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A STUDY OF PRAIRIE FALCON POPULATIONS IN CALIFORNIA^{1/}

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ABSTRACT

Two hundred and eighteen prairie falcon (Falco mexicanus) territories were observed throughout California during 1969-1972. Active prairie falcon eyries were widely distributed geographically in California; however, occupancy of traditional territories around the perimeter of the Central Valley was extremely low. This observation was notable around the western edge of the San Joaquin and Sacramento valleys. Regionally, the prairie falcon has maintained local centers of successful production and in some instances at near historic nesting densities. Local centers of successful production were characterized by faunal diversity and relatively high densities of prey species.

Major emphasis in this study occurred during 1971 and 1972 when we observed 127 and 190 traditional nesting locations. Less than 50 percent of these territories were occupied by pairs, and only 50 percent of these pairs produced young. Statewide, the average number of fledgings per productive pair during 1970-1972 was 3.20; however, the average number of fledgings for all pairs observed during the same period was low, 1.59 fledgings per pair. This production rate was below the average 2.56 fledgings per all pairs (observed) required to maintain a stable population based on the age of first breeding and the reported mortality rates. Low average production rates were attributed to an inordinately high frequency of nonproductive pairs.

This study represents a basis for an intensive investigation of prairie falcon population dynamics. We urge that a comprehensive study of California prairie falcon populations be done. Low average fledging success per pair; inordinately high frequency of nonproductive pairs; and other factors mentioned in the text provide reasonable justifications for intensive studies of this species.

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RECOMMENDATIONS

This investigation is another reminder of the fragile balance between predator and prey and man's impact upon the biota. A foundation now exists for continued studies of prairie falcon population dynamics. We have studied the simplest relationships--occupancy and productivity at traditional eyries. Clearly, the need for continued research was shown. The following recommendations are made in the hope that future investigations and management decisions relating to the prairie falcon are properly directed:

1. Annual surveys of prairie falcon populations be conducted to determine productivity and population trends.
2. Banding and retrapping studies be continued to determine the age structure and mortality rates of prairie falcon populations.
3. Experimental manipulation of prey species abundance and diversity in several isolated areas be undertaken to provide basis for rigorous management programs in other regions of the state.
4. An educational program utilizing television and other communication media be immediately undertaken to reduce the shooting of raptors.
5. Intensive studies of pest control programs be undertaken to determine their long-term effects on raptor populations.
6. A prairie falcon "recovery plan" directed to increasing prairie falcon numbers and territorial distribution in California be developed.
7. Evaluation be made of a management plan, supervised by the Department of Fish and Game, allowing for the removal of a limited number of prairie falcons for falconry purposes.

INTRODUCTION

This paper describes the status of prairie falcon (Falco mexicanus) populations in California. Demands for this study were made due to the uncertainty regarding the status of this species and were an outgrowth of The International Peregrine Symposium held in Madison, Wisconsin in 1965. This conference addressed itself to the decline of the peregrine falcon (Falco peregrinus) in Europe and North America and to the status of several other raptorial species (Hickey, 1969).

Prairie falcon populations in Colorado through 1965 apparently were stable and normal reproductive success was observed (Anderson, 1969). Subsequently, a 34 percent decline of nesting pairs at traditional eyries in western Canada was shown (Fyfe, et al., 1969). A clear relationship existed between high DDE a metabolite of DDT levels and low production of young. Unfortunately, little was known about the prairie falcon populations in California. However, in 1956 the absence of nesting prairie falcons at traditional eyries in southern California prompted speculation that recent land use changes in the once sparsely developed desert regions were responsible for the decline (Cooper's Society Meeting, 1956).

We limited this paper to observations made at prairie falcon nesting territories; data from four reproductive seasons are presented. However, in 1971 and 1972 we conducted an extensive survey of traditional eyries. The prairie falcon, like other cliff-nesting falconiforms, tends to be faithful to a breeding territory (Bent, 1938; Brown and Amadon, 1968). This nesting fidelity allows verification of site utilization and an evaluation of reproductive success during the spring. Thus major emphasis was placed on fledging success and occupancy at traditional nesting locations.

PROCEDURE

Prior to the spring of 1971, various organizations and individuals were solicited for field assistance and nest location information. We received reports of approximately 400 nesting locations; these were obtained from museums, ornithologists, falconers, egg collectors, state and federal biologists, and personal records. From these reports, 256 prairie falcon territories were sufficiently documented to warrant further investigation. We anticipated observing approximately 200 of these traditional nest locations; this included 38 locations with pre-1971 data.

Territories were observed for the presence of adult birds. Occupied sites were subsequently studied during the reproductive period. Clutch size, hatching success, fledging success and prey species utilization were determined. Often the precise location of an eyrie was determined late in the incubation period or shortly after the eggs hatched; in these instances clutch size measurements were not included in this paper because the possibility of egg loss was great.

birds were repeatedly observed carrying prey items to a particular region of the cliff.

In this report fledging success is calculated from two considerations of the data. First, the fledging success of productive pairs is the observed number of young fledged per the observed number of pairs producing young. Second, the fledging success of all pairs is the total number of young fledged (observed plus estimated) per total number of pairs observed.

Some terms are used in special context. The term "occupancy" refers to the presence of a "bachelor," either male or female, or a pair of prairie falcons maintaining a territory. "Complete" occupancy of a territory refers to the presence of a pair which may or may not be reproductively active. An "incomplete" territory means that a "bachelor" is present.

RESULTS

From 1969 through 1972 we observed 218 prairie falcon territories. Two hundred and two of these sites were traditional nesting locations; 16 locations were first noted by the authors in 1971 or 1972 (7 and 9 locations respectively). A majority of the territories were observed during these two years; however, some territories were studied for three or four years. During four reproductive seasons (1969-1972) we studied 19 territories and 19 additional sites were studied for three years (1970-1972). Sixty-one locations were studied for two years (1971-1972), and 119 territories were observed only one year (28 and 91 territories during 1971 and 1972, respectively). Thus, during four reproductive seasons 19, 38, 127 and 190 territories were observed in successive years, 1969-1972.

Distribution of Occupied Territories

Distribution of occupied sites observed during this study differs from the distribution of historic sites in one respect (Figures 2 and 3). Traditional nesting sites, approximately 30 kilometers or less from the Central Valley, were virtually 100 percent unoccupied. Only one pair per year was observed at a total of 33 traditional nesting sites. During 1971 one pair produced three young. In 1972, at a second location, three eggs were laid which failed to hatch. These observations were particularly notable along the eastern slopes of the Coast Range, Northern and Central regions.

In general, most areas of California which traditionally supported nesting prairie falcons continue to do so; however, at territories studied for two or more years the number of occupied eyries decreased annually (Tables 1-3). The frequency of "complete" occupancy in Northern and Southern California decreased considerably (Tables 1 and 3); however, the Central region reflects a modest increase during 1972 (Table 2).

Intraspecific Nesting Densities

Closely associated eyries were frequently observed. In the Central region, five locations were in adjacent canyons along a 17 kilometer stretch of dry creek bed (San Luis Obispo County). The two closest locations were approximately 125 meters apart. These sites were located in a horseshoe-shaped dirt canyon which overlooked a wide ephemeral creek. Both pair nested in dirt potholes, one was located near the top of a 50-60 meter cliff; the other pair was situated 20 meters from the canyon floor. These pairs produced three and four young. From the top of the dirt ridge, which separated these sites, a third location was visible downstream about five kilometers to the west. Two additional pairs were located approximately 12 kilometers and 13 kilometers upstream. A possible sixth site was located four kilometers to the east, but access to this region was not granted by the landowner.

Other areas of Central and Northern California also supported closely associated pairs. In Northern California, during 1936 and 1937, six and three pairs of prairie falcons, respectively, were present on a two kilometer length of rimrock (Bond, 1939). Two eyries were 400 meters apart. During 1969-1972, three to five pairs utilized this traditional nesting region annually; all nesting sites were within an area of less than 100 square kilometers. In 1971, three pairs were productive; the sites were 300 meters apart, and a fourth pair of prairie falcons nested four kilometers to the northeast. In 1972, two productive pairs nested 100 meters apart, fledging five young per pair. An additional pair occupied a third location; we believed they were productive but at an alternate site two kilometers to the northeast. Additional territories were noted by local biologists; however, we were unable to make observations at these sites.

High density nesting in other areas of the state involved as many as six pairs within a six square kilometer area. These locations were separated by altitudinal and lateral spacing. Other areas supported closely associated pairs, varying between 300 and 600 meters apart.

Territory Utilization by Region

As shown in Tables 1 and 3, fewer productive territories were observed during 1972 in the Northern and Southern regions. In 1971, only 17 territories from the Northern region and nine locations from the Southern region were productive (Table 4). During 1972, approximately 50 percent of these territories were again productive as compared with 65 percent from the Central region.

Successive utilization of eyries in the Central region contrasted with other regions (Table 4). Twelve productive locations were observed during 1971, but only 10 of these sites were productive in 1972. In total, however, 17 productive territories were observed during 1972; 41 percent of the productive sites were previously inactive territories. In other regions only one territory from an inactive category was productive during 1972 (Table 4A). State-wide a general decrease in utilization at historic territories was shown (Table 4D).

TABLE 4.

Utilization of Prairie Falcon territories during 1971 and 1972.
(UC, unoccupied; B, bachelor present; NON, nonproductive pair present; and PRD, productive pair present)

NORTHERN: 1971	UC	1972			PRD	CENTRAL: 1971	UC	1972			PRD
		B	NON	PRD				B	NON	PRD	
UC	4	3	0	0	1	UC	10	8	0	0	2
B	10	7	2	1	0	B	4	2	0	1	1
NON	7	3	2	2	0	NON	8	1	1	2	4
PRD	17	2	3	3	9	PRD	12	1	0	1	10
N =	38	15	7	6	10	N =	34	12	1	4	17
			A.						B.		
SOUTHERN: 1971	UC	1972			PRD	CALIFORNIA: 1971	UC	1972			PRD
		B	NON	PRD				B	NON	PRD	
UC	9	8	0	1	0	UC	23	19	0	1	3
B	7	4	1	2	0	B	21	13	3	4	1
NON	2	2	0	0	0	NON	15	5	3	3	4
PRD	9	1	1	3	4	PRD	40	5	4	7	24
N =	27	15	2	6	4	N =	99	42	10	15	32
			C.						D.		

TABLE 5.

Reproductive success of pairs observed with complete clutches through fledging

	<u>1969</u>	<u>1970</u>	<u>1971</u>	<u>1972</u>
PAIRS WITH COMPLETE CLUTCH	6	10	12	18
NUMBER OF EGGS	25	38	48	78
NUMBER OF FLEDGLINGS	16	29	31	65
PERCENT FLEDGING	64	76	65	83
EGGS PER COMPLETE CLUTCH	4.16	3.80	4.00	4.33
YOUNG FLEDGED PER PAIR	2.67	2.90	2.58	3.61

Reproductive Success

The average number of eggs per complete clutch differed slightly between 1969-1971. Clutch size was greatest in 1972 and a higher fledging rate was also observed (Table 5). During 1971, of the 48 eggs observed 17 eggs did not produce young: four eggs were destroyed by ravens, one pair of birds laid a single egg and subsequently abandoned the site, and the remaining eggs failed to hatch for undetermined reasons. In 1972, 83 percent of the 78 eggs laid resulted in fledged young. However, 13 eggs failed to hatch; 9 eggs were added; and the fate of 4 eggs was undetermined.

During 1971, the Southern California population produced more young per successful pair (Table 3). Northern California was the second most productive region (Table 1). Productivity per successful pair in 1972 was greatest in Northern California, followed closely by the Southern and Central regions (Table 1-3). Average production (fledglings per successful pair) was calculated from Tables 1-3 for 99 territories. These values compare well with 2.86 and 3.45 fledglings for all productive pairs during 1971 and 1972 (Table 6).

Statewide, the estimated total fledglings per total pairs from three regions ranged between 1.56 and 2.88 young for all pairs studied. A slight annual increase was shown for Northern region territories, ranging between 2.14 and 2.38 (Table 1). However, major differences in the number of fledglings per total pairs studied were observed in the Central region (Table 2). The greatest production was about 2.8 young during 1970 and 1972, but production in 1971 was an average 1.70 fledglings.

TABLE 6.

Comparison of reproductive data from three regions of North America ^{1/}

	<u>CENTRAL ROCKY MOUNTAINS (1)</u>			<u>SOUTHERN CENTRAL CANADA (2)</u>		<u>CALIFORNIA*</u>	
	<u>1960</u>	<u>1961</u>	<u>1962</u>	<u>1968</u>	<u>1970</u>	<u>1971</u>	<u>1972</u>
NUMBER OF PAIRS STUDIED	24	28	25	62	28	65	80
NUMBER OF PRODUCTIVE PAIRS	17**	19**	19**	44	16	28	42
NUMBER OF FLEDGLINGS OBSERVED	31	32	28	157	50	80	145
NUMBER OF FLEDGLINGS PER PRODUCTIVE PAIR	1.82	1.68	1.47	3.57	3.12	2.86	3.45
NUMBER OF FLEDGLINGS PER PAIR STUDIED	1.29	1.14	1.12	2.53	1.78	1.23	1.81

^{1/} (1) Enderson, 1964; (2) Fyfe, et al., 1969; (*) excludes pairs suspected of production and fledging estimates (Tables 1-4); and (**) pairs completing clutches.

DISCUSSION

Geographically the prairie falcon is widely distributed throughout California in most life-zones, but is particularly common in Upper and Lower Sonoran Zones (Miller, 1951). Nesting pairs were observed from sea level to elevations greater than 10,000 feet. In recent years marked reductions of nesting prairie falcons were observed in areas which traditionally produced substantial numbers of young (Figures 1 and 2).

Abandonment of traditional eyries in the foothills adjacent to the Central Valley has significantly altered prairie falcon distribution. The importance of this observation is twofold: first, the foothills around the perimeter of the Central Valley no longer support a major breeding population and hence a serious loss of production; second, desertion of traditional nesting territories is characteristic of the "decline syndrome" (Prestt and Ratcliffe, 1972). Numerous investigators have observed similar trends (Ratcliffe, 1963, 1967, 1969; Cade, et al., 1971; Herman, 1970, 1971; and others). The so-called "decline syndrome" is characterized by a combination of symptoms usually observed over a period of years: loss of production; eyrie abandonment by pairs; occupancy of territory by a single bird; and finally total desertion of the territory (see Hickey, 1969 and Prestt and Ratcliffe, 1972 for details). These effects are most frequently encountered where insect control practices are such that raptors nesting or wintering in such areas accumulate sublethal levels of the applied pesticidal material--in short, the symptoms of sublethal effects and "delayed expression" of pesticides through trophic concentration (Rudd, 1966: 248-267).

A significant loss of occupied territories in the Northern region occurred around the perimeter of the Sacramento Valley. Unfortunately, desertion of these traditional territories in the Central Valley (Figure 1) reduced the average productivity of the population (Table 1). The Modoc Basin, however, supported a relatively stable raptor population, and we observed a sharp increase in average fledging success at productive sites in 1972 (Table 1). Increased fledging success appeared related to increased densities of prey species. Throughout the Modoc Basin raptorial species were relatively abundant compared to other regions. On one 100 kilometer square area four pair of red-tailed hawks (Buteo jamaicensis) produced two and three young each. These pair were located within an area of high raptor concentration; several pairs of prairie falcons and great horned owls (Bubo virginianus) and an extremely large population of barn owls (Tyto alba) were associated on a long rimrock previously described (Dixon and Bond, 1937; Bond, 1939). Short-eared owls (Asio flammeus) were extremely abundant in the adjacent lands, about 50 birds were observed in one area (Dennis G. Raveling, personal communications). These observations tend to support the thesis that prey availability was great in this region and favored particularly high production during 1972.

Throughout the Central Valley, but particularly in the Central region (Figure 1 and 2), a notable reduction of nesting prairie falcons was observed (Table 2). The reduction of nesting falcons in this region of California is not linked to a single cause. Certainly the influence of pesticidal material on other falconiforms such as the peregrine falcon population in California has extracted its toll (Herman, 1971). Other factors such as recent changes

in land use have created major ecological tragedies in just a few decades. A case in point is the draining of Buena Vista Lake (Kern County) in the southern San Joaquin Valley. During the late 1940s, drainage of this lake significantly altered the winter habitat of many waterfowl and the availability of potential prey species of both peregrine and prairie falcons. Changes in land use throughout the Central Valley is the rule. There is no means to measure the extent of damage done to various species. We cannot re-establish the landscape as it originally evolved.

Vertebrate control programs are common to California and the Central Valley; many reviews are available which deal with this subject (see Rudd, 1966: 112-140). The facts remain: control programs have taken their toll over the years. For example, between 1966-1972 roughly one million passerines were killed annually (California Bird Control Report--50 CFR 16.23); horned larks (Eremophila alpestris) represent approximately 30 percent of this annual kill. To the prairie falcon, the horned lark is a particularly important prey species during the winter (Enderson, 1964). What is lacking, however, is an evaluation of what effect bird depredation control activities have on other species. The possibility of secondary poisoning via such chemicals as strychnine or compound 1080 deserves added attention.

Small mammal control campaigns conducted annually, in some regions, remove such prey species as the Beechey ground squirrel (Citellus beecheyi). These efforts appear to have significantly reduced nest densities and distribution, particularly in the southern San Joaquin Valley where historically the Beechey ground squirrel was the main prey species caught by prairie falcons during the reproductive season (Bent, 1938; Bond, 1936; Dawson, 1913). In contrast, however, small passerines were the main prey species captured by nesting prairie falcons during this study (unpublished observations). A change in prey species utilization has clearly occurred. Certainly, the solution is open to experimental evaluation.

For a number of years we observed losses of nesting falcons in the Southern region (Table 3). Intensive observations in these regions disclosed prairie falcons were not reproducing. Pairs established their territories, but egg laying was not initiated. At first this situation seemed to fit the "decline syndrome"; however, at many sites adult falcons were observed nearly every month of the year, suggesting the adults remain at their territories year-round. Second, in the Mohave Desert prairie falcons were observed preying primarily on reptiles and mammals (unpublished observations). Hence, we conclude there is no reasonable source of pesticidal material to influence reproduction. What appears probable, however, is that an extended period of drought in the Southern region has restricted prairie falcon abundance and distribution. At best, this conclusion is highly speculative. Nevertheless, from our observations it appears that prey species availability was reduced with a corresponding reduction in the total population and a general lowering of fledging success. This does not imply, however, that productivity of successful pairs was low. In fact, the average number of observed fledging success per productive pair exceeds three young (Table 3), but at the population level substantial production was offset by the disappearance of pairs at traditional territories and an increased frequency of nonproductive pairs. The latter two observations are symptomatic of the "decline syndrome," but good productivity is not. This situation requires further study.

The numbers of nesting prairie falcons declined in many regions of California

during the past few years. However, low productivity per se does not reasonably account for this decline. Fledging success at productive eyries was less than three young per pair only once in four years (Tables 1-3). Statewide (1970-1972), average fledging success did not drop below 2.70 young per productive pairs (Table 6). This rate of productivity does not indicate pesticide influence; the fact that an inordinately high frequency of pairs are nonproductive remains something of a mystery.

Many ornithologists over the years have pointed to the fact that cliff-nesting falconiforms tend to demonstrate fidelity to a particular site (Hickey, 1969; Cade, 1960; and others). What we observed during 1970 and 1971, however, was an extensive shifting of production between locations; few territories supported productive pairs in both years (Garrett and Mitchell, 1972). During 1972, only 60 percent of the previously productive locations were again productive (Table 4D). We may infer from these data that prairie falcons are either more ephemeral than previously realized or that the mortality rate is far greater than the evolutionary limits. It appears that recruitment into the population is not sufficient to prevent losses of breeding pairs (Table 4). We observed peripheral changes, the loss of pairs or singles, and infrequently a pair establishing a territory at a previously unoccupied location. We do not know how far a pair will move, or if indeed they will move at all. We have studied territories which have a history of occupancy, but we know little about the prairie falcon population itself, i.e., rates of dispersion, age distribution or migratory patterns. Clearly banding and recapture studies are needed to clarify the issue.

The question of mortality rates is a major concern. What are the current adult and immature mortality schedules of prairie falcons? Banding recovery data prior to 1951 showed prairie falcons ringed as nestlings sustained an immature mortality rate of 74 percent and an adult mortality rate of 25 percent. Available data through 1962 revealed mortality schedules of 75 and 26 percent, respectively (Enderson, 1969). For our immediate purposes we are interested in prairie falcon mortality rates which were prevalent prior to major declines in raptor populations. The following equation,

$$\bar{m} = 1 - s / s_0 s_1 (1 - s + s_2),$$

provides an estimate of adult survivorship (s_1), immature survivorship (s_0), or the average number of female fledglings (\bar{m}) per breeding age female required to maintain a stationary population (Henney, et al., 1970). Assuming an equal sex ratio, $2\bar{m}$ equals the total number of fledglings for any species that produces young for the first time at the end of their second year of life. Thus, knowing any two parameters such as the mortality rates, a reasonable estimate of normal productivity can be calculated, noting that $s = s_1 = s_2$ since the mortality schedules are reported for only two age classes (Henney, et al., 1970).

During this study we did not observe any first year breeding pairs. However, some individuals may breed after their first year (Webster, 1944). Based on banding and retrapping of prairie falcons for several years, it is generally concluded that the age of first breeding is after year two (Enderson, 1964). Thus, calculating fledging success for all breeding age females, based on an adult mortality rate of 25 percent and a 74 percent immature mortality rate, an average 2.56 fledglings per breeding age female are required to maintain a stationary population.

Statewide, average production was 1.59 fledglings per pairs studied (Table 6). In only the Central region of California has the rate of 2.56 fledglings per total pairs been observed (Table 2). In southern central Canada, average fledging success was very close to the calculated rate (Fyfe et al., 1969, Table 6, and a three year study in the central Rocky Mountains revealed that average fledging success of all pairs studied was substantially below 2.56 young (Enderson, 1964). It appears that some prairie falcon populations throughout North America were showing symptoms of inadequate production as early as 1960 (Table 6). We conclude the observed rates of production in California during 1971 and 1972 were below expectation and indicate a declining population.

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