the cliff ($\bar{x}$= 68.6 ft, 21 m; range, 25–250 ft, 8–76 m; n=13) than did those of the Prairie Falcon ($\bar{x}$= 25.3 ft, 7.7 m; range, 4–175 ft, 1–53 m; n=41).

The average height of the Prairie Falcon eyries in Utah (64 ft; 20 m) was greater than that recorded by Enderson (1964) in Colorado and Wyoming (34.7 ft; 11.1 m), and less than that reported by Leedy (1972) in Montana (80 ft; 24.4 m). The average cliff height of 101.7 feet (31 m) for the Prairie Falcon in Utah is nearly twice that recorded by Enderson (1964) for this species in Colorado and Wyoming, and about 25 feet (7.6 m) less than that recorded by Leedy (1972) in Montana. Table 3, which compares the heights of cliffs and eyrie sites of the Prairie Falcon with those of the peregrine, illustrates the difference in height preferences between the two species.

The more marginal sites, including those on the smaller or more accessible cliffs at sites such as 1, 3, 11, and 20 (Table 1), probably were abandoned by the peregrine earlier in the century. Both their sizes and locations made them marginal sites. Several investigators (Hickey, 1942; Ratcliffe, 1962) have indicated that the marginal sites were the first to become inactive following the advent of early settlers.

Eyrie Type Preferences

The Prairie Falcon uses a wider variety of nesting situations than does the peregrine (see Figs. 39-45). For example, nearly half (45.8 percent) of 72 Prairie Falcon nesting sites in Utah were in potholes and crevices (Figs. 42-44) in the face of a cliff, whereas only a third of them (31.9 percent) were on an open ledge of a cliff (Fig. 39). An additional third of the eyries were in the

Fig. 40. The Prairie Falcon eyrie that was situated on an old Common Raven's (*Corvus corax*) nest and was later reclaimed by the raven. Note the accumulation of fecal material and detritus suggesting that the eyrie had been used by the falcons for a long period of time (eyrie site faces southwest). Photo by R. D. Porter, 1951.

Fig. 41. Raven's nest built upon prairie eyrie (shown in Fig. 40). Photo by R. D. Porter, 1951.

nests of other species of raptors and Common Ravens, which suggests that these species may be beneficial to the Prairie Falcon by providing additional nesting sites. Table 10 gives the kind of nesting situations used by Prairie Falcons in Utah.

Sometimes these competitors may preempt their old nests from the Prairie Falcon. An occurrence of this kind took place at an eyrie in Weber County observed by Porter and Erwin. The falcons were using an old raven's nest which apparently had been occupied for many years by falcons, since it was almost entirely buried in excrement (Fig. 40). Without the old raven's nest as a base, a falcon's eyrie would have been impossible. When first located on 5 June 1950, five fully grown young were present in the nest. The following year the eyrie contained three fresh eggs on 7 April. When it was next visited on 8 May, a raven flushed from the eyrie site, exposing six raven eggs in a newly constructed stick nest over the old prairie eyrie (Fig. 41). The whereabouts of the previous tenants was not determined.

Table 10. Percentage use of various categories of eyrie sites by Prairie Falcons in Utah (see photos by Wolfe, 1928)[1]

Kind of Site	Usage of eyrie types	
	n	Percent
Potholes[2]	26	36.1
Open cliff ledges	23	31.9
Crevices	7	9.7
Stick nests	16	22.2
Red-tailed Hawk's on cliff face	7	9.7
Common Raven's on cliff face[3]	5	6.9
Tree nests	2	2.8
Golden Eagle's on cliff face	1	1.4
Unknown species of hawk	1	1.4
Totals	72	99.9

[1]From unpublished data of authors, fieldnotes of R. G. Bee, A. B. Boyle, and R. J. Erwin, and from ornithological literature for the state.
[2]Five or 6.9 percent of the eyries were in old ravens' nests located within potholes.
[3]Including the five that were in old ravens' nests within potholes, a total of 10 or 13.8 percent were in old ravens' nests.

Peregrines apparently were more restrictive in the selection of their eyrie sites. They used predominantly open ledges or shelves which usually were under an overhung portion of the cliff (See Figs. 26-38). Only two Utah eyries, to our knowledge, were situated in potholes on the sides of cliffs [sites 4 (alternate) and 23, Table 1 (See Fig. 44]. We have no evidence of a beneficial relationship between the peregrine and other cliff-nesting species similar to that previously discussed for the Prairie Falcon.

Both species of falcon apparently prefer to nest under overhangs. Although our data on the

Fig. 42. Prairie Falcon eyrie in crevice on face of west-facing cliff. Peregrines nested up side canyon (site 8, Table 1). Much of the wood in the crevice was carried there by wood rats (*Neotoma* sp.). Photo by R. D. Porter, 1951.

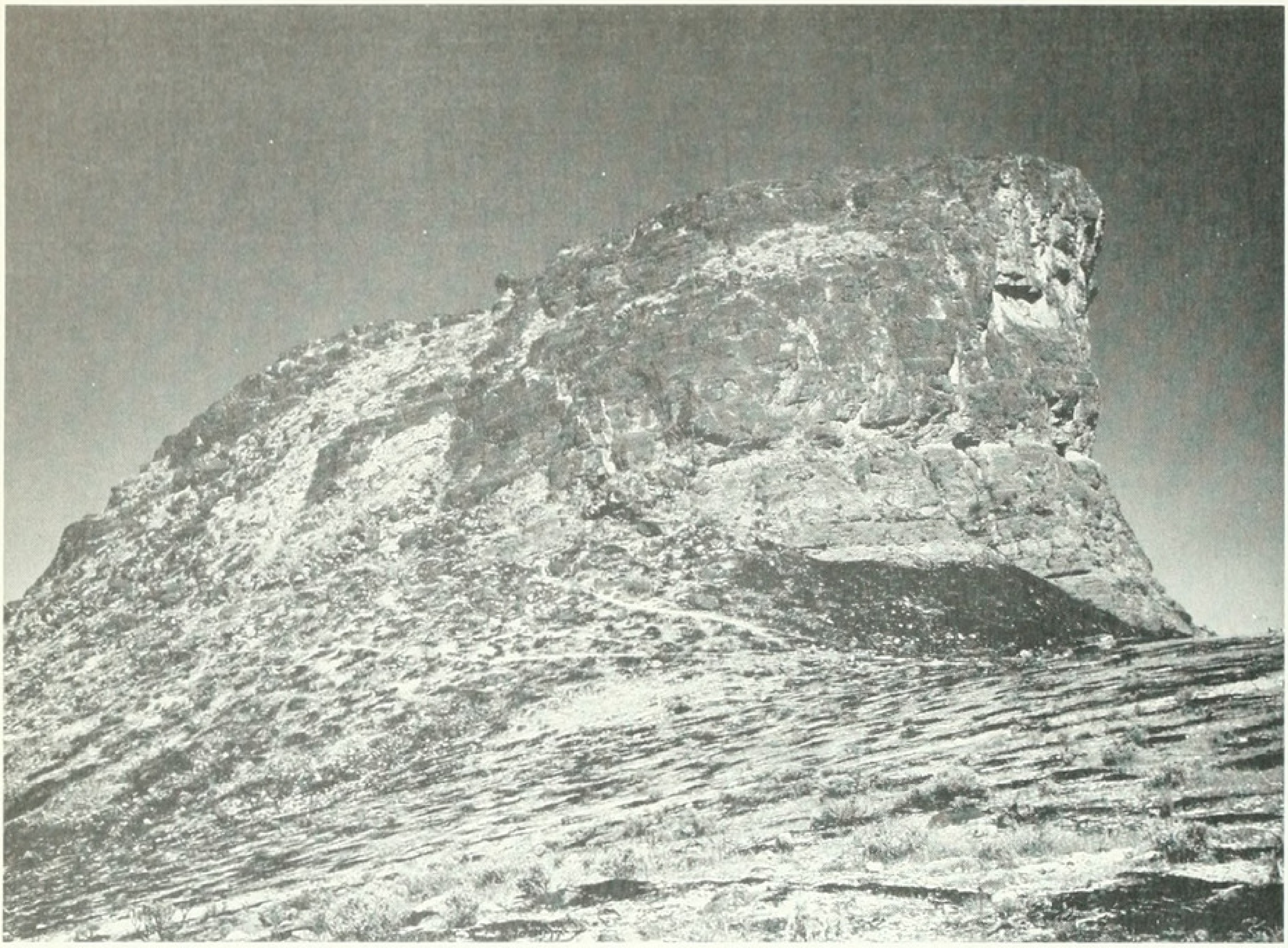

Fig. 43. A cliff used alternately by Prairie Falcons and ravens. Nesting site is situated in a pothole similar to that shown in Figure 46. Cliff is less than 2 miles (2.6 km) from the peregrine eyrie shown in Figure 22, and this cliff may also have been used historically by peregrines. Photo by R. J. Erwin, August 1972.

Prairie Falcon are incomplete in this regard, all but one of 36 Prairie Falcon eyries in Colorado and Wyoming reported by Enderson (1964) were directly overhung by a portion of the cliff.

Size Preference for Nesting Area

The Prairie Falcon appears to be less selective than the peregrine in the size of its nesting or egg-laying area. White (unpubl. data), for instance, observed a Prairie Falcon nesting in a pothole that was apparently too small for a large family of young because, before the young had fledged, all but one were forced from the eyrie to an untimely death on the talus below (Figs. 45-46). This nest was used for five consecutive years. The female laid five eggs each year and each year only one young fledged. The eyrie was then abandoned. We have also, however, seen prairies successfully fledge large broods from ledges equal to or smaller than the site mentioned above.

The aforementioned Prairie Falcon eyrie in Weber County that was taken over by ravens had a total nesting area of only about 310 sq inches (2,000 cm^2) (measured from photographs). A Prairie Falcon eyrie in Box Elder County, found by Erwin, was in a crevice in the face of a cliff which was only 20 inches (51 cm) wide at the point where the eggs were laid. The crevice was over 80 inches in depth (ca. 200 cm) and nearly high enough for a man to stand in (measured from a photograph).

In the Wasatch Mountains, peregrines usually laid their eggs on wider ledges with a relatively more spacious nesting area (frequently with grass on them) than did the Prairie Falcon. The area and/or volume available for nesting on open ledges and within potholes used as eyrie sites in Utah are given in Tables 9 and 11. The average available nesting area for peregrine eyries in Utah is nearly twice that of prairie eyries (Table 11).

The wider variability in size and height of the Prairie Falcon's nesting sites would appear to be advantageous to the Prairie Falcon in its competition with the peregrine. If the better quality sites were already utilized, one of lesser quality,

Table 11. Size of area available for nesting at Prairie and Peregrine Falcon eyrie sites in Utah.[1]

Types of sites and units of measure	PRAIRIE FALCONS			PEREGRINE FALCONS		
	n	$\bar{x}$	range	n	$\bar{x}$	range
POTHOLE SITES						
Avail. nest. area						
sq feet	5	11.6	8.0 -18.8	–	—	— —
sq meters	5	1.1	0.74- 1.7	–	—	— —
Volume of potholes						
cubic feet	4	20.2	9.0 -43.7	–	—	— —
cubic meters	4	0.6	0.3 - 1.2	–	—	— —
LEDGE AND POTHOLE SITES, combined						
sq feet	8[2]	16.3	2.2 -38.8	7[3]	27.8	10.0-52.0
sq meters	8[2]	1.5	0.2 - 3.6	7[3]	2.6	0.9- 4.8

[1]Data were collected between 1943 and 1972 by R. D. Porter, C. M. White, and R. J. Erwin. See Table 8 for more detailed data on peregrine eyrie site 7.
[2]Two of the eyrie sites were alternate sites at site 7 (Table 1); one was used in common with peregrines.
[3]Data are from four different eyrie sites, including three alternate eyrie sites at site 7 (Table 1, figs. 26-39).

and possibly not suitable for peregrines, could be used, thus giving additional pairs of Prairie Falcons the opportunity to nest. Prairie Falcons nesting in the more arid desert areas of Utah frequently use sites which probably would not be used by the peregrine.

Aggressive Interactions between Peregrines and Prairie Falcons

Nelson's (1969) reported decline in active peregrine eyries around the Great Salt Lake probably involved the use by Prairie Falcons of abandoned peregrine eyries (Nelson, pers. comm., 1971), and as mentioned earlier, the peregrine also is known to have occupied an eyrie which earlier in the century was used by Prairie Falcons (see White, 1969b).

No direct competition between the two species for nesting sites was recorded during the years that the earlier mentioned Wasatch Mountain eyries (Table 1, site 7) were under observation by Porter and Erwin, despite the fact that the eyrie sites were only about 300 feet (91 m) apart (Figs. 22 and 23), and that the peregrines frequently flew within 100 yards (91 m) or so of the prairie's eyrie. Neither of the eyries were visible from the other (see Fig. 22). White and Cade (1971) found peregrines and Gyrfalcons nesting on the same cliffs simultaneously and successfully. They postulated that perhaps peregrines and Gyrfalcons can coexist in close juxtaposition if their nests are not visible to one another and if their schedules or routes of going to and from their nests to hunt are different.

Other instances of amicable interspecific coexistence between the peregrine and the prairie have been reported. Bond (1946), for example, tells of the two species nesting peaceably only a few hundred feet apart. Pettingill and Whitney (1965) noted the nesting of a pair of peregrines and prairies 400 yards (366 m) apart in South Dakota without apparent conflict. French (1951) found the two species nesting 200 yards (183 m) apart, but not in view of each other. He watched the peregrines attack the prairies at least three times, but only during one of several visits to the eyrie. It is possible that his disturbance of the prairies at their eyrie helped provoke the attack by the peregrines. Lanner Falcons (*Falco biara-*

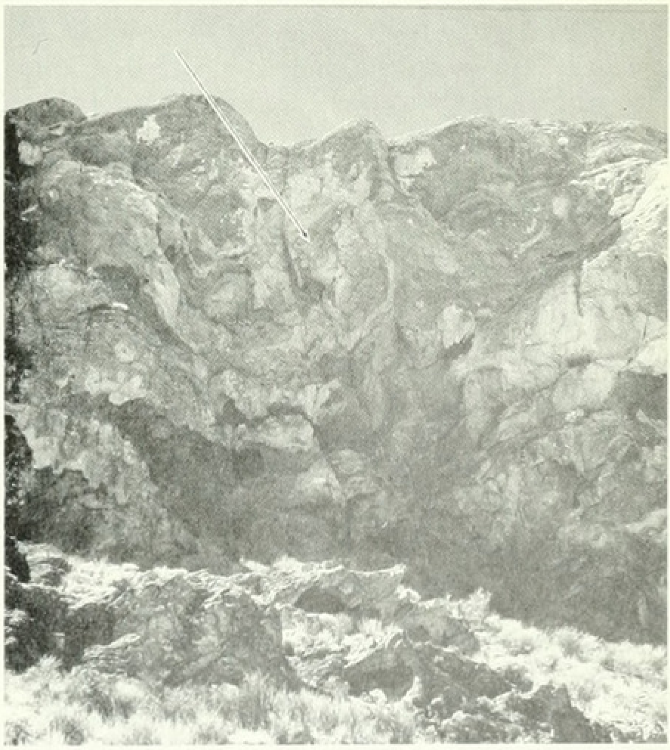

Fig. 44. Cliff in Great Basin desert (site 23, Table 1). Peregrine eyrie was situated near the horseshoe-shaped depression, "pothole," at the center of the cliff indicated by arrow. Photo by R. J. Erwin, August 1972.

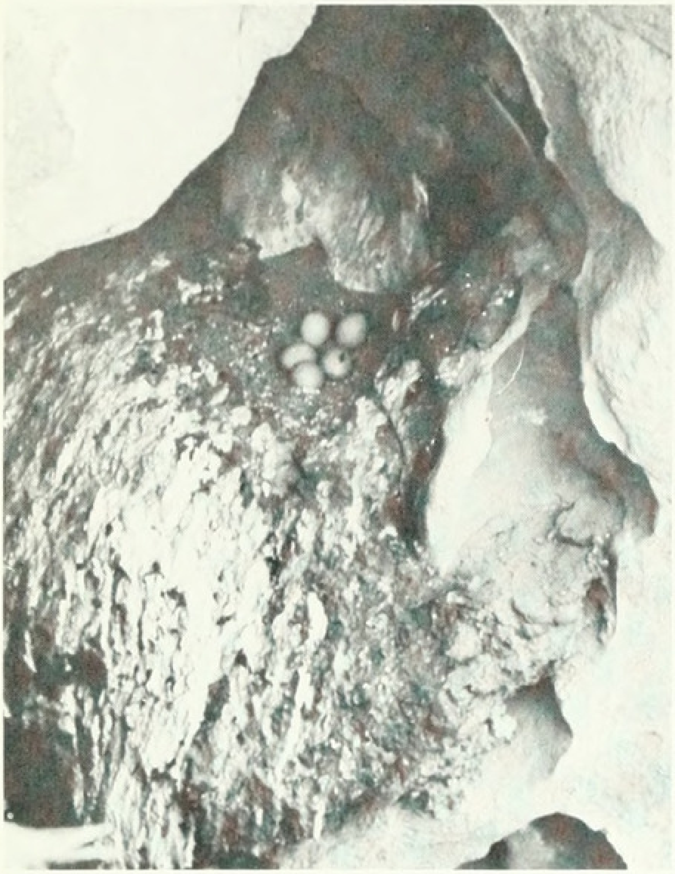

Fig. 45. Prairie Falcon eyrie in pothole on side of sandstone cliff. Photo by Gary D. Lloyd and C. M. White, 1958.

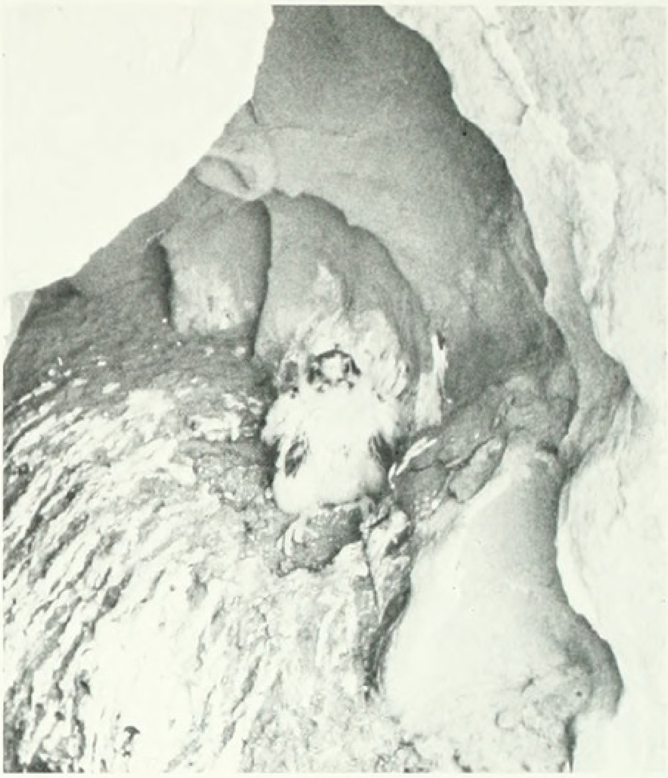

Fig. 46. Young Prairie Falcon in pothole eyrie illustrated in Fig. 43. Photo by Gary D. Lloyd and C. M. White, 1958.

micus) and peregrines in Sicily have been reported by Mebs (in Fischer, 1967) to nest only 500 meters apart with no apparent conflict during the nesting period.

On the other hand, Nelson (1969) watched a pair of Prairie Falcons in aerial combat with a pair of peregrines in Utah near the nesting site of the latter (Table 1, site 11); the two pairs nested about one-fourth mile (402 m) apart (Nelson, pers. comm., 1971). In discussing the aerial battles between the two species, Nelson (1969), indicated that the Prairie Falcons seemed to win them. Later in the paragraph he writes, "The battles were not definite and always ended in sort of a draw, with observers deciding that the Prairie Falcons won." He also noted that although the Prairie Falcons had command of the air, when the two species parted they returned to their respective sites. Hence, he did not consider the aggression to result in the abandonment of eyries by either species. Webster (in Beebe and Webster, 1964) gives a vivid account of an aerial attack in Colorado by a female Prairie Falcon on a peregrine presumably carrying food to its young in which the Prairie Falcon robbed the peregrine of its prey. The Prairie Falcon nested nearby, but the location of the peregrine's eyrie was not ascertained by the observer.

Not all encounters between the two species are won by Prairie Falcons. Ogden (1972) sighted an adult female peregrine along the Snake River of southwestern Idaho on 31 March and 6 April 1972. Although unmated, she forced a pair of Prairie Falcons to abandon their established territory and clutch of eggs following about two weeks of conflict between the two species (Ogden, pers. comm., 1972). The female peregrine remained and defended the cliff through the remainder of the nesting season and on several occasions she made reproductive overtures toward male Prairie Falcons (ibid.). Richard Fyfe (pers. comm., 1972) made an observation similar to Ogden's on 11 April 1972 in Alberta, Canada. A pair of Prairie Falcons was well established and the female was about to lay eggs in a "pothole" eyrie on a high dirt river bank at the time that the female peregrine arrived at that eyrie on 11 April. The male peregrine preceded her arrival by a few days. Within a matter of hours on the day of her arrival, the peregrines had driven the prairies away and usurped the pothole.

Despite these observations of conflict, both species are able to establish and hold an eyrie site in close proximity to its congener. The near equality in size and strength between the two species seems to reduce their dominance over each other. This is unlike the competition between the peregrine and the Gyrfalcon in the Arctic, where the larger and stronger Gyrfalcon, due to its earlier nesting and superiority to the peregrine in aerial combat, is able to establish and hold the most propitious nesting sites (Cade, 1960).

Both peregrines and prairies may use one another's alternate nesting sites, the availability of which may enable the two species to nest in closer proximity to each other than would two pairs of peregrines or two pairs of Prairie Falcons. Mebs (*in* Fischer, 1967) reported a similar relationship between the Lanner Falcon, a near ecological equivalent of the Prairie Falcon, and the peregrine in Sicily. A nesting cavity (hole) under his observation for three years was occupied in 1957 by lanners and in 1958 and 1959 by peregrines.

In some instances, the Prairie Falcon may occupy sites which otherwise would be used by additional pairs of peregrines—as well as the reverse—thus possibly limiting each other's breeding density.

Each species is known to maintain distances between eyries in parts of its geographic range not occupied by the other species which are much less than the distances between their eyries along the Wasatch escarpment. Few of the distances, however, averaged less than the distance between the alternate nesting sites used by the peregrine and Prairie Falcon at site 7.

Hickey (1942), for example, mentions that two pairs of peregrines nested only a half mile (805 m) apart in Canada, and Ratcliff (1962) gives an instance in Great Britain of four pairs breeding on a mile (1.6 km) stretch of cliff. White and Cade (1971) found peregrines nesting a quarter of a mile (1.40 km) apart in the Arctic, but this was the exception, not the rule. Beebe (1960) noted five to eight pairs nesting on a linear mile (1.6 km) of cliff in the Queen Charlotte Islands, the highest density known for the peregrine.

The highest Prairie Falcon density, to our knowledge, is along the Snake River in southwestern Idaho, where in 1971 Ogden (1971) found 74 active nest locations along a 53 mile (85.3 km) stretch of river, for an average of 1.4 occupied areas per linear mile (1.6 km). The eyrie sites averaged less than one mile (1.6 km) apart (one pair/3,771 ft; 1,149 m).

Date of Egg Laying as a Competitive Factor

We have observed in Utah that the Prairie Falcon generally initiates egg laying earlier in the spring than does the peregrine, and Nelson (1969) also noted this relationship between the two species. In Utah, peregrines have initiated egg laying as early as 22 March and as late as the second week in May. We have records of Prairie Falcon clutches in the Great Salt Lake area containing three eggs on 7 April, four eggs on 10 April (R. L. Porter and J. F. Poorman, unpubl. notes), and five eggs on 22 April. Newly hatched young were present on 13 May; young capable of flight were present on 10 June. A nest in extreme northern Utah found by Erwin in 1969 contained fully fledged young on 1 June. Woodbury et al. (unpubl. ms) recorded 51 sets of eggs from Tooele, Salt Lake, and Utah counties collected from 3 March to 15 June 1939. The average date of collection for 16 of the clutches, for which sufficient dates are available, was 20 April (range: 3 April-22 May). This did not, however, represent the dates of the laying of the first eggs. Wolfe (1928) records complete clutches of Prairie Falcon eggs in Utah from 5 to 20 April. The average nesting date for 36 records in Utah County was 18 April (range: 3 March-15 June) (data from Bee and Hutchings, 1942).

An earlier nesting date would give the Prairie Falcon first choice of eyrie sites. We have very little precise information for Utah on the arrival dates of either species at their eyrie sites, although White has seen Prairie Falcons at cliffs where eyrie sites were situated in February and early March and Porter has recorded them at a nesting cliff in the west desert of Utah as early as 3 February (1953) (Porter, Bushman and Behle, unpubl. ms). Wolfe (1928) noted the first appearance of Prairie Falcons in the Salt Lake Valley about the middle of March, and earlier farther south. He indicated that in some of the warmer valleys many of the falcons probably remain during the entire winter. Morlan Nelson (pers. comm., 1971) has seen this species at its desert eyries in Utah the year around. He believes that only the young leave the area of the nesting site (ibid.), although Enderson (1964) recorded the earliest arrivals in northern Colorado on 22 February in 1961 and observed that most adults became associated with the cliffs by mid-March.

Judging from the observation of adult male peregrines at eyries the year around in New Mexico (T. Smylie, pers. comm., 1971), it is quite possible that peregrines remain at or near some of the Utah eyries the year around, particularly the desert sites. Paul Newey (pers. comm., 1952) observed peregrines chasing his pigeons near the Wasatch Mountains during the last week in January 1950 and again on 18 February 1950. The falcons were probably from a nearby eyrie. The nesting cliff was climbed on 25 February by R. D. and R. L. Porter, but no falcons were seen. Both peregrines and Prairie Falcons, however, were seen by 4 April.

Reproductive Potential as a Competitive Factor

The Prairie Falcon appears to have a greater reproductive potential than does the peregrine. This, however, among other things such as food availability and winter mortality of young, may be a reflection of the greater vulnerability of the Prairie Falcon's eggs and young to predation due to its selection of eyries at sites which are more easily accessible to predators. The average clutch size for the Prairie Falcon is 4.5 for 55 completed clutches in Wyoming and Colorado (Enderson, 1964), 4.3 for 20 nests in western Montana (Leedy, 1972), 4.25 for 31 eyries along the middle Snake River in Idaho (Ogden, 1971), and 4.35 for the 65 clutches from the Utah eyries in the present study. These are compared with an average clutch size of 3.8 for peregrines in Utah, 3.7 for peregrines elsewhere in the United States (Hickey, 1942; Bond, 1946), and 2.9 for peregrines in northern Alaska (Cade, 1960).

PLEISTOCENE AND PREHISTORIC PEREGRINE AND PRAIRIE FALCON DISTRIBUTIONAL RELATIONSHIPS

Although Nelson's (1969) climatic change hypothesis probably is not the complete answer to the recent reduction in active eyries in Utah, it has a great deal of merit on a long-term basis. Perhaps the peregrine's present distribution in Utah can be elucidated best by an examination of the possible distribution of the peregrine and prairie falcon during prehistoric and Pleistocene times.

Pleistocene Distributional Records

Both the peregrine and the Prairie Falcon are known from late Pleistocene deposits in western North America (Howard, 1962b; Miller, 1943). Hence, both species probably were present in Utah during the late Pleistocene. White and Cade (1971) suggest that the peregrine may have originated in midlatitude regions of Eurasia, then spread northward into the Arctic, and from there into North America (White 1968b). The Prairie Falcon apparently evolved *in situ* in western North America.

Both species were present in the Los Angeles area of California contemporaneously (Howard, 1962b) throughout much of the late Pleistocene period covered by fossils found in the La Brea Tar Pits. The fossils in these pits are believed to range from 5,000 to 40,000 years old (Berger and Libby, 1966; Ho, Marcus, and Berger, 1969; and Downs and Miller, 1971).

Pit 16 contained fossils of three each of both the peregrine and the Prairie Falcon. Fossil wood from two depths, 6½ and 12 feet (2-3.7m), in this pit has been dated back $\geq$40,000 years by radiocarbon dating (Berger and Libby, 1966).

The occurrence of these two species together in this and other pits (Howard, 1962b) suggests a long association between the two species. Since there is, however, a considerable variation in the ages of the fossils from the various pits and from the various depths of each pit, and since the greatest depths have not always yielded the oldest fossils (pit 9, Berger and Libby, 1966), the exact age of the peregrine fossils is not known. In addition, Howard's (1962b) published account of the fossils present in the various pits does not indicate the depths from which the fossils were obtained nor if the fossils of the two species discussed here intermixed within the same depth. Therefore, a more definitive interpretation regarding the duration of a sympatric association between the two species and the age of their fossil remains must await carbon dating of the actual peregrine and Prairie Falcon fossils.

Additional specimens of the Prairie Falcon from Pleistocene deposits are known from Smith Creek Cave in Nevada (Howard, 1952), from Rocky Arroyo (Wetmore, 1932) and Howell's Ridge Cave (Howard, 1962a) in New Mexico, from Lubbock Reservoir in Texas (Brodkorb, 1964), and from Nuevo Leon in Mexico (Miller, 1943). Specimens of the peregrine also have been found at Potter Creek Cave and at McKittrick in California (Miller, 1911 and 1927), Shelter Cave in New Mexico (Howard and Miller, 1933), and at American Falls in Idaho (Brodkorb, 1963). Vertebrate fossils from the late Pleistocene American Falls bed B, where this latter specimen apparently originated, have been dated as having an age greater than 29,700 B. P. (ibid.).

Post-Pleistocene Distributional Records

The Prairie Falcon was distributed widely during prehistoric times. It is known from Oregon (Miller, 1957; <8,000 B. P.), California [(Howard, 1929; ≤1,000 B. P.) and (DeMay, 1942; ≤500 B. P.)], Arizona (Miller, 1932; 1,000 A. D.), and Utah [(Harper and Alder, in press; ≤8,500 B. P.) and (Steward, 1937; remains not dated, but probably very recent)]. The peregrine, on the other hand, has been found, to our knowledge, only at prehistoric sites in California (Howard, 1929; ≤1,000 B. P.) and Utah (Steward, 1937; remains not dated, but one of the two specimens probably was very recent; the other may have been somewhat older; one apparently was within strata containing artifacts of the Promontory culture).

These records suggest that both species were rather widely distributed geographically during the late Pleistocene, and that the peregrine probably was more common then than now; but following the Pleistocene period, the relative distribution and abundance of the two species probably were much the same as they have been historically.

Lake Bonneville and Peregrine Distribution in Utah

Ancient Lake Bonneville was formed during the thrusts of the most recent Pleistocene glaciers some 60,000 to 70,000 years ago (Blackwelder, 1948, and Antevs, 1948). At its greatest height (the Bonneville level), this lake covered 19,750 sq miles (51,153 km^2) of Utah's Great Basin (Antevs, 1948) and had a shoreline of 2,550 miles (4,103 km) (Fenneman, 1931). After standing at the Bonneville level for a long period of time, it is believed to have receded below the present level of the Great Salt Lake (Marsell *in* Durrant, 1952). Then, some 25,000 years ago during the Provo pluvial it rose to the Provo level [Lake Provo, 13,000 mi^2 (33,670 km^2) area, Antevs (1948)]. It then receded (Antevs, ibid.; Marsell, op. cit.), after which it again filled back up to the Provo level (Marsell, op. cit.). In the last 12,000 years it receded to the present level (op. cit.).

A warmer interval of some 4,000 years began about 5,550-4,000 years B. C. (Blackwelder, 1948), at which time the lake receded to a level below that of the Great Salt Lake, with average temperatures distinctly higher than those of the present (Antevs, 1948; Blackwelder, 1948). Beginning about 2,500 years ago, a reduction in mean temperatures and evaporation caused an expansion of the lake to its historic levels (Antevs, 1948).

The present environmental conditions in the Arctic may be near optimal for the peregrine, judging from its recent distribution and population density there. Climatic conditions in Utah during the late Pleistocene glacial periods probably were much less arid than at present and consequently closer to those presently occurring in the Arctic. According to Blackwelder (1948), temperatures in the Great Basin during the coldest ages probably were 8-12° F below the long-term average, and the rate of evaporation was much slower than at present. The extent of the ecological changes that took place in the southern part of the Great Basin during the latest glacial age are revealed in the dung of extinct ground sloths found in Gypsum Cave of southern Nevada (Laudermilk and Munz, 1935). The dung contained species of plants which now occur 3,000 feet (914 m) higher in the mountain ranges some 20 miles (32.2 km) away.

Recent data collected by Harper and Alder (in press) from an anthropological site in northern Utah, although agreeing in the sequence of events, indicate that the date of the actual onset and termination of these periods may be in error as might the extent of temperature change. At Hogup Cave, which is located just north of the Great Salt Lake, Harper and Alder (in press) found that all but one of the plant species that were present in the 14 feet of deposit dating back 8,500 years presently occur within 40 miles (64 km) of the cave. During this period, the upland areas were dominated by a xeric desert shrub community, although the first 500 years were somewhat more mesic in nature. They (ibid.) found that the lowlands had undergone a greater degree of change than had the uplands, as suggested by both plant and animal remains in the deposits. From about 7,800 B. P. to 2,500 years B. P. (except for a brief period about 6,000 years B. P.), the temperature increased at least 1° C and the open water and marshlands decreased. Then some 1,500 years ago and continuing for about a millenium, there was a relative increase in grasses on the uplands [suggesting an increase in rainfall]. Harper and Alder (ibid.) believe that the last 500 years were more arid and that the climate around the cave became as dry and inhospitable as at anytime during the past 8,500 years.

Historically, with the utilization for irrigation of the river waters which support the Great Salt Lake and a general increase in mean temperatures and decrease in precipitation during the past several decades, as was discussed earlier, the Great Salt Lake reached its minimum level for historic times in about 1961. Since then it now has risen about seven feet (2.1 m) above its historic low.

The climate and ecological conditions present during the past 8,500 years would not seem to have been sufficiently arid to have eliminated completely the peregrine as a breeding bird in the area surrounding the Great Salt Lake. This is especially so if one considers the apparent extent of the aridity during the past 500 years and the persistence of the peregrine as a breeding bird in Utah despite the dry harsh climate of the past half century.

The occurrence of the Prairie Falcon at the oldest level (at least 8,350 years B. P.), along with numerous remains of nine species of water birds, at a time when ecological conditions probably were more optimal for the peregrine than at present, would suggest that the region surrounding the Great Salt Lake was even at that time an area of sympatry for these two species. The presence of both species in Black Rock Cave, south of Great Salt Lake (Steward, 1937), gives credence to this hypothesis.

The date of the first occurrence of the peregrine in the intermountain area, of course, is not known, but one can speculate that it appeared during one of the pluvial periods when the environmental conditions were most propitious for its survival and for its competition with the Prairie Falcon for food and nesting sites.

It is probable that it was present in Utah during the late Pleistocene, contemporaneously with its occurrence at Rancho La Brea. The presence of this species among fossils at the American Falls bed B, dating back at least 29,700 years, tends to confirm this supposition.

During the Bonneville and Provo pluvials, Lakes Bonneville and Provo, with their extensive shorelines and numerous islands, must have provided innumerable nesting sites, an abundance of prey species, and a near optimal climate for the peregrine. Pleistocene rivers and smaller lakes also must have provided correlative conditions which may account for eyries in areas outside of Bonneville Basin.

If the peregrine was present during the Bonneville and Provo interpluvials, it may have encountered environmental conditions of even greater aridity than at present. It would be of interest to know if peregrine eyries were maintained during these periods of extreme aridity or if, as suggested by Nelson (1969) for present conditions, altitudinal and latitudinal adjustments were made. If the latter were true then the eyries became reactivated when the lake gradually increased again to its maximum historic level.

The overlap between the breeding distribution of the Prairie Falcon and peregrine in the intermountain area during the cooler, wetter pluvial period was probably dominated by the peregrine, but as the climate slowly ameliorated, populations of the Prairie Falcon likely increased in density and gradually extended northward, probably at the expense of the peregrine. As the environmental conditions became more arid, the peregrine eyries that were near lakes or streams where sufficient food was available may have remained active. Those where the water disappeared probably either were taken over by the better adapted Prairie Falcon or else were deserted. Peregrines at the active eyries may have gradually adapted to the increasing aridity, but they would have been able to compete with the Prairie Falcon only at sites where water was available. This hypothesis seems to be supported by the geographical and ecological distribution of the peregrine in Utah during historic times (Fig. 1). For instance, of the 40 known and suspected eyries in Utah, 26 were located in or near the Bonneville Basin. The greatest concentrations of breeding pairs occurred near the largest remaining bodies of water, particularly in the area surrounding the Utah and Great Salt lakes.

The eyries in the harsh environment of the Great Salt Lake Desert were adjacent to small expanses of marsh (Figs. 20 and 23). Most astounding is that these eyries existed at all, considering the harsh nature of the environment. It is evidence of the adaptability of the species and of the species' tenacity at its eyrie sites. How long these eyries would have remained active in the absence of human interference is a question that may never be answered. The tenacity of peregrines at their eyrie sites as discussed by Cade (1960) and Hickey (1942), and the tendency toward a genetic continuity in eyrie maintenance as proposed by White (1969a) (for a more complete discussion, see White, 1968b) would suggest the possibility that some of the eyrie sites that were active during recent times may have had long histories of activity; some perhaps, even extended back into Lake Bonneville times. This possibility seems especially plausible when one considers the relative recency of some of the later pluvial periods. Thus, the relationship between the Prairie Falcon and peregrine probably extends back many thousands of years, which may be a factor in the relative compatibility of the two species.

Data presented previously regarding the contemporaneity of the two species at Rancho La Brea; the occurrence of the peregrine in a fossil bed at American Falls, Idaho, dating back to at least 29,700 years B. P. (Brodkorb, 1963); the presence of both species at anthropological sites just south of the Great Salt Lake (Steward, 1937; Black Rock Cave); and the climatic and environmental evidences from Hogup Cave in northern Utah (Harper and Alder, in press) tend to corroborate this supposition. The lack of aggression between them also suggests a long sympatric relationship.

White and Cade (1971) believe that traditional use of an eyrie site will in the long run reduce the total impact of intolerant behavior and promote stability in the peregrine populations of the Arctic. If so, a long history of occupancy at Utah eyries probably would have enhanced the peregrine's competitive position with the Prairie Falcon and thus strengthened the peregrine's hold on its optimal eyrie sites.

SUMMARY AND CONCLUSIONS

Utah's rugged topography and ecological variability is conducive to its inhabitation by a wide variety of raptorial species. This includes the Peregrine Falcon, which now has virtually disappeared as a breeding bird in the state.

Although sparsely distributed throughout Utah, the species apparently found conditions especially suitable for nesting in the environs of the Great Salt Lake and Utah Lake valleys, where its nesting sites in the adjacent mountains were within flying distance of a plentitude of preferred prey species which inhabited the marshes and shorelines surrounding the two lakes. Despite the aridity of the environment, the 20 eyries that occurred there, when and if they all were active simultaneously, comprised a population comparable to some populations elsewhere in North America where the environment is considered to be more congenial to the peregrine. On the average, there was one eyrie site for every 225 sq miles (583 km^2) in an area of about 4,500 sq miles (11,655 km^2) surrounding the Utah and Great Salt lakes. The average distance between 13 eyries along 130 linear miles (209 km) of the Wasatch Mountains was 10.0 miles (16.1 km) (range, 2-20 mi; 3.2-32.2 km).

Elsewhere in the state, the species was more sparsely distributed, and then only at sites where suitable nesting cliffs were adjacent to marshes or rivers. Only nine additional eyries have been verified for the remainder of the state [one pair per 7,732 mi^2 (20,025 km^2) in area, exclusive of the aforementioned 4,500 mi^2], although 11 others are suggested by the presence of adult birds and/or young during the nesting season. If all 40 known and suspected eyries are included, there would be about one eyrie for every 2,123 sq miles (5,499 km^2). If 11 unverified eyries are excluded, there would be about one eyrie for every 2,928 sq miles (7,584 km^2) of the state.

Peregrines have reproduced successfully in the deserts of Utah's Great Basin and Colorado Plateau under some of the harshest climatic conditions to which the species is subjected. All eyries in Utah's deserts have been situated near marshes, lakes, or rivers. Peregrine nesting sites in the desert generally were closer to extensive marshes than were those along the Wasatch escarpment. The average distance from eyrie to hunting sites in the marshes was only 1.3 miles (2.1 km) (range, 0.19–2.8 mi; 0.31–4.5 km) for three desert eyries. For the nesting sites in the region of the Utah and Great Salt lakes, the distances averaged 3.3 miles (5.3 km) (0.19-9.7 mi; 0.31-15.6 km). Marshes used by peregrines at the desert eyries usually were less than 3 sq miles (7.8 km^2) in extent (Table 4).

Although the Peregrine Falcon has been known to occur in Utah since the early 1870s, most of our knowledge of its nesting distribution and abundance dates back only three or four decades. The status of the species in Utah prior to the late 1930s is largely unknown. Its past history and present status in Utah, therefore, has been postulated on the basis of all records available to us, both before and after 1939. Data are too sketchy for a thorough understanding of the kinetics of local populations. Eyries that survived the longest are those farthest from areas of intensive agricultural practices and also dense human populations. Those at the poorest quality sites appeared to have been deserted first. Abandonment of active eyries first became apparent in the 1940s. The known breeding population in Utah was reduced by the late 1960s to less than 10 percent of the pre-1940 estimates.

The several factors, in order of relative importance, that may have contributed to these changes are as follows: (1) the inimical effects of DDT, its metabolites, and other chlorinated hydrocarbons on peregrine reproduction; (2) a drying up of marshes which supported the peregrine's prey species, due to a decline in annual precipitation; an increase in the average daily temperatures; and the diverting of river waters for irrigation purposes; (3) the killing of adult and young falcons with firearms; (4) the death of peregrines due to botulism toxins; (5) the robbing of eyries for their eggs or young; and (6) the destruction of nesting cliffs for mining and construction operations and general human encroachment.

Reproductive failure typical of the pesticide syndrome was recorded at three peregrine eyries and one Prairie Falcon eyrie in Utah during the period following the extensive use of DDT to control mosquitoes and agricultural pests in Utah and elsewhere. All of these factors combined probably have contributed to the near extirpation of the peregrine in Utah, although the use of organochlorine pesticides probably was the most important contributory factor, especially when combined with a prolonged drought which occurred during the first half of the century.

The average clutch size at one peregrine eyrie site in Utah for five years between 1943 and 1952 was 3.8, and an average of 2.4 young hatched during these years; and for seven years between 1943 and 1953 a total of 19 young were produced for an average of 2.7 young per year. This is in close agreement with figures recorded at other eyrie sites in North America at an equivalent latitude. The incubation period at the aforementioned eyrie site was estimated to exceed the 28 to 29 days reported elsewhere by four or five days. An unusually long incubation period of about 40 days in 1948 was explained on the basis of renesting, if based on a 28- to 29-day incubation period.

Nestling peregrines in Utah were given a wide variety of avian prey species. Pairs nesting along the Wasatch Mountains (near the Great Salt Lake) fed their young mostly shore- and marshbirds, many of which were obtainable only from Great Salt Lake marshes up to 17 miles (27.4 km) distant. Avocets and Willets were the species of shorebirds most used. Mourning Doves, Rock Doves, Red-shafted Flickers, and Western Meadowlarks were most used of the nonaquatic prey species. Bats, which were the only mammalian prey species present in Utah eyries, represented less than one percent of the diet. Passerine and gallinaceous prey species were of greater importance and aquatic prey species of lesser importance in the desert eyries. The selection of eyrie sites by peregrines in Utah appears to be associated with the availability of suitable nesting sites adjacent to a marsh or stream where prey species are available in adequate numbers. The utilization of aquatic prey species as food for nestling peregrines in Utah undoubtedly is a major factor in the species's proclivity for nesting sites near water.

The Golden Eagle and Prairie Falcon are the two species most likely to compete with the peregrine for food and nesting sites. Direct competition between the peregrine and Golden Eagle for food probably is minimal, since mammalian prey species contribute greatly to the eagle's diet, and no direct evidence of competition between the two species for nesting sites has been observed in Utah.

The Prairie Falcon, on the other hand, is a probable competitor, which is expected because both species belong to the same genus, both are basically equivalent in ecological function, and both are approximately equal in size and strength. Although the habitat of the two species overlaps, habitat separations are present. The Prairie Falcon, for example, may nest in the desert many miles from water. In the zone of contact between the two species, its selectivity in habitat and food encompasses and exceeds that of the peregrine. The zone of contact between the two species appears to be restricted only by the paucity of suitable nesting habitat adjacent to an adequate supply of food for the peregrine.

Where they occupy the same habitat their diets are somewhat different, thus mitigating the possibility of strong competition for food, although where they nested side by side in the Great Salt Lake Valley their food niches did overlap considerably. Both species preyed rather extensively on the same two prey species, the avocet and Willet, which probably was a response to the abundance of these two shorebirds. In general, the Prairie Falcon was much less selective in its food requirements in the area surrounding the Great Salt Lake than was the peregrine in the same area, and it was more prone to supplement its diet with rodents, ground nesting birds, and reptiles. Thus, in this respect, it appeared to have an adaptive advantage over the peregrine.

Competition between the two species for food did not appear to have been an important factor in controlling their relative densities along the escarpment of the Wasatch Mountains, especially when populations of avocets, Willets, and other species of shorebirds were sufficiently large to support them both.

We have no data regarding the food niches of the Prairie Falcon in the zones of contact between the two species at river sites in the desert. However, we would expect a greater overlap in the avian prey of the food niches of the two species in these areas due to the elimination of a great portion of aquatic birds from the diet of the peregrine (see Gabrielson and Jewett, 1940). Our data, however, suggest that the extensive utilization of rodents, particularly ground squirrels (*Citellus* sp.), by the Prairie Falcon in the desert areas would tend to lessen the impact of the competition between the two congeners for avian prey in those regions.

In regions of Utah where the populations of the peregrine were greatest, pairs of Prairie Falcons and peregrines nested much closer together than did pairs of peregrines or pairs of prairies. The two species sometimes even used one another's alternate nesting sites. When they nested close together, their nesting sites were not known to be visible from one another. Although they were observed in aerial combat, neither species appeared to be able to consistently dislodge its congener from its nesting site.

Our data suggest that both species select eyrie sites on the basis of availability, but when given a choice they seemingly select them on the basis of directional exposure to the sun. The peregrine shows a preference for north- and east-facing cliffs, and the Prairie Falcon shows a preference for south- and west-facing cliffs. This relationship between the two species needs additional investigation to further test its validity in Utah and to test its applicability elsewhere in the arid West.

The Prairie Falcon was less selective than was the peregrine in its choice of nesting sites, sometimes selecting sites which were seemingly shunned by the peregrine. The former species, for example, utilized sites that were located on smaller ledges with a smaller total nesting area, as well as sites located on lower cliffs nearer the base of the cliff or otherwise more easily accessible to humans and to mammalian predators, than did the latter species. Furthermore, ravens which are common in Utah, seemingly alter the nesting habitat in a beneficial way for Prairie Falcons by providing additional nests that are frequently used by the falcons, whereas the peregrine apparently is little affected by the presence of ravens.

The Prairie Falcons initiated egg laying earlier in the season, thus giving them first choice of nesting sites; and on the average they laid larger clutches than did the peregrine.

The Prairie Falcon is a true desert species. It apparently evolved in the arid environment of western North America, and as expected, in its association with the peregrine it appears to be the dominant competitor in the following ways: (1) it has a greater reproductive potential than does the peregrine, based on its larger clutch size; (2) it is less selective than is the peregrine in choice of nest sites and thereby has more nesting situations to choose from; (3) it lays earlier in the season than does the peregrine; thus it may have first choice of cliffs and eyrie sites; (4) it shows less selectivity in its choice of prey species as food for its young; consequently it has a wider range of species to choose from, including birds, mammals, and reptiles; and (5) because of its selection of prey species other than birds, it is not as obligate to open water for food, nor is it as obligate to open water for bathing, and thus it may nest many miles from water.

The Prairie Falcon, then, would appear to have a marked adaptive advantage over the peregrine, especially in marginal areas where the peregrine's ecological tolerance is restricted and where the peregrine's preferred food and/or nesting sites are in short supply. The Prairie Falcon's adaptive advantage over the peregrine may contribute to the restriction of the peregrine to the more optimal aquatic habitats near streams and marshes where food and nesting sites are not in short supply, and where the peregrine competes successfully with its congener.

Some of the reasons the peregrine in Utah is able to compete successfully with the Prairie Falcon for food and quality nesting sites may be: (1) the relative tolerance of the two species for each other while nesting close together; (2) the utilization of one another's alternate eyries, coupled with the inability of either species to consistently gain a dominance over the other in aerial combat, although recent observations by Ogden (1972) and R. Fyfe (pers. comm.) suggest that the peregrine may occupy the most propitious sites because it is capable of forcing the Prairie Falcon from them; (3) the possible partitioning of the nesting cliff with each species having distinct preferences for different types of nesting sites or a wide variability in acceptable nesting situations. There is, for example, the peregrine's preference for open ledges and the Prairie Falcon's acceptance of a wide range of nesting situations, illustrated by its use of potholes in the face of the cliff, open ledges, and old stick nests of other raptorial species. The pothole eyries probably enhance the survival prospects of young reared on west-facing cliffs and probably offer greater protection from predation than do the open ledges; (5) a variation between the two species in the size of the nesting area and in the height of the cliffs and eyrie sites; (6) the presence, in abundance, of the prey species preferred by the peregrine in areas of Utah where the peregrine was most common, with partial partitioning by the two species of their food niches; and (7) the peregrine's fidelity to the cliff.

We have hypothesized that the peregrine probably invaded the intermountain region during a pluvial period of the Pleistocene, when the environmental conditions favored the peregrine in its competition with the Prairie Falcon. Moreover, the ancient Pleistocene Lakes Bonneville and Provo undoubtedly presented the peregrine with both an abundance of food and a sufficiency of nesting sites. Fossil remains of peregrines from the La Brea Tar Pits dating back 40,000 years or more and from American Falls in Idaho dating back nearly 30,000 years support this hypothesis.

There may have been times during the cooler pluvial periods when the geographic ranges of the two species were mutually exclusive, at least in some localities of Utah. During the drier interpluvials, the Prairie Falcon probably took over nesting sites no longer tenable to the peregrine. However, the peregrine probably persisted at those sites where the ecological conditions were most propitious to its survival and where it gradually adapted to the more arid condition of the interpluvial, as is the present case. The peregrine is noted for its fidelity to certain cliffs over many generations of breeding birds. Traditional occupancy may not be the rule with the Prairie Falcon. Finally, one would expect that the longer the existence of a sympatric relationship between two closely related congeners, the more extensive would be the partitioning of their resources and the greater the reduction in the conflict between them. The partitioning of the resources between the peregrine and prairie seems to be sufficiently defined to suggest that this phenomenon has been in operation for a considerable period of time. The low level of interspecific aggressiveness as well as the paleontological records suggest that the relationship between the two species is probably of long standing.

Fluctuations in peregrine populations concomitant with fluctuations in height and length of the shoreline of the Pleistocene lakes probably have been of natural occurrence down through the ages. Peregrine populations possibly have been declining slowly in Utah over the past several centuries concurrent with a general amelioration of climate and accompanying reduction in suitable habitat based on climatic and biotic evidence from Hogup Cave dating back 8,500 years, while populations of the Prairie Falcon may have slowly expanded to fill the void as suggested by Nelson (1969).

Evidence that the southern extremity of the peregrine's geographic range historically shifted northward along with an associated shift altitudinally (Nelson, 1969) has not been demonstrated for Utah. With the drastic decline in the species' breeding populations that is presently taking place throughout North America, a hypothesis of this kind is difficult to test. A general cooling trend in Utah and elsewhere in the Northwest which started about 1961, however, should result in more suitable ecological conditions for the peregrine. The extent to which old eyrie sites are recolonized should be a test of the validity of Nelson's (1969) climatic change hypothesis for the peregrine decline in the western United States.

The presence of the peregrine at desert sites on the periphery of its ecological range as late as 1959-60 in the Great Basin (Table 1, site 23) and the early 1960s in the Colorado Plateau (Table 1, site 28) emphasizes the species's ability to adapt and its tenacity for survival.

The competitive roles of the peregrine and the Prairie Falcon apparently change according to locality, based on availability of food and nesting sites, and on the behavior and ecology of the raptorial species with which they must compete. For example, in the Arctic the Peregrine Falcon is a generalist, both in terms of its selection of nesting sites and in regards to trophic relationships with its competitors (White and Cade, 1971); there, this species utilizes a wide variety of food, which is not a restrictive aspect of its economy in the Arctic, and a broad selection of nesting sites. Its chief competitors in the Arctic are the Common Raven, the Gyrfalcon, and the Rough-legged Hawk (*Buteo lagopus*). The Gyrfalcon, the peregrine's most closely related competitor, on the other hand, is a specialist in terms of nest site and food selection. The raven and Gyrfalcon have similar nesting requirements, and since both are early nesters they have an earlier choice of eyrie sites. Thus, when the later-nesting peregrines and rough-legs arrive, the late arrivals are more or less limited to the remaining sites. Consequently, the peregrine utilizes "marginal" sites where it may have to compete with the rough-legs. Apparently, however, the peregrine is capable of usurping the rough-legs's nest. In addition, the two species may jointly occupy the same cliffs, thus lessening the competition between them. White and Cade (1971) believe that since ravens and peregrines do not get along well together, the earlier nesting raven may force the peregrine into "marginal" and "submarginal" sites on those occasions when peregrines try to nest too close to the ravens. They believe that the same thing applies when peregrines attempt to settle too close to Gyrfalcons on the same cliff. The peregrine, nevertheless, does use "optimal" sites in the Arctic when they are available.

In the desert, however, the peregrine's role is the reverse of its role in the Arctic. Here the peregrine is forced into the role of a specialist because the harsh arid environment produces few of the prey species preferred by the peregrine and because the Prairie Falcon competes more successfully for both the former's marginal food niche and its marginal nesting niche. The specialization in the peregrine's food requirements is apparent only when compared with that of the Prairie Falcon in the zones of contact between the two species. Here the utilization by the Prairie Falcon of rodents (especially ground squirrels), reptiles, and birds (to a great extent the same principal shore birds used by peregrines) makes it a generalist in its food habits. In areas of allopatry, as in the deserts, the Prairie Falcon often uses predominantly one or two species of rodents and/or birds and, therefore, in these regions, it is seemingly a specialist.

In its nesting site requirements, the Prairie Falcon is a generalist when both allopatric and sympatric with peregrines. In its selection of nesting sites, it seems to prefer sites which we would consider to be marginal for the peregrine. This more or less limits the peregrine to the more optimal nesting sites and to the role of a specialist. Distribution of free water, and its concomitant supply of suitable prey species, is the most important environmental factor dictating the distribution and abundance of the Peregrine Falcon in the arid West. Conversely, lack of free water and its associated supply of suitable prey species is a limiting factor in the distribution and abundance of this species.

Climate, on the other hand, appears to be a major factor restricting the geographic distribution of the Prairie Falcon as is its strong proclivity to nest on cliffs, thus nearly eliminating the use of tree nests as eyrie sites. In general, however, the selection by the Prairie Falcon of a wide variety of prey species, encompassing three classes of vertebrates, its utilization of several different types of nesting situations, its relatively high reproductive potential, and its ability to exploit successfully the arid environments of western North America points out the extent to which this species has become adapted to its particular environment. With its versatility in selection of prey species and nesting sites, but more especially the former, the Prairie Falcon is among the better adapted and more successful of North American raptors.

Because of its extensive utilization of rodents for food, its frequent occurrence in areas many miles from water and many miles from civilization, and its relatively nonmigratory nature, the Prairie Falcon is much less likely to become a permanent victim of the indiscriminate use of the chlorinated hydrocarbons than is the peregrine.

The current precarious status of the Peregrine Falcon in Utah is probably a result both of a change in climate and of the inimical effects of man's activities. The future of the species in Utah, as elsewhere, appears bleak. Many of the factors responsible for its decline are still in evidence. DDT and other harmful pesticides are still being used in Utah. In 1969, for example, 7,593 pounds (3,440 kg) of DDT were used in Utah for the control of noxious insects (in the pesticide policy statement of the Utah State Department of Natural Resources) and this was increased to 11,348 pounds (5,140 kg) in 1970 (Work Unit A, Pesticides Applied—State of Utah, Utah State Health Dept., 1970; Stephen L. Warnick). The impact on raptors of polychlorinated biphenyls and of the heavy metals, such as mercury, lead, and cadmium, are still poorly understood, and other chemical hazards of unknown kinds also may be involved.

Although man is still encroaching on the activities and habitat of the peregrine and on its environment, with the construction of artificial lakes such as those formed in Glen Canyon and in the Flaming Gorge and with a general cooling of the climate which is resulting in the reestablishment of certain lakes and marshes, nesting pairs of peregrines may yet be attracted into new and old areas, hopefully away from the harmful activities of man. Inimical environmental factors must first be eliminated. The use of management methods, such as construction of manmade marshes near suitable nesting cliffs or manmade eyrie sites near suitable marshes, has not yet been attempted. Management techniques have worked well with other species, and may prove successful with the peregrine.

The few peregrine eyries still remaining active, as well as the many active Prairie Falcon eyries in the state, should be given the strictest protection and/or management. All peregrine eyries should be guarded zealously that future generations may have the pleasures which have been ours; that is, to see, to study, and to enjoy this magnificent species alive in its native haunts.

Addendum

After the final manuscript was in press, we learned of two more localities used by peregrines. Ralph B. Williams (pers. comm.) told us of an eyrie that the late Charles Springer of Salt Lake City, an avid birder and falcon enthusiast, located sometime in the late 1930s and early 1940s. The eyrie was west of the general area of the Bear River marshes. From the description of the eyrie it appeared to be about 12 to 15 straight-line miles from eyrie number 9 (Table 1) and within region A as outlined on Figure 1. It was apparently inactive after the early 1940s since that area was searched for falcons in the mid-1940s. The second locality occupied by a pair of territorial peregrines would also be included in the area of region A but to the east of the boundary lines, as shown in Figure 1. This locality was adjacent to several pairs of Prairie Falcons, but the exact canyon in which it was located could not be determined from a map, as it was located in the late 1930s and details are vague (Morlan Nelson, pers. comm., 1973).

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APPENDIX—ADDITIONAL HISTORY OF DDT USAGE AS A MOSQUITOCIDE IN UTAH

According to Collett (1955), Salt Lake County sprayed 310 acres (125 ha) by airplane in 1949 and in 1950, according to Smith (1951), both Weber and Salt Lake City Mosquito Abatement districts (MAD) hired planes for aerial spray work, and the latter treated more than 1,300 acres (526 ha). From 1950 through 1953 the Salt Lake City district treated 10,680 acres (4,322 ha) by aircraft (Collett, 1955) and Davis County sprayed 3,000 acres (1,214 ha) by aircraft in 1953 (Stewart, 1954). Aerial spraying greatly increased in 1954, according to Graham and Rees (1958). In that year the Salt Lake City district (Collett, 1955) aerially treated 12,128 acres (4,908 ha), of which 2,286 acres (925 ha) were in cooperation with the Davis County MAD. Insecticides used by the Salt Lake City MAD in 1954 were DDT in number 2 fuel oil, DDT and water emulsion, and heptachlor emulsion in water; DDT was applied at the rate of two gals per acre (19 l/ha), containing 0.4 lbs (181 g) of DDT; heptachlor was applied at the rate of 0.06 lbs/acre (67 g/ha) for larvae and 0.08 lbs/acre (90 g/ha) for adults (Collett, ibid.).

The Weber County MAD sprayed over 10,000 acres (4,047 ha) by air in 1952 and 19,825 acres (8,023 ha) in 1953. DDT was applied at 0.2 lbs/acre (224 g/ha) for 15,812 acres (6,399 ha) and at 0.4 lbs/acre (448 g/ha) for 1,793 acres (726 ha) in 1953, for a total of 3,880 lbs (1,760 kg) of DDT applied to 17,605 acres (7,124 ha) of marsh and pasture lands (Fronk, 1954). In 1954 Weber County aerially treated

13,300 acres (5,382 ha) at 0.1 to 0.4 lbs of DDT per acre (112–448 g/ha) (Fronk and Jenne, 1955), while Box Elder County similarly sprayed 5,000 acres (2,023 ha) (Josephson, 1955).

An abatement district was not operative in Utah County until 1963, and the chemicals used were Baytex, parathion (both in pastures), and DDT (where residues were considered to be no problem) (Davis, 1964). DDT was not used by the South Salt Lake County district. Heptachlor was used in this county starting with the inception of the MAD in 1953 (Graham and Rees, 1958; Graham *in* letter). It was applied at 0.04 lbs per acre (45 g/ha). Dieldrin was used extensively in this district also at the same concentrations as heptachlor. Other districts then began using heptachlor, and by 1958 it became as commonly used as DDT (Graham and Rees, 1958). Malathion and parathion were used in 1956, and parathion became the insecticide preferred by the Salt Lake County MAD in 1957 when resistance to heptachlor developed in the mosquitoes (Graham and Rees, 1958). By 1962 nearly all mosquito abatement districts in Utah had abandoned the use of DDT because pastures, milk, and food were becoming polluted with residues, and by 1970, only Box Elder County was still using DDT.

LITERATURE CITED

Allen, J. A. 1872. Notes on an ornithological reconnaissance of portions of Kansas, Colorado, Wyoming, and Utah. Bull. Mus. Comp. Zool., 3(6):113-183.

Antevs, E. 1948. The Great Basin with emphasis on glacial and postglacial times. III. Climatic changes and prewhite man. Bull. Univ. Utah 38(20), Biol. Ser. 10(7):167-191.

A.O.U. Checklist of North American Birds. 1957. 5th ed., (Amer. Ornith. Union) The Lord Baltimore Press, Inc., Baltimore, Md.

Baird, S. F. 1852. Birds, pp. 314-335. In H. Stansbury, An expedition to the valley of the Great Salt Lake of Utah. Lippincott, Grambo and Co., Phila.

Bartholomew, G. A., and T. J. Cade. 1963. The water economy of land birds. Auk 80(4):504-539.

Bee, R. G. Unpubl. Field notes, deposited with Department of Zoology and Entomology, Brigham Young University.

Bee, R. G., and J. Hutchings. 1942. Breeding records of Utah birds. Great Basin Nat. 3(3-4):61-85.

Beebe, F. L. 1960. The marine peregrines of the Northwest Pacific coast. Condor 62(3):145-189.

Beebe, F. L., and H. M. Webster. 1964. North American falconry and hunting hawks. Publ. Priv., N. Am. Falconry and Hunting Hawks, Box 1484, Denver, Colorado. 315 p.

Behle, W. H. 1958. The bird life of Great Salt Lake. Univ. Utah Press, Salt Lake City, Utah. XIII+203 p.

———. 1960. The birds of southeastern Utah. Univ. Utah Biol. Ser. 12(1):1-56.

Behle, W. H., J. B. Bushman, and C. M. Greenhalgh. 1958. Birds of the Kanab area and adjacent high plateaus of southern Utah. Univ. Utah Biol. Ser. 11(7):1-92.

Benge, M. K., and L. E. Fronk. 1970. Effects of pesticides on nontarget aquatic organisms on the Ogden Bay Waterfowl Management Area, Utah. Utah Mosq. Abate. Assoc. Proc. 23:34-40.

Bent, A. C. 1938. Life histories of North American birds of prey (pt. 2). U.S. Natl. Mus. Bull. 170: VIII+482 p.

Berger, D. D. and H. C. Mueller. 1969. Nesting Peregrine Falcons in Wisconsin and adjacent areas, pp. 115-122. In J. J. Hickey, [ed.], Peregrine Falcon populations, their biology and decline. Univ. Wisconsin Press, Madison. XXII+596 p.

Berger, R., and W. F. Libby. 1966. University of California at Los Angeles radiocarbon dates V. Radiocarbon 8:467-497.

Birch, L. C. 1957. The meanings of competition. Amer. Nat. 91:5-18.

Bitman, J., H. C. Cecil, S. J. Harris, and G. F. Fries. 1969. DDT induces a decrease in eggshell calcium. Nature 224(5214):44-46.

Bitman, J., H. C. Cecil, and G. F. Fries. 1970. DDT-induced inhibition of avian shell gland carbonic anhydrase: a mechanism for thin eggshells. Science 168(3931):594-596.

Blackwelder, E. 1948. The Great Basin, with emphasis on glacial and postglacial times. I. The geological background. Bull. Univ. Utah 38(20), Biol. Ser. 10(7):3-16.

Bolen, E. G. 1964. Plant ecology of spring-fed marshes in western Utah. Ecol. Monog. 34:143-166.

Bond, R. M. 1936a. Eating habits of falcons with special reference to pellet analysis. Condor 38(2): 72-76.

———. 1936b. Some observations on the food of the Prairie Falcon. Condor 38(4):169-170.

———. 1936c. Observations on the food of the Duck Hawk. Condor 38(5):217-218.

———. 1946. The peregrine population of western North America. Condor 48(3):101-116.

Brodkorb, P. 1963. Pleistocene birds from American Falls, Idaho. Quart. Jour. Florida Acad. Sci. 26(3): 280.

———. 1964. Catalogue of fossil birds: Pt. 2 (Anseriformes through Galliformes). Bull. Florida State Mus. Biol. Sci. 8(3):196-326.

Brown, L., and D. Amadon. 1968. Eagles, hawks, and falcons of the world. Vol. 2. McGraw-Hill Book Co., New York. (Hamlyn Publ. Group, Ltd., Middlesex, England). 945 p.

Cade, T. J. 1960. Ecology of the peregrine and Gyrfalcon populations in Alaska. Univ. Calif. Pub. Zool. 63(3):151-290.

Cade, T. J., C. M. White, and J. R. Haugh. 1968. Peregrines and pesticides in Alaska. Condor 70(2): 170-178.

Collett, G. C. 1955. Airplane operations in the Salt Lake City Mosquito Abatement District. Utah Mosq. Abate. Assoc., Abstr. and Proc. 8:15-16.

CRAIGHEAD, J. J., AND F. C. CRAIGHEAD, JR. 1956. Hawks, owls, and wildlife. Stackpole, Harrisburg, Pa. XIX+443 p.

DAVIS, T. 1964. Mosquito control in Utah County. Utah Mosq. Abate. Assoc. Proc. 17:21.

DE MAY, I. S. 1942. An avifauna from Indian kitchen middens at Buena Vista Lake, California. Condor 44(5):228-230.

DEMENTIEV, G. P. 1951. [The Peregrine Falcon in the USSR], pp. 87-105. In G. P. Dementiev and N. A. Gladkov [ed.], Birds of the Soviet Union. [in Russian]. Vol. 1. 645 pp. (Translated 1966 by Israel Program for Scientific Translations, Jerusalem; U.S. Dept. Comm. Clearinghouse for Fed. Sci. and Tech. Inf.)

———. 1957. On the Shaheen *Falco peregrinus babylonicus*. Ibis 99(3):477-482.

DIXON, J. B. 1937. The Golden Eagle in San Diego County, California. Condor 39(2):49-56.

DOWNS, T., AND G. J. MILLER. 1971. Asphalt cemetery of the ice age, pp. 52-63. In 1972 Britannica Yearbook of Science and the Future. Encyclopedia Britannica, Inc., Chicago, 448 p.

DURRANT, S. D. 1952. Mammals of Utah. Univ. Kansas Publ. Mus. Nat. Hist. 6:1-549.

ENDERSON, J. H. 1964. A study of the Prairie Falcon in the central Rocky Mountain region. Auk 81(3): 332-352.

———. 1965. A breeding and migration survey of the Peregrine Falcon. Wilson Bull. 77(4):327-339.

ENDERSON, J. H., AND D. D. BERGER. 1968. Chlorinated hydrocarbon residues in peregrines and their prey species from northern Canada. Condor 70(2): 149-153.

FENNEMAN, N. M. 1931. Physiography of western United States. McGraw-Hill Book Co., Inc., New York, XIII+534 p.

FERGUSON-LEES, I. J. 1951. The peregrine population of Britain. Bird Notes 24:200-205, 309-314 [original not seen; quoted by Ferguson-Lees, 1957 and Ratcliffe, 1969].

———. 1957. [The rarer birds of prey; their present status in the British Isles.] Peregrine (*Falco peregrinus*). British Birds 50(4):149-155.

FISCHER, W. 1967. Der Wanderfalk [The Peregrine Falcon] (*Falco peregrinus* und *Falco pelegrinoides*). (A. Ziemsen Verlag, Wittenberg Lutherstadt; Berlin Zoological Park, Book No. 13); 150 pp (Translated 1972 for U.S. Dept. Interior, Bureau of Sport Fisheries and Wildlife and the National Science Foundation, Washington, D.C. by the Indian National Scientific Documentation Center, Hillside Road, New Delhi, India.)

FREMONT, J. C. 1845. Report of the exploring expedition to the Rocky Mountains in the year 1842, and to Oregon and North California in the years 1843-44. Blair and Rives Printers, Washington. 693 p.

FRENCH, N. R. 1951. Duck Hawks nesting in Colorado. Condor 53(1):54.

FRONK, L. E. 1954. Use of the airplane in the application of insecticides in mosquito control. Utah Mosq. Abate. Assoc., Abstr. and Proc. (Mimeo) 7:24-26.

FRONK, L. E., AND E. A. JENNE. 1955. Highlights of the Weber County Mosquito Abatement District for the year 1954. Utah Mosq. Abate. Assoc., Abstr. and Proc. 8:20-21.

GABRIELSON, I. N., AND S. G. JEWETT. 1940. Birds of Oregon. Oregon State Monogr., Studies in Zool. 2., Oregon State College, Corvallis, Oregon, XXX+650 p.

GRAHAM, J. E., AND D. M. REES. 1958. Chemical control of mosquitoes in Utah. Proc. and Papers, 26th Ann. Conf., Calif. Mosq. Contr. Assoc., pp. 16-19.

GRATER, R. K. 1947. Birds of Zion, Bryce, and Cedar Breaks. Zion-Bryce Mus. Bull. 5. Zion Nat. Park. 93 p.

HAINES, A. L. 1955. Osborne Russell's journal of a trapper. Univ. Nebraska Press, Lincoln, XVIII+191 p.

HALL, E. R. 1946. Mammals of Nevada. Univ. Calif. Press, Berkeley, XI+710 p.

HALL, G. H. 1955. Great moments in action, the story of the Sun Life Falcons. Mercury Press, Montreal, Canada (reprinted 1970. Canadian Field Nat. 84(3):211-230).

HARPER, K. T. AND G. M. ALDER. The macroscopic plant remains of the deposits of Hogup Cave, Utah, and their paleoclimatic implications. Univ. Utah Anthro. Papers, in press.

HARRIS, W. R. 1909. The Catholic Church in Utah. Salt Lake City; Intermountain Catholic Press.

HEATH, R. G., J. W. SPANN, AND J. F. KREITZER. 1969. Marked DDE impairment of Mallard reproduction in controlled studies. Nature 224(5214):47-48.

HEATH, R. G., J. W. SPANN, J. F. KREITZER, AND C. VANCE. 1972. Effects of polychlorinated biphenyls on birds. Proc. XV Internat. Ornithol. Congr., E. J. Brill, Leiden. pp 475-485.

HENSHAW, H. W. 1874. An annotated list of the birds of Utah, Annals New York Lyceum Nat. Hist. 11:1-14.

———. 1875. Report upon the ornithological collections made in portions of Nevada, Utah, California, Colorado, New Mexico, and Arizona, during the years 1871, 1872, 1873, and 1874, pp. 131-507, 977-989. In George M. Wheeler, Rept. Geog. and Geol. Expl. and Surv. West 100th Meridian, Vol. 5.

HERBERT, R. A., AND K. G. S. HERBERT. 1965. Behavior of Peregrine Falcons in the New York City region. Auk 82(1):62-94.

HICKEY, J. J. 1942. Eastern population of the Duck Hawk. Auk 59(2):176-204.

———. 1969. Peregrine Falcon populations, their biology and decline. J. J. Hickey [ed.], Univ. Wisconsin Press, Madison, XXII+596 p.

HICKEY, J. J., AND D. W. ANDERSON. 1968. Chlorinated hydrocarbons and eggshell changes in raptorial and fish-eating birds. Science 162:271-273.

———. 1969. The Peregrine Falcon: life history and population literature, pp. 3-42. In J. J. Hickey [ed.], Peregrine Falcon populations, their biology and decline. Univ. Wisconsin Press, Madison, XXII +596 p.

HO, T. Y., L. F. MARCUS, AND R. BERGER. 1969. Radiocarbon dating of petroleum-impregnated bone from tar pits at Rancho La Brea, California. Science 164:1051-1052.

HOWARD, H. 1929. The avifauna of Emeryville shellmound. Univ. Calif. Publ. Zool. 32(2):301-394.

———. 1952. The prehistoric avifauna of Smith Creek Cave, Nevada, with a description of a new gigantic raptor. Bull. So. Calif. Acad. Sci. 51, pt. 2:50-54.

———. 1962a. Bird remains from a prehistoric cave deposit in Grant County, New Mexico. Condor 64(3):241-242.

———. 1962b. A comparison of avian assemblages from individual pits at Rancho La Brea, California. Los Angeles County Mus. Contr. Sci. 58:1-24.

Howard, H., and A. H. Miller. 1933. Bird remains from cave deposits in New Mexico. Condor 35(1): 15-18.

Jefferies, D. J. 1967. The delay in ovulation produced by p,p'-DDT and its possible significance in the field. Ibis 109:266-272.

Johnson, H. C. 1899. A successful day with the Duck Hawks. Condor 1(3):45-46.

Josephson, K. L. 1955. Mosquito activities for 1954 of the Box Elder Mosquito and Fly Abatement district. Utah Mosq. Abate. Assoc., Abstr. and Proc. 8:18-19.

Keith, J. O., and E. G. Hunt. 1966. Levels of insecticide residues in fish and wildlife in California. N. Am. Wildl. Conf. 31:150-177.

Korns, J. R. 1951. West from Fort Bridger; the pioneering of the immigrant trails across Utah 1846-1850. Utah State Hist. Soc. Salt Lake City, 296 p.

Laudermilk, J. D., and P. A. Munz. 1935. Plants in the dung of Nothrotherium from Gypsum Cave, Nevada. Carnegie Inst. Wash., Publ. 453:29-37.

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. Montana, unpublished.

Lincoln, F. C. 1933. A decade of bird banding in America: A review. Ann. Rpt. Smithsonian Inst. for year ending June 30, 1932. Publ. 3185: 327-351.

Linsdale, J.M. 1937. The natural history of magpies. Pacific Coast Avifauna 25:1-234.

Longcore, J. R., F. B. Samson, and T. W. Whittendale, Jr. 1971. DDE thins eggshells and lowers reproductive success of captive Black Ducks. Bull. Envir. Contam. and Toxicol. 6(6):485-490.

Longcore, J. R., F. B. Samson, J. F. Kreitzer, and J. W. Spann. 1971. Changes in mineral composition of eggshells from Black Ducks and Mallards fed DDE in the diet. Bull. Envir. Contam. and Toxicol. 6(4):345-350.

Low, J. B. 1966. Waterfowl interests in relation to vector control programs. Utah Mosq. Abate. Assoc. Proc. 19:25-30.

McFarland, L. Z., R. L. Garrett, and J. A. Nowell. 1971. Normal eggshells and thin eggshells caused by organochlorine insecticides viewed by the scanning electron microscope. Scanning Electron Microscopy (pt. 1). Proc. 4th Ann. Scanning Electron Microscope Symposium. IIT Research Inst. Chicago, Ill. pp. 377-384.

McGahan, J. 1968. Ecology of the Golden Eagle. Auk 85(1):1-12.

Mees, F. 1949. Waarnemingen over het vangen van Vleermuizen door Roofvogels op West-Java. Ardea 37:173-175.

Miller, A. H. 1932. Bird remains from Indian dwellings in Arizona. Condor 34(3):138-139.

Miller, L. 1911. Avifauna of the Pleistocene cave deposits of California. Univ. Calif. Publ. Bull. Dept. Geol. 6(16):385-400.

———. 1927. The falcons of the McKittrick Pleistocene. Condor 29(3):150-152.

———. 1943. The Pleistocene birds of San Josecito cavern, Mexico. Univ. Calif. Publ. Zool. 47(5): 143-168.

———. 1957. Bird remains from an Oregon Indian midden. Condor 59(1):59-63.

Nelson, M. W. 1969. The status of the Peregrine Falcon in the Northwest, pp. 61-72. In J. J. Hickey [ed.], Peregrine Falcon populations, their biology and decline. Univ. Wisconsin Press, Madison, Wisc. XXII+596 p.

Nelson, N. F. 1954. Factors in the development and restoration of waterfowl habitat at Ogden Bay Refuge, Weber County, Utah. Utah State Dept. Fish and Game Publ. No. 6:1-87.

———. 1966. Waterfowl hunting in Utah. Utah State Fish and Game Publ. No. 66-10:1-100.

Nelson, R. W. 1972. The incubation period in Peale's Falcons. Raptor Research 6(1):11-15.

Nice, M. M. 1954. Problems of incubation periods in North American birds. Condor 56(4):173-197.

Nielson, L. T. 1962. The Utah Mosquito Abatement Association—a brief history of mosquito control in Utah. Utah Mosq. Abate. Assoc. Proc. 15:12-15.

Odum, E. P. 1959. Fundamentals of ecology, 2nd ed. W. B. Saunders Co., Phila., XVII+546 p.

Ogden, V. 1971. A nesting study of the Prairie Falcon. Quarterly Report, Idaho Cooperative Wildl. Res. Unit 24(2 and 3):18-20, 16-17.

———. 1972. Nesting density and reproductive success of Prairie Falcons (*Falco mexicanus*) in southwestern Idaho. Quarterly Report, Idaho Cooperative Wildl. Res. Unit 25(1 and 2):13, 13.

Olivier, G. 1953. Nidification du faucon pelerin sur les edifices. L'Oiseau et la Revue Franc. d'Ornithol. 23(2):109-124.

Peakall, D. B. 1969. Effect of DDT on calcium uptake and Vitamin D metabolism in birds. Nature 224(5225):1219-1220.

———. 1970. p,p'-DDT: Effect on calcium metabolism and concentration of estradiol in the blood. Science 168(3931):592-594.

———. 1971. Effect of polychlorinated biphenyls (PCB's) on the eggshells of Ring Doves. Bull. Envir. Contam. and Toxicol. 6(2):100-101.

Pettingill, O. S., Jr., and N. R. Whitney, Jr. 1965. Birds of the Black Hills. Cornell Lab. Ornithol. Spec. Publ. No. 1:VII+139.

Phillips, A., J. Marshall, and G. Monson. 1964. The birds of Arizona. Univ. Arizona Press, Tucson. 212 p.

Platt, J. B. 1971. A survey of nesting hawks, eagles, falcons, and owls in Curlew Valley, Utah. Great Basin Nat. 31(2):51-65.

Porter, R. D., J. B. Bushman, and W. H. Behle. Birds of the Great Salt Lake Desert. Unpubl. Ms. (in preparation).

Porter, R. D., and S. N. Wiemeyer. 1969. Dieldrin and DDT: Effects on Sparrow Hawk eggshells and reproduction. Science. 165:199-200.

———. 1972. Reproductive patterns in captive American Kestrels (Sparrow Hawks). Condor 74 (1):46-53.

———. 1972. DDE at low dietary levels kills captive American Kestrels. Bull. Envir. Contam. and Toxicol. 8(4):193-199.

Powell, J. W. 1879. Report on the lands of the arid region of the United States, with a more detailed account of the lands of Utah. (2nd Ed.), U.S. Gov. Print. Office, Washington.

Ratcliffe, D. A. 1958. Broken eggs in peregrine eyries. British Birds 51:23-26.

———. 1962. Breeding density in the peregrine *Falco peregrinus* and raven *Corvus corax*. Ibis 104: 13-39.

———. 1963. The status of the peregrine in Great Britain. Bird Study 10(2):56-90.

———. 1965. The peregrine situation in Great Britain 1963-64. Bird Study 12(2):66-82.

———. 1967a. Decrease in eggshell weight in certain birds of prey. Nature 215(5097):208-210.

———. 1967b. The peregrine situation in Great Britain 1965-66. Bird Study 14(4):238-246.

———. 1969. Population trends of the Peregrine Falcon in Great Britain, pp. 239-269. In J. J. Hickey [ed.]. Peregrine Falcon populations, their biology and decline. Univ. Wisconsin Press, Madison, XXII +596 p.

———. 1970. Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British birds. J. Appl. Ecol. 7(1):67-115.

REMY, J., AND J. BRENCHLEY. 1861. A journey to Great Salt Lake City. Vols. I and II. W. Jeffs, London 501 & 605 p.

RIDGWAY, R. 1874. Notes on the bird fauna of the Salt Lake Valley and adjacent portions of the Wahsatch Mountains. Bull. Essex Institute 5: 168-173.

———. 1877. Ornithology, pp. 303-669. *In* "ornithology and paleontology," Clarence King. U.S. Geol. Expl. 40th Parallel, Vol. 4, Pt. 3. pp. 303-669.

SMITH, D. A. 1961. Participation in mosquito control by the Department of Fish and Game. Utah Mosq. Abate. Assoc. Proc. 14:4-5.

SMITH, J. V. 1951. Progress of mosquito abatement in Utah. Proc. and Papers, 19th Ann. Conf., Calif. Mosq. Contr. Assoc. pp. 42-43.

STAGER, K. E. 1941. A group of bat-eating Duck Hawks. Condor 43(3):137-139.

STANSBURY, H. 1852. An expedition to the valley of the Great Salt Lake of Utah, including a reconnaissance of a new route through the Rocky Mountains. U.S. Senate; Lippincott, Grambo and Co., Phila. 487 p.

STEWARD, J. H. 1937. Ancient caves of the Great Salt Lake region. Smithsonian Inst. Bureau of American Ethology, Bull. 116:1-131.

STEWART, G. W. 1954. Davis County. (In Reports from Mosquito Abatement Districts), Utah Mosq. Abate. Assoc., Abstr. and Proc. (Mimeo.) 7:34-35.

TINBERGEN, L. 1946. Der Sperwer al roofvijand van Zangvogels. Ardea 34:1-213 [original not seen, quoted by F. and J. Craighead (1956) and Cade 1960)].

TWOMEY, A. C. 1936. Climographic studies of certain introduced and migratory birds. Ecology 17 (1):122-132.

———. 1942. Birds of the Uinta Basin, Utah. Ann. Carnegie Mus. 28, Art. 17:341-490.

TYLER, J. G. 1923. Observations on the habits of the Prairie Falcon. Condor 25(3):90-97.

U.S. DEPARTMENT OF COMMERCE. 1965. Climatography of the United States 86-37; Decennial census of the United States climate; Climatic summary of the United States, Supplement for 1951 through 1960, Utah.

VAURIE, C. 1961. Systematic notes on Palearctic birds. No. 44 Falconidae: The genus *Falco* (Part 1, *Falco peregrinus* and *Falco pelegrinoides*). Am. Mus. Novitates No. 2035, pp. 1-19.

WARNICK, S. L. 1971. The Utah community pesticide study. Utah Science, Agr. Exp. Sta. 32(2):53-55.

WAUER, R. H., AND D. L. CARTER. 1965. Birds of Zion National Park and vicinity. Zion Nat. Hist. Assoc., Zion National Park 92 p.

WELLER, M. W., B. H. WINGFIELD, and J. B. LOW. 1958. Effects of habitat deterioration on bird populations of a small Utah marsh. Condor 60(4): 220-226.

WETMORE, A. 1915. Mortality among waterfowl around Great Salt Lake, Utah. Bull. U.S. Dept. Agr. No. 217:1-10.

———. 1918. The duck sickness in Utah. U.S. Dept. Agr. Bull. No. 672:1-25.

———. 1932. Additional records of birds from cavern deposits in New Mexico. Condor 34(3):141-142.

———. 1933. The eagle, king of birds, and his kin. Nat. Geogr. Mag. 64(1):43-95.

WHITE, C. M. 1963. Botulism and myiasis as mortality factors in falcons. Condor 65(5):442-443.

———. 1968a. Diagnosis and relationships of the North American tundra-inhabiting Peregrine Falcons. Auk 85(2):179-191.

———. 1968b. Biosystematics of North American Peregrine Falcons. Ph.D dissertation, Univ. of Utah, unpublished. 195 p.

———. 1969a. Is there a genetic continuity concerned in eyrie maintenance? pp. 391-397. *In* J. J. Hickey [ed.], Peregrine Falcon populations, their biology and decline. Univ. Wisconsin Press, Madison, XXII+596 p.

———. 1969b. Population trends in Utah raptors. pp. 359-362. In J. J. Hickey [ed.], Peregrine Falcon populations, their biology and decline. Univ. Wisconsin Press, Madison, XXII+596 p.

WHITE, C. M., W. B. EMISON, AND F. S. L. WILLIAMSON. 1971. Dynamics of raptor populations on Amchitka Island, Alaska. BioScience 21(12):623-627.

———. 1973. DDE in a resident Aleutian Island peregrine population. Condor (in press).

WHITE, C. M., AND G. D. LLOYD. 1962. Predation on peregrines by ringtails. Auk 79(2):277.

WHITE, C. M., AND T. J. CADE. 1971. Cliff-nesting raptors and ravens along the Colville River in arctic Alaska. The Living Bird, Laboratory of Ornithology, Cornell Univ., Ithaca, N. Y. 10th annual: 107-150.

WIEMEYER, S. N., AND R. D. PORTER. 1970. DDE thins eggshells of captive American Kestrels. Nature 227(5259):737-738.

WILLIAMS, R. B., AND C. P. MATTESON, JR. 1948. Wyoming hawks. Wyoming Game and Fish Dept., Bull. No. 5, Cheyenne, Wyoming, 84 p.

WITHERBY, H. F., C. R. JOURDAIN, N. F. TICEHURST, AND B. W. TUCKER. 1939. The handbook of British birds. Vol. 3, H. F. and G. Witherby, London, 399 p.

WOLFE, L. R. 1928. The breeding Accipitres of Utah. Oologists' Record 8(4):90-102.

———. 1929. Collecting rent from falcons and ravens. Oologist, whole no. 501, 46(2):16-20.

WOODBURY, A. M., AND H. N. RUSSELL, JR. 1945. Birds of the Navajo country. Bull. Univ. Utah. 35(14), Biol. Ser. 9(1):1-160.

WOODBURY, A. M., C. COTTAM, AND J. W. SUGDEN. 1949. Annotated checklist of the birds of Utah. Bull. Univ. Utah 39(16), Biol. Ser. 11(2):1-40.

———. The birds of Utah. Unpublished Ms. (deposited with Lynn Hayward, Brigham Young University).

WOODBURY, A. M., AND C. COTTAM. 1962. Ecological studies of birds in Utah. Univ. Utah Biol. Ser. 12(7):V+28 p.