

A STUDY OF THE PRAIRIE FALCON IN THE CENTRAL ROCKY MOUNTAIN REGION

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THE Prairie Falcon (*Falco mexicanus*) is more easily studied in the field than most North American falcons. All others, except the Sparrow Hawk (*Falco sparverius*), are either rare, seasonal in occurrence, or occupy relatively inaccessible areas. However, although the Prairie Falcon is a year 'round resident in central regions, reaches high densities compared with other large falcons in most areas, and persists in readily accessible areas, it has been little studied. I therefore located areas where this species occurs in appreciable numbers. There I determined its abundance and seasonal status, studied breeding biology, and investigated the seasonal movements of individuals and segments of the population. Because of increasing and potentially detrimental popular interest in this species, I have not given exact localities in this paper.

METHODS

Observations were made at nesting sites in spring and early summer, and on automobile trips in areas where Prairie Falcons were numerous in late summer, fall, and winter.

Trapping and recognition.—I attempted to trap, band, and mark as many birds as possible.

Trapping devices employed included nets, snares, and the bal-chatri trap (see Berger and Mueller, 1959).

All birds trapped were fitted with U. S. Fish and Wildlife Service bands and marked (see Figure 1) by cutting the vanes from the shafts of neighboring remiges and rectrices, the positions of the marks being varied to distinguish individuals (usually the vanes were removed in a circular area less than two inches in diameter on 3 or 4 neighboring remiges or in a strip across all 12 rectrices). Neither trapping nor the marks appeared to affect the falcons adversely.

The age classes and sexes of individuals not trapped were determined with the aid of a 20 \times telescope. Males, less slim in appearance than females, were recognized by their small size and relatively large heads. It was harder to distinguish immatures from adults. Immatures have pale bluish feet, tend to be buffy instead of white below, and are streaked on the flanks; adults, especially males, tend to be barred on the flanks.

Counting.—This was conducted by means of standardized automobile cruises. Since the Prairie Falcons often used electric poles as perches, and were most obvious there, count routes were established, insofar as possible, along pole lines. The hunting range of any falcon may center on a favorite perch (Bond, 1936), or in this case, on a series of poles along an electric pole line.

Generally counts were taken in the morning and only when the wind velocity was less than five miles (eight km) per hour. No extensive efforts were made to locate falcons away from the utility poles, although other likely perches were scanned with binoculars.



Figure 1. Adult male Prairie Falcon showing wing mark.

All birds seen were noted, with reference to age, sex, location, and date of observation. Statements concerning the time of appearance, duration of stay, and observed range of marked birds, of course, can be made with relative confidence, while statements concerning unmarked birds must be made with reservation. Counts were conducted in several areas and at two seasons.

1. Winter. In winter Prairie Falcons tend to concentrate in certain areas and are almost totally lacking elsewhere. A favored area in northern Colorado, of 152 square miles (389 square km) found in the winter of 1959–1960 became the *winter study area*. The counting route here established was 45 miles (72 km) in length and the birds were recorded by the numbers conveniently attached to the poles on which they perched (43 counts: 6 in 1960, 19 February–18 March; 20 in 1960–61, 12 November–15 April; 17 in 1961–62, 27 September–16 March). Subsequently two other wintering areas were located, one in eastern Wyoming (2 counts: 15 and 21 October 1960) and one in eastern Colorado (4 counts: 27 and 28 January 1961; 12 January and 25 February 1962). Most counts were made at more or less regular intervals, near two weeks apart.

2. Post-breeding season. A concentration of Prairie Falcons was located on the Laramie Plains, Albany County, Wyoming, in June, 1960. Here a 38.9-mile (62.2 km) counting route was selected through areas where utility poles were most numerous (16 counts: 6 in 1960, 4 July–14 October; 10 in 1961, 13 June–14 October).

Breeding season.—Beginning in 1960, 65 active nesting sites of Prairie Falcons (all I could find) were located in southern Wyoming and northern Colorado. Of these, only 36 could conveniently be studied. Trips were usually made to the occupied nest sites just after egg laying, after hatching of young, and just prior to the time when the young left the nest. Nestlings were banded and marked on the tail.

RESULTS

Winter.—The chief crop on the northern Colorado area was dry-farmed winter wheat, strip-farmed so that in winter the area had strips of wheat

stubble and nearly bare strips of wheat seedlings. The terrain is gently rolling; the elevation above sea level is about 5,200 feet (1,580 m).

Other birds important on the area were Horned Larks (*Eremophila alpestris*) and Rough-legged Hawks (*Buteo lagopus*). Golden Eagles (*Aquila chrysaetos*), Marsh Hawks (*Circus cyaneus*), Black-billed Magpies (*Pica pica*), and Western Meadowlarks (*Sturnella neglecta*) occurred occasionally. Rock Doves (*Columba livia*) occurred infrequently, generally near farms.

The number of Prairie Falcons seen per count on the study area, in the three seasons counts were taken, varied from zero to eight (one per 5.6 miles, or 9 km). This area was not found until late in the winter of 1959–60, hence data are incomplete for that season. In 1960–61, counting was begun on 12 November, when Prairie Falcons were already present. However, on 27 September and 12 October 1961, trips were taken before they arrived; they were first seen on 20 October. Generally, Prairie Falcons did not arrive until mid-October, and left around the last of March.

On 12 July 1960, a count was taken on the winter study area as well as on the central Colorado area. Although slightly more than 175 miles (280 km) were traveled, and counting conditions were excellent, no falcons were seen. Apparently, these areas are little used by Prairie Falcons except in winter.

In two winters, 38 adult and 23 immature Prairie Falcons were seen on the winter study area and on the eastern Wyoming and central Colorado areas (Table 1).

The time and duration of occurrence of residents on the study area in 1960–61 and 1961–62 are shown in Figure 2. A falcon was considered to be a winter resident if it was observed at least twice and was on the area more than a week.

The duration of residence on the study area varied from 9 to 117 days. The latter value is for an adult female in the 1960–61 period. In the 1960–61 winter period, 12 resident birds spent an average of 58 days on the area, and 24 days was the average time spent in the 1961–62 period, by 4 residents. Of the winter resident birds in the first period, 3 arrived near

TABLE 1
SEX AND AGE OF PRAIRIE FALCONS CHIEFLY ON THE WINTER STUDY AREA,
1960–61 AND 1961–62

| | 12 November 1960 to 29 March 1961 | | | 20 October 1961 to 9 March 1962 | | |
|----------|-----------------------------------|---------|-------|---------------------------------|---------|-------|
| | Males | Females | Total | Males | Females | Total |
| Immature | 6 | 5 | 11 | 2 | 10 | 12 |
| Adult | 9 | 12 | 21 | 5 | 12 | 17 |
| Totals | 15 | 17 | 32 | 7 | 22 | 29 |

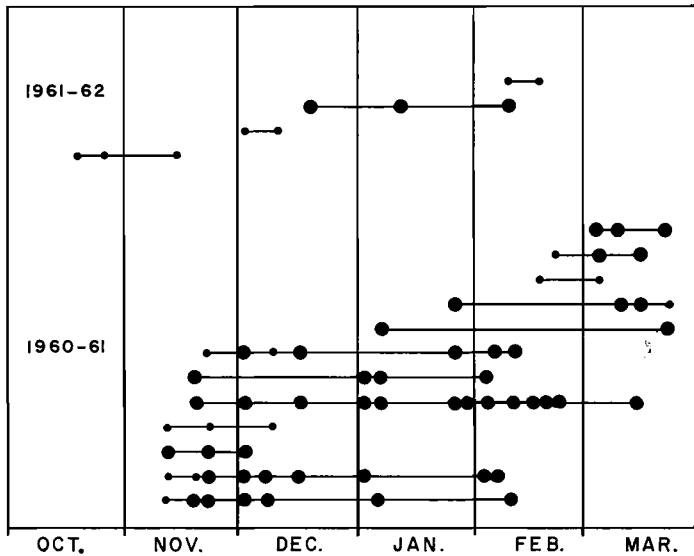


Figure 2. Time and duration of occurrence of marked and unmarked winter resident Prairie Falcons on the winter study area, northern Colorado, 1960-1961 and 1961-1962. The first (left) large dots on the lines indicate the banding dates for those individuals; other large dots indicate subsequent observations of marked and banded birds. Small dots represent sightings not substantiated by marks. Some birds were undoubtedly on the area for a time before being caught and marked. Marks were not always visible. Birds not certainly displaying marks were assigned to the occurrence lines of the birds they probably represented.

the end of February and stayed for a relatively short time. These could have been moving to nest sites.

The number of residents in 1960-61 was greater than that in 1961-62. Only once did more than one resident occur on the area at the same time in the latter period, while in 1960-61 three to seven were present concurrently. Not only were there fewer residents in 1961-62, but these left sooner and all were gone by 18 February. In 1960-61, residents were seen until the last week of March.

Immature Prairie Falcons were winter residents infrequently—two in each of the winters. However, immatures often wandered through the region as transients. I recorded 14 apparently transient Prairie Falcons in 1960-61, and 11 in 1961-62. Generally, these were birds observed only once. Of these 25 transients, 10 were immature and 15 were adult, and 11 were trapped, marked, and banded. Transients were most abundant in November and February, but were observed in every month of the winter.

The most convenient measurement of a Prairie Falcon's range is length of a line between the two most distant points of observation. Since the

counting route on the study area followed roads which paralleled each other, it was possible to observe falcons at many locations. Marked winter residents were observed or retrapped at different points; thus I could plot their movements over the period. The most accurately determined ranges are for repeatedly observed marked birds in the 1960-61 winter. The maximum observed range for 11 marked and unmarked birds was 12.1 miles (19.4 km) for a marked adult female; the average for that winter period was 5.5 miles (8.8 km).

The average range of four marked males in the two winter periods was 3.8 miles (6.1 km), while that for six marked females was 7.2 miles (11.5 km), suggesting that females have larger ranges than males. However, these means are not significantly different (t-test at the 95 per cent level of confidence), perhaps because of the small sample sizes.

Prairie Falcons sometimes return to the same winter area in subsequent years, but the number returning is evidently small. Only 4 of 27 Prairie Falcons banded on the winter study area were recovered there in later winters. Two, an immature and an adult female, were banded in the winter of 1959-60 and recovered the following winter. Two others, both immature males, were banded in the 1960-61 period and were recovered one year later.

From 21 to 26 January 1962, I attempted to determine the population density, and sex and age group of individuals, of Prairie Falcons wintering in the Calgary area of Alberta, Canada. South and east of Calgary the major crop is winter wheat. North and west of Calgary is aspen parkland. Calgary lies near the northern limit of wintering Prairie Falcons east of the Rocky Mountains, apparently because of the lack of suitable winter habitat north of that city. Here, as in Wyoming and Colorado, I attempted to follow utility pole lines; however, because of windy conditions Prairie Falcons were often seen perched on haystacks or fence posts.

In the area bordered by Calgary, Bassano, and Nanton, Alberta, I saw 11 birds in 408 miles (653 km) of travel, or one bird per 37.1 miles (59.4 km). This figure may indicate fewer birds than were actually in the area because of strong winds on two of the five count days. Six adult females and two males were seen in the Calgary area. The ages of three other females were not determined. No immatures were identified. Perhaps winter conditions this far north are unfavorable for immature birds.

Much of the daily activity of Prairie Falcons in winter was concerned with obtaining food. When prey was abundant, they spent much time perching on utility poles. I saw 11 attempts to secure natural prey. These consisted of a shallow dive from a perch, followed by a series of rapid wing beats close to the ground for a distance usually less than 400 m; finally, the last few meters of the approach consisted of a swift glide.

The falcon tried to follow the evasive action of the prey. If the falcon was unsuccessful, immediate second attempts were seldom made. Prairie Falcons did hunt while on the wing, especially if prey was not abundant, and flew at a rapid pace up to 40 feet (12.3 m) above the ground. Attempts were made to capture prey flushing in front of the bird.

I saw over 70 Prairie Falcons feeding on prey while I was trapping. Feeding falcons were alert and sensitive to the presence of other raptors. They always attempted to fly when Rough-legged Hawks, Marsh Hawks, or Golden Eagles approached. When the prey was too heavy to carry, the falcons would leave their food and chase the intruder, often succeeding in driving it away. Sometimes they flew to attack Rough-legged Hawks while the latter were several hundred meters away. Occasionally Prairie Falcons crouched motionless over their prey, sometimes remaining undetected, flying only at the close approach of another raptor. If successful in chasing another raptor away by a series of dives, they almost always returned to feed, and seldom had difficulty in relocating the prey. Since the Prairie Falcons normally preyed on smaller animals which they could carry in flight, theft by other raptors probably was not significant. Intraspecific competition for food was observed only once. In this case two female Prairie Falcons fought on the ground for a dead Rock Dove.

The breeding period.—Not all nest sites within the area were found, because of the inaccessibility of some of the region. Prairie Falcons nest only on cliffs where there are ledges suitable for the placement of eggs, and all such formations that could be found were checked.

In all, 36 nesting cliffs were examined (Table 2). These included 14 of sandstone, 10 of sedimentary conglomerate, 7 of limestone, and 5 of granite. The cliffs varied from 7.7 m to 38.7 m in height (average, 15.8 m). Prairie Falcons placed their eggs in depressions scraped in the debris on ledges. These "scrapes" were located in various situations on the cliffs; 16 were

TABLE 2
NESTING SUCCESS OF PRAIRIE FALCONS

| | 1960 | 1961 | 1962 | Average |
|---------------------------------|------|------|------|---------|
| Nest sites visited | 27 | 34 | 33 | 31 |
| Nest sites occupied | 24 | 31 | 27 | 27 |
| Nest sites studied | 24 | 28 | 25 | 26 |
| Pairs laying eggs | 19 | 25 | 23 | 22 |
| Pairs completing clutches | 17 | 19 | 19 | 18 |
| Total eggs in complete clutches | 76 | 87 | 85 | 83 |
| Eggs per complete clutch | 4.5 | 4.6 | 4.5 | 4.5 |
| Total young hatched | 58 | 45 | 42 | 48 |
| Young hatched per pair studied | 2.4 | 1.6 | 1.7 | 1.9 |
| Total young fledged | 31 | 32 | 28 | 30 |
| Young fledged per pair studied | 1.3 | 1.1 | 1.1 | 1.2 |

on open shelves, 16 in "potholes," and 4 in larger caves. The average nest was 11.1 m above the base of the cliff. With one exception, all "scrapes" were directly overhung by a portion of the cliff. They varied in their accessibility to mammalian predators; 28 were deemed inaccessible to such predators, because of the smooth vertical faces surrounding the shelf. Of the 36 sites, 22 ledges faced south, 5 faced north, and 9 faced east or west. In successive years, Prairie Falcons tend to use alternate shelves on the same cliff.

Adult female Prairie Falcons, the earliest arrivals observed, were seen at two northern Colorado nest sites on 22 February 1961. Most adults became associated with nesting cliffs by mid-March. Although Webster (1944) stated that males arrive first at the nesting cliffs, 9 of 11 first arrivals at cliffs in the present study, in February and March, were females. Adult male and female Prairie Falcons seemed not to be associated on the wintering areas in February and March, suggesting that pair formation occurs after their arrival at the cliffs. At no site did a falcon remain unmated.

I visited only 25 of the 36 nest sites in all three years. Of these 25 sites, 14 were used by pairs of falcons in the three years, 9 were used in two years, and the remaining 2 were used only once. In 1962 33 sites were visited and of these 6 were unused. These data suggest that many available nesting cliffs are vacant each year. Three former sites in the region have not been used in the last four or five years.

In 1960 and 1961, I trapped 18 adult Prairie Falcons at their nest sites (9 in each year). In 1961 and 1962, I tried to determine how many returned, but because some deserted their cliffs before they could be trapped, or would not respond to the trap, in only 14 instances was I able to ascertain if specific birds returned. In 6 of these instances, individuals were retrapped at their original cliffs. The other 8 birds did not return (the sites were unoccupied, or new, unbanded birds were present), and were not identified elsewhere. Of the 6 retrapped birds, 5 had been banded the year before, and 1 two years previously.

At one nest site in 1960, both adults were banded. The following year the banded male failed to return and was replaced by another male which was then caught and banded. The third year the second male and the original female nested at the site.

The incubation period in three instances was apparently between 29 and 31 days. The young hatch over two or three days, indicating that incubation does not commence until the clutch is nearly complete. The length of the fledging period appears more variable; 15 broods remained in the nest for periods varying from 36 to 41 days.

Generally, clutch completion occurred around 25 April, hatching around

25 May, and fledging around 3 July; but these varied from 12 April to 9 May, 12 May to 8 June, and 21 June to 19 July, respectively. Some pairs of Prairie Falcons were estimated to be as much as 28 days out of phase with others in the region. Only twice was renesting observed. In these cases the first clutches were destroyed early in the incubation periods.

The average complement of 55 known complete clutches was 4.5 eggs.

I recorded data on the reproductive performance of Prairie Falcons (Table 2). Occasionally I could not determine the number of eggs originally laid, especially if the count was made late in the incubation period, in which time egg loss could have occurred. Young were considered fledged when they left the nest ledge and were able to fly several hundred meters. It was impossible to make observations at every nest site at this specific time and when nearly fledged young were seen they were considered fledged. Over the three-year period, the pairs studied at nest sites fledged 1.2 young per pair. There was a general year-to-year agreement in production figures, except that in 1960 a seemingly larger proportion of the eggs laid hatched.

The causes of egg losses and nestling mortality were largely unknown. Two clutches failed to hatch in 1960; three sets failed to hatch in both 1961 and 1962. I found remains of nestlings at four deserted nest sites. There was evidence of a predator at one nest and of human disturbance at the other three. Apparently the young had been pushed out of the nest with a stick at one of the latter sites. At another of these the adult female was shot on the ledge by someone, resulting in the death of the small young, and at another site the female was found shot and the young eventually died.

At one nest site in 1960 the adult female was drowned in a stock tank, after entering the water either to bathe or to obtain one of several Western Meadowlarks floating in the water. At all other sites which failed to fledge young, both eggs and young inexplicably disappeared.

The sex ratio of 91 nestling Prairie Falcons handled was very near 50:50 (45 ♂♂ : 46 ♀♀).

In all, 75 nestlings were banded in 1960 and 1961, and 63 are known to have fledged. Three were recovered and reported through the U. S. Fish and Wildlife Service. Three others, banded as nestlings, were observed later at nest sites of the study. A male, banded in 1961, appeared at a nest site in 1962 as a member of a pair, but no eggs were laid. A female, banded in 1959 by another worker, was retrapped in 1961 as a breeding bird 30 miles from where she was banded. This bird laid four eggs which disappeared before hatching. A second female, banded in 1960, returned to within one mile of that nest site to breed in 1962 but was replaced by the previous year's occupant.

Prior to laying eggs, the adults perched for long periods near the nest site and the males occasionally hunted. Copulation is frequent in this period, certainly occurring several times each day. Once I saw a male investigating ledges on a cliff, presumably before scraping a depression to hold the eggs.

Females do most of the incubating. Males incubated only while females fed on prey brought by the male. During the incubation period, males apparently do all the hunting and are thus sometimes absent from the nest site. After the eggs have hatched, the female hunts and by the time of fledging of young, the female may be away from the nest site much of the time.

The nest is defended by both adults, the male being more aggressive but less persistent than the female. Once I was struck three times by a male Prairie Falcon when small young were in the nest. Another time, while I was at a nest site, the adult female attacked a female from a nearby site. These two sites were only 200 meters apart but did not face each other, a characteristic of Peregrine Falcon (*Falco peregrinus*) sites in areas of high breeding density (Beebe, 1960). This intraspecific conflict was probably caused by my presence and evidently is unusual. It was seen only once, although several of the nest sites studied were less than 200 m apart. On yet another occasion I flushed a Great Horned Owl (*Bubo virginianus*) from a cliff. The owl was struck by both falcons and soon killed.

I did not try to estimate quantitatively the prey brought to the nest for young Prairie Falcons. Fowler (1931) stated that some prey remains are apparently carried from the nest. I found remains of Horned Larks and Richardson's ground squirrels (*Citellus richardsonii*) most often, and sometimes exclusively. Horned Larks are one of the most widely distributed birds of open areas in the region (Cassel, 1952), being found at even the highest elevations (Finzel, 1962); with McCown's Longspur (*Rhynchophanes mccownii*), they were abundant near many of the nest sites in the present study. Western Meadowlarks were the third most frequent species used. Remains of a White-throated Swift (*Aeronautes saxatalis*), a Loggerhead Shrike (*Lanius ludovicianus*), and a Vesper Sparrow (*Pooecetes gramineus*) were found in three different nests, while one nest contained only the remains of Black-billed Magpies. Parts of McCown's Longspurs were found infrequently, as were remains of thirteen-lined ground squirrels (*Citellus tridecemlineatus*).

The post-nesting period.—A counting route was set up on the Laramie Plains in June, 1960. This intermontane basin has an area of more than 2,000 square miles (5,120 square km) and an elevation of about 7,400 feet (about 2,200 m). The Laramie Plains are bordered by mountains on the east, south, and west, all of which exceed 8,000 feet (2,430 m). Their

topography is generally flat, with occasional low ridges and gentle swales. Vegetation is a mixture of several kinds of grasses, herbaceous plants, and sagebrush, the latter being most abundant to the north. Average annual precipitation is 11.2 inches (28.4 cm).

Other summer birds important on the prairie were McCown's Longspurs, Western Meadowlarks, Ferruginous Hawks (*Buteo regalis*), and Horned Larks. The last was the most numerous species; its breeding territories were found almost continuously along the counting route. Pronghorns (*Antilocapra americana*), thirteen-lined ground squirrels, Richardson's ground squirrels, and white-tailed prairie dogs (*Cynomys leucurus*) were the most numerous diurnal mammals. Both species of ground squirrels estivate by 10 August and are not frequently seen after that date.

In 1960, 6 complete trips were made over the 38.9-mile (62.2 km) post-nesting area counting route, while 10 trips were made in 1961. Many more trips initiated were not completed because of increasing wind. The greatest number of Prairie Falcons seen in this period in 1960 was 11 on 4 August, while in 1961, 16 birds were seen on 28 July, averaging 1 per 2.4 miles (3.8 km). In 1960, 11 falcons were trapped between 4 July and 14 October, and in 1961, 14 were trapped on the area from 13 June to 14 October.

A resident was defined as a falcon remaining on the study route for more than 7 days. The duration of the occurrence of these birds varied from 8 to 102 days. In the 1960 post-nesting period, 9 females and 5 males were resident; 18 females and 6 males were resident in 1961. All these falcons were adults; immature birds occurred only as transients.

Thirteen post-nesting residents were marked and subsequently resighted in 1960 and 1961. The average stay of these falcons on the study area was certainly at least 31 days. However, these 13 probably remained for an average period of 44 days, a value obtained by adding to the observations of definitely marked falcons those sightings in which the marks were not seen, or made before the individual was marked.

Figure 3 shows the number of residents along the counting route in the post-nesting periods of 1960 and 1961. Averaging the number of observed residents by five-day periods tends to smooth the curve, eliminating sharp peaks and depressions caused by nearly coinciding arrival and departure dates of individuals. More importantly, averaging generalizes the figure, reducing error introduced by including in the graph observations of birds not substantiated as residents by the sighting of marks.

The build-up of the 1960 post-nesting resident population is uncertain because counts were not begun until 4 July, when some resident birds were already on the area. In 1961, counts were begun on 13 June, prior to their arrival. An averaged maximum of approximately 9 resident falcons was

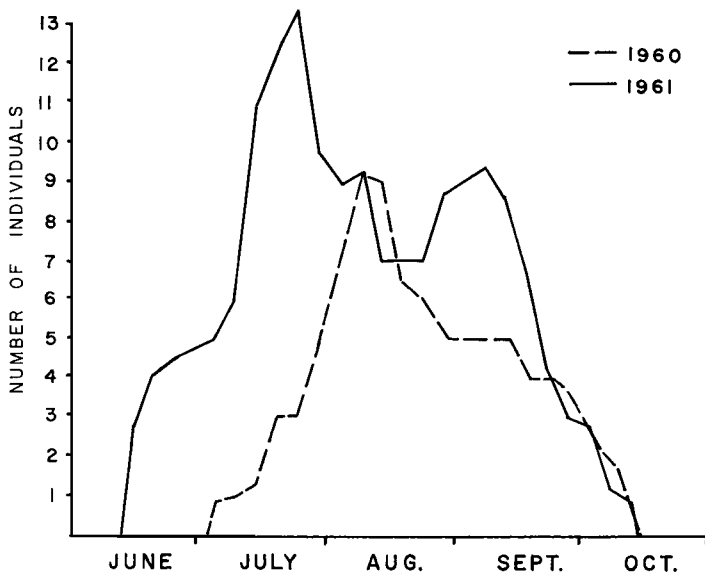


Figure 3. Generalized estimates (see text) of marked and unmarked post-breeding resident Prairie Falcons on the Laramie Plains study area in 1960 and 1961.

on the study route in 1960. This number occurred on 9 August. After that, the resident population decreased until all falcons were gone on 15 October. A maximum of about 13 individuals was resident in 1961, the first appearing in the second week of June, the last leaving in mid-October (Figure 3).

Of 39 transient Prairie Falcons (12 males and 27 females) in the post-nesting periods of 1960 and 1961, 9 were caught and marked. Transients were seen in every month of the post-nesting periods with as many as 10 occurring in June, 1961.

Observations of Prairie Falcons in this period were restricted to the linear counting route adjacent to an electric line; there was little opportunity to observe them elsewhere. The locations of falcons were recorded each trip and the distances of movement tabulated. These distances may not show the size of their ranges because nothing is known of their movements away from the pole line. However, I suspect that lateral movements were not great. The average maximum movement of 6 marked birds in the 1960 post-nesting period was 1.8 miles (3.1 km) and that of 6 marked birds in the 1961 period was 2.7 miles (4.3 km). The maximum distance of movement was 4.8 miles (7.7 km), recorded in 1961 for two adult females. These two values are responsible for the larger 1961 average.

There is no evidence that the same Prairie Falcons return to the post-

nesting area. Of 11 birds trapped there in 1960, none was recovered in 1961.

Although 21 adults, 3 immature birds, and 32 nestlings were banded within 150 miles (240 km) of the post-nesting area by the beginning of the 1960 period, none was among 11 birds captured there in that period. By 1961, 58 adults, 19 immature birds, and 75 nestlings had been banded in the region, but none was among 14 captured in the 1961 post-nesting period. Prairie Falcons which spend the summer and early fall on the Laramie Plains appear to be birds from regions other than the nesting and wintering areas studied.

Prairie Falcons were not evenly distributed along the counting route, but tended to be grouped in certain areas. Often three or four were found on a low ridge in the first mile of the route. Although two individuals of the same age and sex were sometimes perched on poles less than 200 meters apart, no antagonism was noted.

In contrast to the winter period, only two instances of interaction were observed between Prairie Falcons and other raptors. On 5 September 1961 an adult female chased an immature Peregrine Falcon which was pursuing a Rock Dove. The Peregrine Falcon retreated to a perch while the Prairie Falcon captured the prey. One week later I saw the same thing again.

Molt.—Molt was observed in 21 female and 9 male Prairie Falcons trapped at nesting sites and in the post-nesting period. Molting begins with the remiges, then involves the body feathers, and finally the rectrices. Three males and three females caught in late May and in early June provided extensive data on the order of molting the remiges. Five dropped the fourth primary first, while one dropped the fifth first. Generally, the molt of the remiges is in the order 4–5–6–3–7–2–1–9–10 (the outermost), but there is apparently some variability. For example, in different birds 1 fell before 8, 8 before 2, 9 before 8, and 9 before 1. One bird lost 7 and 1 nearly simultaneously, and 9 and 1 were lost at the same time in another, judging by the length of replacement feathers. Primary 10 was the last lost in 15 individuals for which this could be determined.

Molt of the rectrices was in the order 1 (innermost), 2, 6, 3, 4, 5. No variability was observed in this sequence.

Molt of the remiges begins near early May; rectrices are not lost until mid-June. Most birds complete the development of new flight feathers by early October. Those caught about the same date show up to three or four weeks' difference in the progression of this molt. Molt of the body feathers begins in late June and ends in early October.

Weights.—Adult and immature female Prairie Falcons weigh about one-third more than adult and immature males, respectively. Adult males averaged 554 g (range 500–635 g in 15 birds), immature males averaged

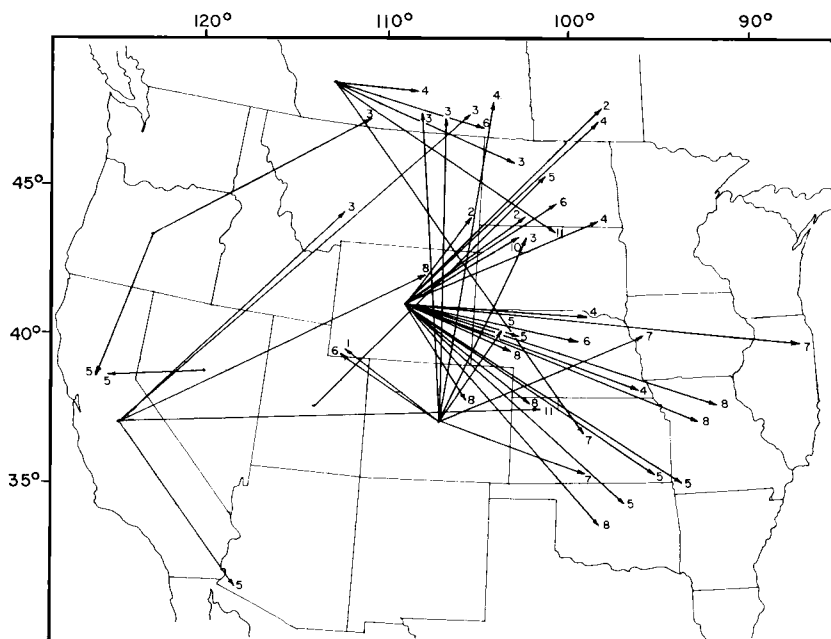


Figure 4. Recoveries of Prairie Falcons banded as nestlings and recovered in their first year in the period from 1930 to 1961. Numbers indicate months between banding and recovery.

539 g (515–570 g in 5), adult females averaged 863 g (760–975 g in 31), and immature females averaged 824 g (675–925 g in 12). All birds weighed had empty crops.

Banding returns.—Prairie Falcon band recoveries to June, 1961, were supplied by the Bird Banding Office, U. S. Fish and Wildlife Service. Of the 100 records, 8 were excluded from analysis for various reasons. Of the remainder, 83 were banded as nestlings and 9 as adults or immatures.

Young birds are evidently less wary, since of banded birds recovered in their first year, 72 per cent were shot, while only 41 per cent of the older ones were shot.

Points of banding and recovery of Prairie Falcons banded as nestlings are shown in Figures 4 and 5. Distances traveled are approximations, and the centers of the states are used as banding points to simplify the figures. Birds recovered within the state in which they were banded are not included in these figures.

There is a strong tendency for young to move eastward from mountain area nests to the plains provinces and states in their first year, but there is little westward movement (Figure 4). Falcons banded in Alberta,

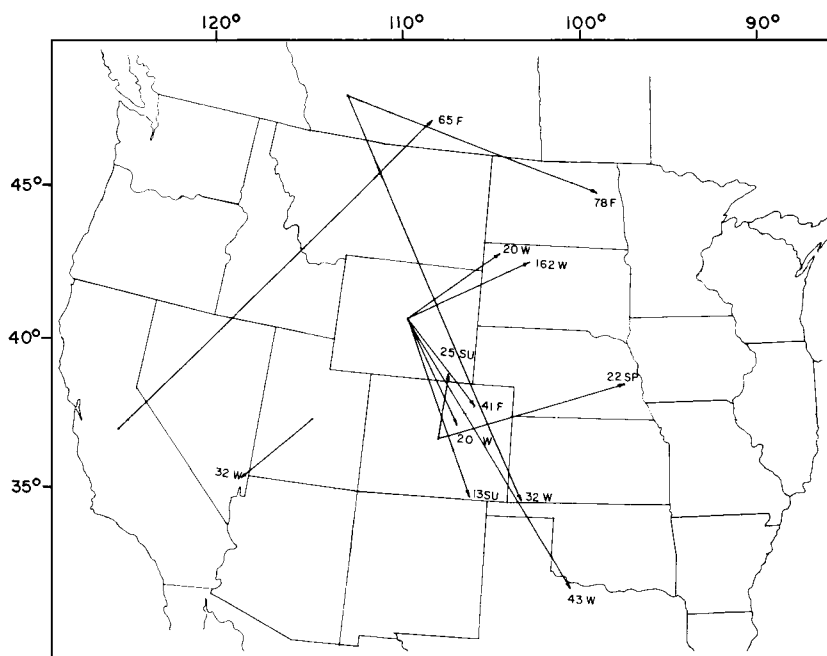


Figure 5. Recoveries of Prairie Falcons banded as nestlings in the period from 1930 to 1961 and recovered after their first year. Time of recovery: W, winter; SP, spring; SU, summer; F, fall. Numbers indicate months between banding and recovery.

Canada, do not move northward since they are near the northern limit of the range. Birds from Wyoming and Colorado moved to the northeast, east, and southeast. Four of 5 birds banded in California were recovered east of the Continental Divide.

Prairie Falcons banded as nestlings and recovered after their first year showed a similar pattern of recovery (Figure 5). Only one falcon, banded in Utah, moved westward. Noteworthy is a California bird recovered in fall in Saskatchewan after 5 years and 5 months, and a falcon from Wyoming recovered in South Dakota in winter after 13 years and 6 months. Apparently the plains are an important Prairie Falcon wintering area.

Of 9 Prairie Falcons banded either as adults or immatures, 7 were recovered in the state where banded. The banded period did not exceed 21 months in any case. Two adult males were recovered in states other than where they were banded. One, banded in July, 1939, in Utah, was recovered in September, 1940, in South Dakota. The other, banded in Colorado on 29 January 1960 was recovered in August, 1961, in Wyoming. More data are needed concerning the movements of adults, and future banding efforts should include them.

DISCUSSION

Southern Wyoming and northern Colorado are typified by great altitudinal variation, ranging from about 5,000 feet (about 1,500 m) above sea level on the plains immediately east of the Rocky Mountains to alpine areas above 12,000 feet (3,600 m). This variability results in many different habitats, some suitable for Prairie Falcons.

Prairie Falcons frequent open areas. The low-level style of hunting, described above, necessitates the absence of tall vegetation. For this reason, forested mountain regions do not support a resident population of these falcons at any time of year, although they were found breeding in fairly open, sagebrush-covered mountain valleys.

Winter distribution.—Two factors are apparently responsible for marked winter concentrations of Prairie Falcons in areas which lack them at other times. These are suitable hunting terrain with the absence of high vegetation, and abundant prey. The Horned Lark, their principal winter food, was the only species whose numbers were conspicuously correlated with those of the Prairie Falcon.

Generally, at the onset of cold weather and snow in late fall, Horned Larks are found in flocks of a few to 50 or more birds. Perhaps because of deepening snow, these flocks drift to winter wheat areas at lower elevations, where 46 per cent of their diet is wheat (Finzel, 1962). The build-up of the Prairie Falcon population on the wintering areas coincided with the increase in the number of Horned Larks. Larks became numerous in November, when Prairie Falcons were arriving. In all three winters, Prairie Falcons were gone by the time most of the Horned Larks had dispersed. No falcons were seen on the area on 24 February 1961, when Horned Larks were few. But on 4 March, when many thousands of Horned Larks were concentrated by heavy snowfall, five falcons were seen. Three trapped had not been banded before, suggesting an influx. I saw Prairie Falcons pursuing Horned Larks about 11 times, and only once pursuing other prey, a vole (*Microtus* sp.). I saw falcons eating Horned Larks several times. In 1960–61, resident falcons were substantially more abundant than in the following winter (Figure 2). Horned Larks were abundant on all but one counting trip in the former period, while in the winter of 1961–62 both larks and falcons were scarce. In most winters, the Laramie Plains supports few Horned Larks. Significantly, Prairie Falcons were rare there in December and January, and I saw only a few in February. However, by March, both Horned Larks and falcons were frequently observed there. Prairie Falcons were numerous near Albuquerque, New Mexico, in the winter of 1961–62 when T. Smylie (pers. comm.) recorded one falcon per 36 miles (57.6 km) traveled. This is also an area where

Horned Larks are numerous in winter; an average of 12 larks per 100 acres has been recorded (Freeman, 1954). These considerations suggest that the distribution of Prairie Falcons is correlated with the distribution and numbers of Horned Larks, which in turn, are apparently related to climatic conditions and the location of suitable winter habitat.

Upon the dispersal of Horned Larks and arrival of migrant birds by March, Prairie Falcons move to nesting cliffs, even at higher elevations. However, falcons are dependent upon the sustained presence of the larks. By 24 February 1961, five falcons were already associated with five nest sites 12 miles from the winter study area. Horned Larks were numerous on the surrounding prairie. But after a snowfall on 2 March these sites were abandoned with the disappearance of Horned Larks from the vicinity.

Continuity of nest site use.—Cade (1960: 240) presents the concept of "tradition as a factor linking generations to the same cliff," stating that continual use of a cliff by Peregrine Falcons requires acquisition of a new mate when one member of a pair is lost. If both members are lost, this tradition is broken and the site will remain unused until the discovery of the cliff by a new pair. This idea is not easily applied to Prairie Falcons.

In this study banding and retrapping showed that slightly less than 50 per cent of the nesting birds failed to return to the nest site they used in a previous year, or to any site I observed. If this high rate of failure to return is extended over three or four years, it is evident that few of the original falcons would remain. It seems that the loss of one member of a pair is a frequent occurrence and that the "tradition of use" at any cliff must be often reestablished. This is borne out by the facts that 44 per cent of the cliffs under observation in this study were not used in at least one of the three years, and in 1962 6 of the 33 cliffs observed were unoccupied. Undoubtedly, some falcons are remarkably faithful to a breeding site. One partially albino female was seen at a Colorado nesting site for nine years (Baily and Niedrach, 1933).

Nesting failure at a site appears not to be a deterrent to its use the next year, since at the 14 nest sites used consecutively for three years, only 21 of the 42 nesting attempts were successful.

Hickey's classification (1942) of Peregrine Falcon cliffs in the eastern United States, based largely on the height of the cliff, cannot be extended to Prairie Falcon cliffs. An ideal Prairie Falcon cliff has a sheltered ledge which provides a location for the placement of eggs, gravel, or loose material on the ledge where the egg depression may be scraped, and the ledge overlooks at least some treeless country for hunting. Given these features, an outcropping can be occupied by falcons even though it may be less than 30 feet (9 meters) in height.

Reproduction and survival.—Prairie Falcons in this region have clutch

sizes larger, on the average, than those reported for the Peregrine Falcon. The 55 completed clutches I saw, and 6 seen by C. White (pers. comm.) in Utah, contained an average of 4.5 eggs. The mean clutch size of Peregrine Falcons in the United States was 3.7 eggs (Hickey, 1942; Bond, 1946) and 2.9 in northern Alaska (Cade, 1960). Although Prairie Falcons lay more eggs than Peregrines, they apparently fledge no more young. Peregrine Falcons on the Colville and Yukon rivers in Alaska (45 records) fledged 1.1 young per pair (Cade, 1960), while Prairie Falcons in Colorado and Wyoming fledged a mean of 1.2 young per nesting pair.

Prairie Falcons in isolated regions may have a higher reproductive rate than the one recorded here. There is no doubt that human interference caused nestling mortality in the present study. One nesting escarpment in Colorado contained 12 of the 36 sites investigated and was visited by people who removed marked and banded nestlings in all three nesting seasons. Partly as a result of this, these 12 nests fledged only three young in 26 nesting attempts, although a nearly normal number of downy young was produced.

Cade (1960) and Beebe (1960) postulate a high rate of mortality of immature Peregrine Falcons in their first year, because neither observer saw year-old falcons at the nesting sites. Similarly, I have seen only one yearling Prairie Falcon at a nest cliff; yearlings seldom attempt to nest. However, 38 per cent of the falcons identified as to age in winter in this region were immature birds. This seems to indicate that a large proportion of the young do survive at least until their first winter. Also, once these immatures have lived into the winter, it is likely that their chances of continued survival are good, since they have become adept at hunting and wary of man. I think that winter is not more critical for immatures than for adults in this region, from the standpoint of food supply, because they were attracted to baited traps no more easily than adults. However, leg band recovery data showed that first-year birds are shot much more frequently than older birds. Nevertheless, in view of the relatively large number of immature birds in the wintering population within the area of this study, it seems unlikely that failure to observe them at the nesting sites is indicative of high mortality in that age group. In fact, the whereabouts of immature Prairie Falcons during the first spring after they are hatched is largely unknown. By this time immature birds are difficult to recognize; the feet have become yellowish, approaching the adult condition, and all feathers are worn and faded.

Miscellaneous comments.—Immature Prairie Falcons are apparently unevenly distributed over the range in winter. I did not see young birds near Calgary, Alberta, and generally they are not observed there later than November (N. Winnick, pers. comm.). Likewise, in a sample of 22

Prairie Falcons handled near Albuquerque, New Mexico, in the winter of 1961-62, only 3 were immatures (T. Smylie, pers. comm.). Perhaps the 38 per cent frequency of wintering immatures in the region of this study is not a representative sample of that age group.

The presence of large numbers of Prairie Falcons on the Laramie Plains in the post-nesting period was probably a result of several factors. After nesting, most adult birds abandoned the nest sites and apparently wandered to a considerable extent, occasionally establishing residency on such suitable areas as the Laramie Plains. Once present, they were held there by a large supply of vulnerable prey.

Although Prairie Falcons move from one area to another at different times of the year, only twice, in late March, 1961, were they seen apparently migrating. On both occasions the birds were high, barely distinguishable without binoculars, and moving north.

Although the winter study area was within 86 miles (138 km) of the most distant nesting site studied, and the late summer study route on the Laramie Plains was only about 50 miles (80 km) from the winter study area and surrounded by studied nest sites, Prairie Falcons banded on either the winter area, the summer counting route, or at nesting sites were very infrequently sighted in areas other than the one where banded. At only three nesting sites were falcons observed that had previously been marked on other areas. In April, 1960, an adult female and an adult male became associated with two nesting sites within 14 miles (22.4 km) of their point of banding on the winter study area. A third falcon, bearing a wing mark applied on the winter study area, was seen at a cliff near there, but apparently did not nest. All this suggests that Prairie Falcons in the region studied are not members of a locally permanent resident population, even though Webster (1944), also writing of Colorado, stated that local Prairie Falcons can be seen at almost any time of year within a short distance of their nest sites. Instead, it is more tenable that falcons in this region are composed of birds from three distinct populations, a wintering population, a breeding population, and a summer and early fall population. Where each population spends the remainder of the year is unknown.

Statements of the abundance of Prairie Falcons in Wyoming and Colorado must be made on a seasonal basis, in view of the seasonal use of different habitats. Since wintering, nesting, and post-nesting habitats are not equally extensive, the number of falcons fluctuates seasonally. In Wyoming less area is used for the production of wheat than in Colorado. Consequently, fewer Prairie Falcons occur there in winter. Much of Colorado is not suitable nesting habitat; the eastern plains offer few nesting cliffs, while the mountainous regions are forested. Webster (1944) estimated that 500 pairs nest in Colorado each year, but I think that the number

certainly does not exceed 300 pairs. Wyoming may have as many, considering the numerous small mountain ranges whose foothills provide suitable nesting habitat. Even the plains areas in Wyoming are occasionally broken by nesting escarpments.

The relative abundance of Prairie Falcons in Wyoming and Colorado in the post-nesting period is unknown because areas other than the Laramie Plains have not been investigated in that period.

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SUMMARY

A three-year investigation of the Prairie Falcon was made in Wyoming and Colorado, and included trapping, banding, marking, and repeated transect counting in different areas to determine population densities and seasonal and yearly movements.

Prairie Falcons became associated with winter-wheat agricultural land in winter probably because of the availability of Horned Larks, an important prey species. Adult and immature falcons entered the 52-square mile (133 square km) winter study area in October, were most numerous in November and February, and left in March. Resident males and females had ranges of 3.8 miles (6.1 km) and 7.2 miles (11.5 km), respectively. Of 27 banded falcons, 4 were recovered on the same area in subsequent years. Adult Prairie Falcons winter as far north as southern Alberta, as shown by 11 (or 1 per 37.1 miles) seen in January, 1962. I saw no immatures there.

Only 14 of 25 nest sites were occupied all three years. Of 14 nesting falcons banded at nest sites which could be rechecked, 5 returned to nest at the same nest site the next year and 1 two years later. This frequent disuse of nest cliffs and moderate rate of return indicate that Prairie Falcons are not very constant in the use of nesting sites.

Of 77 nesting attempts, 32 produced fledged young; human interference occurred at several nest sites and was partly responsible for this low reproductive success.

From June to October the Laramie Plains are used by Prairie Falcons,

and counts were regularly made there in this period of 1960 and 1961. They probably used this area because of a plentiful and vulnerable food supply. In October the area is abandoned and the falcons move to wintering areas at lower elevations.

The principal prey of the Prairie Falcon is Horned Larks and Richardson's ground squirrels. In winter, conflicts over food with buteonine hawks were conspicuous.

A total of 100 banding returns showed that Prairie Falcons banded as nestlings were most frequently recovered in their first year, on the plains as far north as southern Alberta, southern Saskatchewan, and southern Manitoba, and as far south and east as Oklahoma. Birds banded in Wyoming and Colorado showed little tendency to move west of the Continental Divide.

Records from 30 individuals show that molt extends from early May to October, although individuals are not closely synchronized. The sequence of remix replacement is somewhat variable, rectrix replacement quite constant.

Adult and immature female Prairie Falcons weigh about one-third more than adult and immature males, respectively.

Prairie Falcons in the region studied seem to be divided among breeding, post-nesting, and wintering populations, the seasonal distribution of which is related to the presence of suitable cliffs, and in all cases to the seasonal abundance of suitable prey on terrain where it can be caught. Trapping and banding operations strongly suggest that these populations are distinct, and there is no information as to their location during the rest of the year.

There is little doubt that in this region much of the seasonal movements and distribution of Prairie Falcons is related to those of the Horned Lark.

The high rate of mortality postulated for immature Peregrine Falcons by Cade (1960) and Beebe (1960) may not apply to Prairie Falcons, since 38 per cent of the wintering population studied were immature birds.

Prairie Falcons seem more numerous in Colorado than in Wyoming in winter, with numbers probably being similar in the breeding season.

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