

POPULATION FLUCTUATIONS AND AGONISTIC INTERACTION OF PEREGRINE AND PRAIRIE FALCONS IN CENTRAL ALBERTA, 1960–2006

Authors: Dekker, Dick, and Corrigan, Rob

Source: Journal of Raptor Research, 40(4): 255-263

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/0892-1016(2006)40[255:PFAAIO]2.0.CO;2

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <u>www.bioone.org/terms-of-use</u>.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

THE JOURNAL OF RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

Vol. 40

DECEMBER 2006

No. 4

J. Raptor Res. 40(4):255–263 © 2006 The Raptor Research Foundation, Inc.

POPULATION FLUCTUATIONS AND AGONISTIC INTERACTION OF PEREGRINE AND PRAIRIE FALCONS IN CENTRAL ALBERTA, 1960–2006

DICK DEKKER¹

3819–112A Street NW, Edmonton, Alberta, T6J 1K4, Canada

Rob Corrigan

Alberta Conservation Association, P.O. Box 40027, Baker Centre Postal Station, Edmonton, Alberta, T5J 4M9, Canada

ABSTRACT.—The Peregrine Falcon (*Falco peregrinus*) became extirpated during the 1960s, while the Prairie Falcon (*Falco mexicanus*) increased on a sympatric nesting range along a section of river in Alberta, Canada. Following the release of 233 captive-reared juvenile peregrines in 1992–96, some peregrines returned to the river to breed, reaching a high of seven pairs in 2000, but declining again to two pairs in 2006. In an inverse relationship, the number of Prairie Falcon nests dropped from five to two and then went back up to four. We hypothesize that the peregrine's failure to reach former densities in the study area was due to habitat deterioration which resulted in a reduced prey base compared to pre-1960s conditions. Interspecific strife with Prairie Falcons was common at contested nest sites. The Peregrine Falcons were the dominant aggressors, replacing pairs of Prairie Falcons at some, but not all, historical cliff eyries.

KEY WORDS: Peregrine Falcon; Falco peregrinus; Prairie Falcon; Falco mexicanus; nest site competition.

FLUCTUACIONES POBLACIONALES E INTERACCIONES AGONÍSTICAS DE *FALCO PEREGRINUS* Y *F. MEXICANUS* EN ALBERTA CENTRAL, CANADÁ, 1960–2006

RESUMEN.—Las poblaciones de *Falco peregrinus* desaparecieron durante los 60s, mientras que las poblaciones de *F. mexicanus* incrementaron en un rango de nidificación simpátrico a lo largo de un sector de río en Alberta, Canadá. Luego de la liberación de 233 individuos juveniles de *F. peregrinus* criados en cautiverio entre 1992 y 1996, algunos individuos regresaron al río a criar, alcanzando un máximo de siete parejas en el año 2000, pero disminuyendo nuevamente a dos parejas en 2006. De modo inverso, el número de nidos de *F. mexicanus* disminuyó de cinco a dos y luego subió a cuatro. Planteamos la hipótesis de que las poblaciones de *F. peregrinus* no alcanzaron las densidades originales en el área de estudio debido al deterioro del hábitat que provocó una reducción de las presas, en comparación con las condiciones presentes antes de la década del 60. Los conflictos interespecíficos por los sitios de nidificación entre ambas especies fueron comunes. *Falco peregrinus* fue el agresor dominante, reemplazando a las parejas de *F. mexicanus* en algunos, pero no en todos, los acantilados históricos de nidificación.

[Traducción del equipo editorial]

The North American breeding range of the Peregrine Falcon (*Falco peregrinus*) has the entire geographic range of the Prairie Falcon (*Falco mexicanus*)

¹ Email address: ddekker1@telus.net

within it (Palmer 1988). The two species are quite similar in size and physiology. However, they are ecologically separated by habitat and prey preference, with the Peregrine mainly selecting breeding sites near water (Cade 1982), and the Prairie Falcon inhabiting more arid regions (Enderson 1964, Brown and Amadon 1968, Steenhof 1998). Where they occur sympatrically, the Prairie Falcon is usually the more common of the two (Porter and White 1973).

Food availability is an important criterion in the distribution and abundance of the peregrine in its nearly worldwide range (Ratcliffe 1980). In the American west, scarcity of avian prey may contribute to the relative paucity of the peregrine in arid regions (Porter and White 1973). Furthermore, peregrines and Prairie Falcons compete for cliff nesting sites, and where suitable locations are scarce, the presence of one species may influence the numbers and distribution of the other (Newton 1979). Nevertheless, Peregrine and Prairie Falcons are reported to be more or less compatible and to coexist side by side with a minimum of hostilities, even switching nesting sites in different years (Porter and White 1973, Cade 1982, Palmer 1988).

The published literature contains very little and only anecdotal information on agonistic interactions between peregrines and Prairie Falcons. In aerial performance, the latter is considered a match for the peregrine (Walton 1978, Cade 1982), and at higher elevations, the Prairie Falcon – apparently due to its lighter wing loading - is believed to outfly the peregrine (Brown and Amadon 1968:835, Nelson 1969). However, in a few cases, peregrines are known to have replaced Prairie Falcons at nest sites and forced them to abandon their eggs (Porter and White 1973:60). In California, a female Prairie Falcon was struck down and assumed to have been killed in a cooperative attack by a pair of peregrines (Walton 1978). In Utah, the three young of Prairie Falcons nesting 300 m from peregrines were killed by them soon after fledging (White et al. 2002). By contrast, there are no reports of peregrine fatalities caused by Prairie Falcons. Interspecific kleptoparasitism (the robbing of prey by one species from the other) may be expected to occur either way, but in the only two published incidents known to us the peregrine was the loser (Beebe and Webster 1964, Dekker 1999).

Changes in climatic conditions or land management that result in a loss of essential habitat and food resources may favor one falcon species over the other. For example, during a period of drought on a sympatric breeding area in Utah, about 50% of the peregrine eyries became vacant and were taken over by Prairie Falcons (Nelson 1969). A similar switch occurred in central Alberta during the 1960s when the peregrine population died out (Enderson 1969). The primary cause of this extirpation was believed to be toxic chemical residues in the food chain, superimposed on the robbing of nest young by humans (Dekker 1967). Less clear was the detrimental impact of environmental changes, such as modern agricultural practices and the draining of area wetlands. During the process of peregrine extirpation in central Alberta, the number of Prairie Falcons increased, suggesting the possibility that the latter had displaced the peregrines by aggressive competition for prey or nest sites (Dekker 1967). An effort to better understand the relative importance of the above factors was recommended by Rowell et al. (2003).

An opportunity to reexamine the interspecific dynamics arrived between 1992–96 with the reintroduction of captive-reared peregrines in the study area by the Alberta Fish and Wildlife Division (AFWD) in association with the Canadian Wildlife Service (CWS). Similar programs have been very successful across North America (Cade and Burnham 2003). In this paper, we report on: (1) the number of nest sites occupied by Peregrine Falcons in the study area before their 1960's extirpation, (2) peregrine population fluctuations after their 1992– 96 reintroductions, and (3) agonistic interactions between peregrines and Prairie Falcons at contested nest sites.

STUDY AREA AND METHODS

The study area consists of two sections (A and B), 30 and 100 km long respectively, of the Red Deer River valley in central Alberta, Canada (52°N, 112°W). The river is 80-150 m wide and flows in a southeasterly direction through a gently sloping agricultural plain containing widely scattered farm buildings and woodlots. Depressions are filled with shallow wetlands that vary in size depending on annual precipitation. The valley is 0.5-1 km wide and about 80 m lower than the mean elevation (860 m) of the uplands. Portions of the valley bottom are used for agriculture and livestock grazing. South-facing valley walls are semiarid and grassy; the north-facing aspect supports a narrow strip of white spruce (Picea glauca) and trembling aspen (Populus tremuloides). Steep and eroding escarpments feature limestone outcrops and cliffs. The local climate is cold continental, and the river is ice-covered from November to late March.

Depending on pockets of suitable habitat, the original and current nesting range of the peregrine includes all of Alberta (Palmer 1988, Corrigan 2000). The Prairie Falcon's breeding range in North America reaches its northern limit at the latitude of the study area (Steenhof 1998), although there are two isolated nesting records, respectively 150 (Semenchuk 1992) and 500 km farther north in Alberta (R. Corrigan, AFWD, unpubl. data). While the Peregrine Falcon migrates south in early fall, the prairie is a year-round resident in the province (Godfrey 1986, Dekker and Lange 2001). Breeding pairs of peregrines arrive in the study area in the first 2 wk of April. By that time, the local Prairie Falcons are well established and their reproductive season is roughly 3 wk ahead of that of the peregrines (D. Dekker, unpubl. data).

Study area A was first surveyed by D. Dekker, on foot and by canoe, in 1960. Repeat visits (5–7/yr) were made to a 4-km central section, named Valley of the Falcons (VF), which contained five prominent nesting cliffs. Area A was not visited in 1962–64. Seasonal checks resumed in 1965– 69 but dropped to occasional in 1969–96. In 1997–2006, Dekker visited the VF section on 72 d (3–11 d/yr). The nest sites were in plain view from the opposite side of the river and could be watched through binoculars and telescope. Observation time spent at one or more falcon eyries in VF was 3–10 hr/d with a mean of 7 hr/d.

Study area B began downstream from area A and was first surveyed in 1992 when AFWD began a mass-release of captive-reared Peregrine Falcons. During the program's 5 yr of operation, hack boxes were installed on four area B cliffs, two of which were occupied at the time by Prairie Falcons. Their young were removed and taken into captivity. In 1996, a fifth release box was installed in area A at a site which had no known occupancy, past or present, by wild falcons of either species. The total number of juvenile peregrines successfully released on the Red Deer and other southern Alberta rivers was 223 (Holroyd 2003). After the releases had stopped, R. Corrigan traveled the river by boat or helicopter to locate nesting peregrines. Known sites were monitored yearly. One or more captivereared young were added to four pairs with less than four young of their own. At about 3 wk of age, nest young were fitted with standard metal and plastic alpha-numeric bands: red for captive-reared birds and black for wildraised young.

Opportunities for studying the foraging habits of these falcons were limited. We rarely saw them attack prey. Upon leaving the valley, both the peregrines and the Prairie Falcons commonly soared and sailed out of view (Dekker 1993, 1999). Waiting for their return, we recorded the number of food items brought back to the nest. We did not collect prey remains at the eyries.

RESULTS

In 1960, study area A contained five nesting pairs of peregrines, including two in the VF section. Single adults were seen at two additional sites upriver from VF. In 1965, two of the known nesting sites were still occupied: one situated in the VF section, the other 10 km downriver from there. Both were abandoned by 1967 (Dekker 1993).

Area A contained four breeding pairs of Prairie Falcons in 1960, and three in 1965. In addition, two single Prairie Falcons frequented VF cliffs after they had been vacated by peregrines. By 1995, the number of occupied Prairie Falcon eyries in area A increased to five.

Area A cliff sites known to have been occupied over the years by breeding falcons of either species varied in aspect; five were north-facing, and four faced south. By 1995, four of five occupied sites faced north. After 1995, only one VF site has been continuously in use by Prairie Falcons nesting in the same cavity each year. The four other sites alternated in occupancy between Prairie and Peregrine Falcons that used the same or different nest ledges. Aggressive interactions between neighboring pairs were observed only at the two VF sites that were closest together (400 m), only when the pairs were of different species, and only during the early part of the breeding season.

We have no information on the historical Peregrine and Prairie Falcon populations of study area B. No peregrines were found in 1992 when AFWD began its releases of captive-reared peregrines. The number of Prairie Falcons breeding in area B was likely greater than the two pairs recorded at cliffs selected for the placement of hack boxes. In 1996, after the peregrine releases were completed, firstyear peregrines, returning from their migrations, became summer residents at the hack sites. In 1994, the first mated peregrine pair laid eggs and raised young in one of the boxes. Henceforth, up until 2006, one or more of the hack sites were occupied yearly, although the falcons sometimes laid their eggs on nearby rock ledges instead of inside the boxes.

In 1997, R. Corrigan found the first successful nest site at a natural cliff in the valley. This was the very last cliff that had been used by peregrines prior to their extirpation (Dekker 1999). By 2000, there were pairs at three traditional natural sites in area A, and the total number of peregrine nests in areas A and B reached a high of seven (Fig. 1).

The peregrine expansion ended in 2000 and the population began to show a decline. By 2006, the number of eyries had dropped from seven to two (Fig. 1). One of these two pairs used an area B hack box, while area A contained the only nest on a natural cliff ledge. The mean number of fledglings produced (excluding fostered young) was 1.8 per occupied site (N = 54), which is near the average for many peregrine populations (White et al. 2002). However, the turnover of one or both adults was high at eyries that were occupied for two or more years in a row (8/12), and there was a rather high incidence of first-year females (N = 4) in nesting pairs which failed to produce young.

The Prairie Falcon population in area A showed an inverse relationship with the peregrine fluctua258



Figure 1. Breeding pairs of Peregrine Falcons along the Red Deer River, Alberta, in 1994–2006.

tion (Fig. 2). After 1995, the number of resident Prairie Falcon pairs declined from five to two, but increased again to four in 2004–06. The mean number of young at successful Prairie Falcon eyries was 4.4 (N = 25), but not all sites were checked after egg-laying time. In most years, two prairie nestlings were collected under falconry permits. In three instances, entire broods disappeared for unknown reasons.

Interspecific Strife. We recorded agonistic interactions between Peregrine and Prairie Falcons at five different cliff sites on 33 d. The peregrines always were the aggressors and appeared to be faster, more agile and more persistent in pursuit than the Prairie Falcons. In contrast, the latter allowed their opponents to pass by unchallenged. Frequent aerial combat took place at only three cliffs. In years when both species were present early in the breeding season, the peregrines dominated the air space above, below and on either side of the Prairie Falcons' nest ledges. Prey-carrying parent Prairie Falcons that were intercepted by peregrines evaded their attack-



Figure 2. Breeding pairs of Peregrine and Prairie Falcons in the Valley of the Falcons along the Red Deer River, Alberta, in 1995–2006.

ers by dropping down onto the escarpment, often into some vegetation. Bodily contact was seen only once, when a male Prairie Falcon was seized by a male peregrine and forced down to the ground. Nevertheless, the pair of Prairie Falcons prevailed and remained in possession of the superior nest ledge.

We recorded four conflicts in which a pair of peregrines succeeded in evicting Prairie Falcons from their nest sites. However, in four other cases the peregrines were unable to evict the Prairie Falcons, and in two additional cases a site usurped by peregrines reverted back to Prairie Falcons in the subsequent year. The appendix contains details of ownership changes at three of the most contested cliff sites.

DISCUSSION

As falcons "use the same nesting places in different years, monitoring becomes easier and the value of population studies increases the longer they are continued" (Newton 1979). Although our sample size is small, the long-range data for study area A show that the reintroduced peregrines regained 60% (three out of five) of their historical nesting cliffs. Moreover, they succeeded in their comeback in a relatively short time of 3 yr. However, contrary to expectations (Holroyd and Banasch 1990), the successful reintroduction of the peregrine did not lead to continued expansion along the Red Deer River. We can only speculate as to the cause or causes.

On the basis of our observations that the Peregrine Falcon was the dominant aggressor with superior flying skills at all contested nest sites, we feel our data do not support the hypothesis that the 2000–06 peregrine declines were the result of interspecific competition with the Prairie Falcon for nest sites. However, such competition may have been a contributing factor, as suggested by the fact that the peregrines often failed to form pairs of adult age, and that they, either singly or even as a mated pair, were not always successful in driving off nesting pairs of prairies.

We have no indication that the peregrines were subjected to human-caused fatalities in the study area, nor do we have any reason to suspect that agricultural or industrial chemical residues were implicated in the decline. As noted, the proportion of first-year recruits on nest sites was rather high, which is typical of populations that are in flux (Newton 2003, Tordoff and Redig 2003), and peregrines are known to do poorly in their first breeding attempts (Court et al. 1988b).

However, by comparison, most other peregrine reintroduction programs have resulted in sustained growth (Enderson 2003). Even in regions where no releases took place, contemporary peregrine populations have regained or are now exceeding historical densities (Cade and Burnham 2003). Philopatry and site tenacity are typical in Peregrine Falcon ecology, and a numerical increase in recovering populations is an indicator of population viability and normalcy (Cade 2003). In contrast, the absence of such growth in central Alberta is notable, and it spurred us to investigate what might be occurring there.

The Prey Base Hypothesis. The introduced peregrine population in the study area began its downward adjustment 4 yr after the releases were stopped. Apparently, while the captive-reared cohort was dying off, it was not being replaced at the same rate by a younger generation. We suggest that a factor that might be responsible for the failure of these falcons to regain their former population level is an inadequate prey base compared to the pre-1960s. Although the reproductive output was kept near average by the few successful pairs which had secured pockets of adequate habitat, prey scarcity may have been at the root of the high adult turnover and the eventual abandonment of other sites. Factors that have negatively affected the avian community of the region after the 1960s are changes in agricultural practices and land use that have resulted in escalating declines in the number and ecological quality of wetlands (Turner et al. 1987). Although we have no data on the prey base in our study area, habitat deterioration can be expected to have resulted in a downward trend in waterfowl, shorebirds, and other peregrine prey. For example, feral Rock Pigeons (Columba livia), that are a worldwide staple for peregrines (Ratcliffe 1980, Palmer 1988), became much scarcer than formerly in central Alberta after old-style wooden field granaries were destroyed and replaced with metal silos on farmyards (Dekker 1993, 1998). Similarly, Gray Partridges (Perdix perdix) have been negatively affected by the use of herbicides, modern grain storage methods, and early fall tilling (D. Dekker unpubl. data). One species that can be expected to have increased is the European Starling (Sturnus vulgaris), which is a common prey for male peregrines in populated regions (Palmer 1988) as well as in our study area.

We noted that the two remaining peregrine eyries in the study area are within flying distance (3– 10 km) of remnant pockets of "knob and kettle" topography, formed by glacial deposits and characterized by wooded hillocks and many small ponds. By contrast, peregrines are absent from river sections where the adjacent uplands have been cultivated right up to the valley rim.

The prey-base hypothesis is further supported by circumstantial evidence from elsewhere in central Alberta. As of 2006, peregrines have yet to return to historical cliff breeding sites along other major rivers in agricultural regions of the province (R. Corrigan unpubl. data). By contrast, reintroduced falcons have been nesting in both of the province's large cities since the late 1970s (Holroyd and Banasch 1990). Moreover, at least four peregrines dispersing from natural cliff sites on the Red Deer River - identified by their band numbers - have become breeding adults in nest boxes on high city buildings and industrial towers in the province (G. Court pers. comm.). Dispersal from natural habitats to urban breeding sites was also noted in recovering peregrine populations in California (Kauffman et al. 2004). In Alberta, as elsewhere in North America and Europe, there is mortal competition for urban territories (Tordoff and Redig 2003, Van Geneijgen 2005). While dispersal from urban to natural cliff sites is still rare (Tordoff and Redig 2003), city falcons have been moving out to high structures in rural settings for more than a decade. During the 1990s, offspring from the Edmonton city population, as well as those from a river population in western Alberta, spread to four power plants near an Alberta lake, even before nest boxes were placed on the stacks. The main food of these breeding pairs is the Franklin's Gull (Larus pipixcan), which is seasonally common and easily caught (Dekker and Taylor 2005).

The abundant prey base of peregrines nesting on Alberta power plants and in the cities is in sharp contrast to our study area, where we saw the following signs of apparent food shortages. (1) At site A1, only the males were seen to bring in prey for the nestlings. Even after absences of 3-4 hr, the females returned without food, although their swollen crops indicated that they had hunted and fed themselves well away from the nest site. (2) During a failed nesting attempt at cliff A2, the adult male, upon returning from long absences (1-3 hr), alternated brooding duties with the female, but he did not always bring food for her (N = 3). In one additional instance, he refused to share a prey item with the aggressively begging and wailing female. (3) Prey items (N = 60) brought to VF sites included 73% small passerines and swallows; 10% waterbirds; 10% Richardson's ground squirrels (*Spermophilus richardsonii*), and 7% unidentified prey. In terms of biomass, the mammalian portion of the diet is substantial. Ground squirrels are locally common and have not been previously recorded as prey for peregrines in central Alberta. However, during years of cyclic abundance, ground squirrels and other rodents accounted for 33% of prey biomass of peregrines in northern Canada (Court et al. 1988a, Bradley and Oliphant 1991).

We saw no evidence of food shortages at the Prairie Falcon nests. During 64 hr of watching at VF sites, the nestlings appeared well-fed, often with bulging crops, ignoring newly-brought food. Of 28 prey deliveries, 75% were ground squirrels. Ground squirrels and other small mammals are also the main prey of nesting Prairie Falcons in Idaho (Steenhof et al. 1999). In a very large sample of food items brought to Idaho eyries only 4% were birds (Holthuijzen 1990). This contrasts with our study in which birds made up 25% of prey items, including five small passerines and two Killdeer (Charadrius vociferus). Steenhof (1998) did not list shorebirds in the known prey of the Prairie Falcon. However, nonbreeding falcons commonly hunt sandpipers in Alberta wetlands (Dekker 1982), and Prairie Falcons nesting in Utah commonly preved on juvenile American Avocets (Recurvirostra americana). Porter and White (1973) stated that, where both species of falcon occur together, the Prairie Falcon "assumes the role of generalist while the peregrine is the specialist." In our study area, the Prairie Falcon could indeed be called a food generalist. By the same token, the peregrine too is a generalist, as suggested by its use of ground squirrels as well as birds.

Conclusions. In contrast to observations reported by other investigators (Brown and Amadon 1968, Nelson 1969, Walton 1978, Cade 1982), we found the Prairie Falcon no match for the peregrine in the air. In all incidents of territorial conflict, the peregrines were clearly the dominant aggressors, whereas the Prairie Falcon's defense was weak and evasive. As in incidents reported from Utah (Nelson 1969, Porter and White 1973), nest site takeovers in our area included at least one case of forced egg abandonment at the expense of the Prairie Falcons. Nevertheless, the peregrines we observed were not always capable of displacing the Prairie Falcons, which supports the contention that both species can exist side by side (Palmer 1988). By way of explanation, we hypothesize that the decisive factor in interspecific combat derives from individual differences in size, dominance, and tenacity, which can either lead to a swift takeover of a nest site or a long standoff. As reported by Dekker (1999), the reintroduced peregrines were noticeably smaller in size than the historical breeding population. Initially, this may have hampered the species' chances of replacing the Prairie Falcon at contested cliff sites.

Furthermore, it was apparent to us that some cliff sites held by Prairie Falcons were easier to defend than others. For instance, two contested sites were situated on partly-wooded escarpments that allowed the Prairie Falcons to take shelter and evade attacking peregrines. By contrast, two other sites that included sheer rock faces were the first to revert back to peregrines after their 30 yr absence.

In any landscape, the "upper limit to the number of established raptor pairs is set by food or nest sites, whichever is in shorter supply" (Newton 1979). A link between Peregrine Falcon breeding density and the food supply was reported from various habitats (Court et al. 1988a, Ratcliffe 1980, Nelson 1990, Johnstone 1998, Newton 2003). Based on our observations, we believe that the peregrine population in our study area is not limited by the availability of nest sites but by its food resource. The fact that the current number of territorial pairs is well below the 1960 level suggests that the carrying capacity of the region, in terms of the prey base for these falcons, has shrunk. A similar conclusion, also untested, was reached for populations in Fiji and Vanuata (White et al. 2000).

Although the Prairie Falcon population is back at its former level, current numbers appear to have reached a plateau as suggested by the intensity of intraspecific territorial disputes. Against conspecifics, the Prairie Falcon is a fierce defender. Unlike peregrines, which generally fight birds of their own sex, Prairie Falcons attack both sexes (Steenhof 1998). In April of 2003 and again in 2004, there were two pairs of prairies at the same site and the level of hostilities was intense. The resident male repeatedly seized the intruding female, and the intruding male tackled the resident male while the latter was standing on the nest ledge near the brooding female. One day, there were two females disputing the nest ledge while the males were engaged in aerial battle. Eventually, only one of the pairs prevailed. These observations support our conclusion that the Prairie Falcon, unlike the peregrine in the study area, is limited by competition for available nest sites.

ACKNOWLEDGMENTS

R. Corrigan was an employee of the Alberta Fish and Wildlife Division in 1995–96 and of the Alberta Conservation Association in 1997–2006. Both agencies provided generous financial support for Corrigan's field study and reimbursed some of D. Dekker's travel expenses in 1997– 2006. Occasional co-observers were G. Court, H. Killiam, and D. Sturgess. W. Nelson kindly supplied relevant literature. We thank the landowners for their unfailing courtesy in allowing access to the river banks. Referees T.J. Cade and C.M. White made helpful comments on the manuscript that led to numerous improvements and additions in this paper.

LITERATURE CIITED

- BEEBE, F.L. AND H.M. WEBSTER. 1964. North American falconry and hunting hawks. Private Pub. Denver, CO U.S.A.
- BRADLEY, D.M. AND L.W. OLIPHANT. 1991. The diet of the Peregrine Falcons at Rankin Inlet, Northwest Territories: an unusually high proportion of mammalian prey. *Condor* 93:193–197.
- BROWN, L. AND D. AMADON. 1968. Eagles, hawks and falcons of the world. Country Life Books. Hamlyn House, Feltham, U.K.
- CADE, T.J. 1982. The falcons of the world. Cornell University Press, Ithaca, NY U.S.A.
- 2003. Life history traits of the Peregrine in relation to recovery. Pages 2–11 in T.J. Cade and W. Burnham [EDS.], Return of the Peregrine. The Peregrine Fund, Boise, ID U.S.A.
- AND W. BURNHAM. [EDS.]. 2003. Return of the Peregrine. The Peregrine Fund, Boise, ID U.S.A.
- CORRIGAN, R. 2000. Survey of the Peregrine Falcon in Alberta. Species at risk report, No. 2. Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton, AB, Canada.
- COURT, G.S., D.M. BRADLEY, C.C. GATES, AND D.A. BOAG. 1988a. The population biology of Peregrine Falcons in the Keewatin District of the Northwest Territories, Canada. Pages 729–739 in T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.

, ____, ____, AND _____. 1988 b. Turnover and recruitment in a tundra population of Peregrine Falcons. *Ibis* 131:487–496.

DEKKER, D. 1967. Disappearance of the Peregrine Falcon as a breeding bird in a river valley in Alberta. *Blue Jay* 30:175–176.

- ———. 1982. Occurrence and foraging habits of Prairie Falcons at Beaverhills Lake, Alberta. *Can. Field-Nat.* 96:477–478.
- ——. 1993. Valley of the falcons. *Alberta Naturalist* 23:53–56.
- 1998. Prairie water wildlife at Beaverhills Lake, Alberta. Univ. of Alberta Press, Edmonton AB, Canada.
- ———. 1999. Bolt from the blue wild peregrines on the hunt. Hancock House, Surrey, BC, Canada, Blaine, WA U.S.A.
- AND J. LANGE. 2001. Hunting methods and success rates of Gyrfalcons and Prairie Falcons preying on feral pigeons in Edmonton, Alberta. *Can. Field-Nat.* 155: 395–401.
- AND R. TAYLOR. 2005. A change in foraging success and cooperative hunting by a breeding pair of Peregrine Falcons and their fledglings. *J. Raptor Res.* 39:386–395.
- ENDERSON, J.H. 1964. A study of the Prairie Falcon in the central Rocky Mountain region. Auk 81:332–352.
- ———. 1969. Population trends among Peregrine Falcons in the Rocky Mountain region. Pages 73–79 in J.J. Hickey [ED.], Peregrine Falcon populations: their biology and decline. Univ. of Wisconsin Press, Madison, WI U.S.A.
- 2003. Early Peregrine expansion and management: Rocky Mountain West. Pages 57–71 in T.J. Cade and W. Burnham [EDS.], Return of the Peregrine. The Peregrine Fund, Boise, ID U.S.A.
- GODFREY, G.W. 1986. The birds of Canada. National Museum of Canada, Ottawa, ON, Canada.
- HOLTHUIJZEN, A.M.A. 1990. Prey delivery, caching, and retrieval rates in nesting Prairie Falcons. *Condor* 92: 475–484.
- HOLROYD, G.L. AND U. BANASCH. 1990. The reintroduction of the Peregrine Falcon into southern Canada. *Can. Field-Nat.* 104:203–208.
- 2003. The return of the *anatum* Peregrine to southern Canada, 1985–2000. Pages 117–125 *in* T.J. Cade and W. Burnham [EDS.], Return of the Peregrine. The Peregrine Fund, Boise, ID U.S.A.
- JOHNSTONE, R.M. 1998. Aspects of the population biology of Tundra Peregrine Falcons (*Falco peregrinus tundrius*). Ph.D. dissertation, Univ. of Saskatchewan, Saskatoon, Canada.
- KAUFFMAN, M.J., J.F. POLLOCK, AND B. WALTON. 2004. Spatial structure, dispersal, and management of a recovering raptor population. *Am. Nat.* 164:582–597.
- NELSON, M.W. 1969. The status of the Peregrine Falcon in the northwest. Pages 61–72 in J.J. Hickey [ED.], Peregrine Falcon populations: their biology and decline. Univ. of Wisconsin Press, Madison, WI U.S.A.
- NELSON, R.W. 1990. Status of the Peregrine Falcon (F. p. pealei) on Langara Island, British Columbia, 1968– 1989. Can. Field-Nat. 104:193–199.
- NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.

— 2003. The contribution of Peregrine research and restoration to a better understanding of Peregrines and other raptors. Pages 339–347 *in* T.J. Cade and W. Burnham [EDS.], Return of the Peregrine. The Peregrine Fund, Boise, ID U.S.A.

OLIPHANT, L.W. 1991. Hybridization between a Peregrine Falcon and a Prairie Falcon in the wild. *J. Raptor Res.* 25:36–39.

- PALMER, R.S. 1988. Handbook of North American birds. Vol. 5. Diurnal raptors, part 2. Yale Univ. Press, New Haven, CT U.S.A.
- PORTER, R.D. AND C.M. WHITE. 1973. The Peregrine Falcon in Utah, emphasizing ecology and competition with the Prairie Falcon. *Brigham Young Univ. Sci. Bull. Biol. Ser.* 18:1–74.
- RATCLIFFE, D. 1980. The Peregrine Falcon. Buteo Books, Vermillion, SD U.S.A.
- ROWELL, P., G.L. HOLROYD, AND U. BANASCH. 2003. The 2000 Canadian Peregrine Falcon survey. J. Raptor Res. 37:98–116.
- SEMENCHUK, G.P. 1992. The altas of breeding birds of Alberta. Fed. Alberta Nat. Edmonton, AB, Canada.
- STEENHOF, K. 1998. Prairie Falcon (*Falco mexicanus*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 346. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, DC U.S.A.

—, M.N. KOCHERT, L.B. CARPENTER, AND R.N. LEHMAN. 1999. Long-term Prairie Falcon population changes in relation to prey abundance, weather, land uses, and habitat conditions. *Condor* 101:28–41.

- TORDOFF, H.B. AND P.T. REDIG. 2003. Peregrines in the Midwest. Pages 173–187 in T.J. Cade and W. Burnham [EDS.], Return of the Peregrine. The Peregrine Fund, Boise, ID U.S.A.
- TURNER, B.C., G.S. HOCHBAUM, F.D. CASWELL, AND D.J. NEW-MAN. 1987. Agricultural impacts on wetland habitats on the Canadian prairies, 1981–85. *Trans. N. Am. Wildl. Nat. Res. Conf.* 52:206–215.
- VAN GENEIJGEN, P. 2005. Broedresultaten van Slechtvalken in Nederland in 2005. Slechtvalk Nieuwsbrief 11:2– 7.
- WALTON, B.J. 1978. Peregrine Prairie Falcon interaction. *Raptor Res.* 12:46–47.
- WHITE, C.M., D.J. BRIMM, AND J.H. WETTON. 2000. The Peregrine Falcon in Fiji and Vanuata. Pages 707–720 *in* R.D. Chancellor and B.-U. Meyburg [EDS.], Raptors at Risk. Hancock House, Blaine, WA U.S.A.

—, N.J. CLUM, T.J. CADE, AND W.G. HUNT. 2002. Peregrine Falcon (*Falco peregrinus*). *In* A. Poole and F. Gill [EDS.], The Birds of North America, No. 660. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, DC U.S.A.

Received 1 September 2005; accepted 18 September 2006 Associate Editor: James C. Bednarz Appendix

Some chronological occupation changes at contested nesting sites.

Site A1. This north-facing cliff, occupied by peregrines in 1960 and 1961, was used by Prairie Falcons from 1967 onwards. In 1999, the site was frequented by a pair of reintroduced peregrines which successfully raised three foster young placed on the only suitable nesting ledge of this cliff site. The same pair returned in 2000 and fledged three young of their own from the same ledge. The following year, the female of the pair was new and in her first year. That spring, and again in 2003, the nesting cavity was occupied by a breeding pair of Prairie Falcons. Despite aggressive attacks by a pair of peregrines, the prairies held on to the superior nest ledge, while the peregrines made an unsuccessful nesting attempt on an inferior outcrop of rock along the same, largely wooded, escarpment about 100 m away from the Prairie Falcons. In 2004-06, the superior ledge was again occupied by Prairie Falcons, and we saw no peregrines there in April and May. Curiously, in late June and early July of 2005, the prairies were attacked by a pair of adult peregrines that used the inferior ledge of site A1 as a temporary perch or roost. This observation indicates the existence of non-nesting "floaters" in this population.

Site A2. This 0.5-km-wide, south-facing cliff, occupied by peregrines prior to 1967 (Dekker 1999), was taken over by Prairie Falcons in 1967, but reverted back to a pair of reintroduced peregrines in 1997. They held the site until 2001. In June 2001, the adult female Peregrine Falcon was found dead on her eggs inside a narrow cavity at the west end of the rock face. Part of the upper wing coverts near the bend had been plucked, and her chest showed two slashes that looked like they had been inflicted by the talons of a raptor, perhaps a Great Horned Owl (Bubo virginianus). Owl predation is a major mortality factor in many peregrine reintroduction programs (Tordoff and Redig 2003), but its role in the Red Deer study area is unknown. It is also possible that the peregrine might have sustained her mortal wounds in combat with a pair of Prairie Falcons that was perched beside the nest cavity in which the dead peregrine was found 2 d later. The male prairie was actually observed to enter and stay 10-15 min inside the cave, enough time to account for the partly plucked wing coverts of the dead peregrine.

For the next three breeding seasons, site A2 was occupied by a pair of Prairie Falcons until they were again replaced by peregrines in 2004. We did not observe the territorial fights that must have preceded this ownership change. However, the circumstances immediately following the apparent takeover are noteworthy. On 25 April 2004, a pair of peregrines, consisting of an adult male and a firstyear female, was using the same nesting cave that had earlier been occupied by the prairies. We do not know whether the peregrines had laid their own eggs or were brooding those of the prairies. By the end of May, the nesting attempt had failed. Both the peregrines and the pair of prairies were now frequenting opposite parts of the escarpment without any obvious hostilities between them. In 2005 and 2006, Prairie Falcons again bred successfully at site A2 and no peregrines were seen there.

Site B1. In 1997, this cliff site became the scene of prolonged interspecific strife when a pair of peregrines drove off the resident Prairie Falcons, possibly forcing them to abandon their eggs, but the peregrines did not nest. In 1998 and 1999, a pair of prairies used a large nesting cave under an overhang, while the peregrines laid eggs on an exposed ledge near the top of the same escarpment about 35 m from the cave. After their eggs were depredated, probably by a coyote (*Canis latrans*), the Peregrine Falcons remained in the area and were subsequently observed bringing food to the Prairie Falcon nestlings under the overhang. The peregrines appeared to prevent the parent prairies from entering. During our last visit of the 1999 breeding season, there were three fledged Prairie Falcons and two adult peregrines present at the site. Prior to the next breeding season, the overhang collapsed and no young were produced at the site in that year. After a nest box was hung on the escarpment and an enclosure built around it to prevent mammalian entry, the site was used by peregrines for three successive seasons up to 2005, but not in 2006.

Hack Site No. 1. In 1992, the displaced pair of Prairie Falcons, whose own young had been removed by AFWD staff, brought food to the recently-released fledgling peregrines. On 15 July, an adult male peregrine arrived at the site. Alternately attacked by both prairies, the peregrine made vigorous counter-attacks, stayed around for several weeks, and also brought prey items to the hacked fledglings. Identified by his band number, this adult peregrine was captive-reared and had been crossfostered into a Prairie Falcon nest in southern Alberta. Cross-fostering of juvenile peregrines into Prairie Falcon nests was commonly practiced in some western regions of North America (Cade and Burnham 2003). To our knowledge, there is only one record - from Saskatchewan - of a crossfostered male peregrine interbreeding with a female Prairie Falcon and raising hybrid young (Oliphant 1991). In addition, on a hack tower in Utah in the mid-1980s, a male peregrine mated successfully with a female Prairie Falcon that had been a falconry bird (J. Enderson pers. comm.).