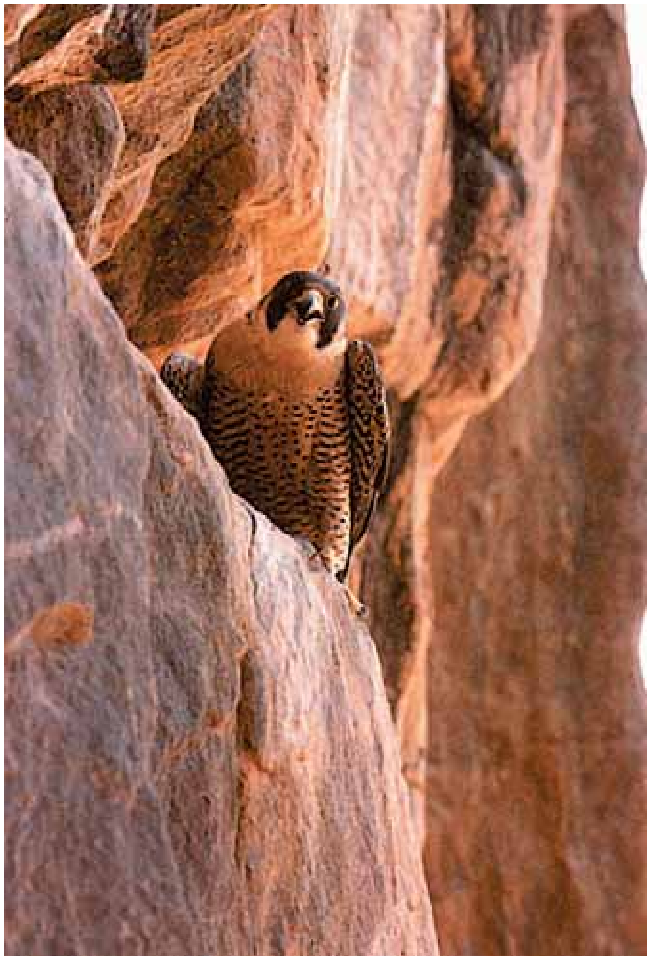

PEREGRINE FALCON BIOLOGY AND MANAGEMENT IN COLORADO

1973 - 2001

STATE OF COLORADO - DIVISION OF WILDLIFE

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ACKNOWLEDGMENTS

In the beginning, we realized that the job of restoration was too large for a single entity. In 1975 the Colorado Division of Wildlife began to monitor and manage wild peregrine falcons. The Peregrine Fund offered to manage captive breeding and oversee most hacking efforts and the land management agencies protected certain nest sites and supported the release of falcons at vacant sites under their jurisdiction. The research and recovery program could not have succeeded without the enthusiastic financial and logistical support of the National Park Service (NPS), U.S. Forest Service (USFS), and the Bureau of Land Management (BLM). Participants from the BLM included Eric Brekke, Hillary Donoghue-Counters, Jim Ferguson, Doug McVean, and Lee Upham. They were dedicated to restoring peregrines on lands under their administration.

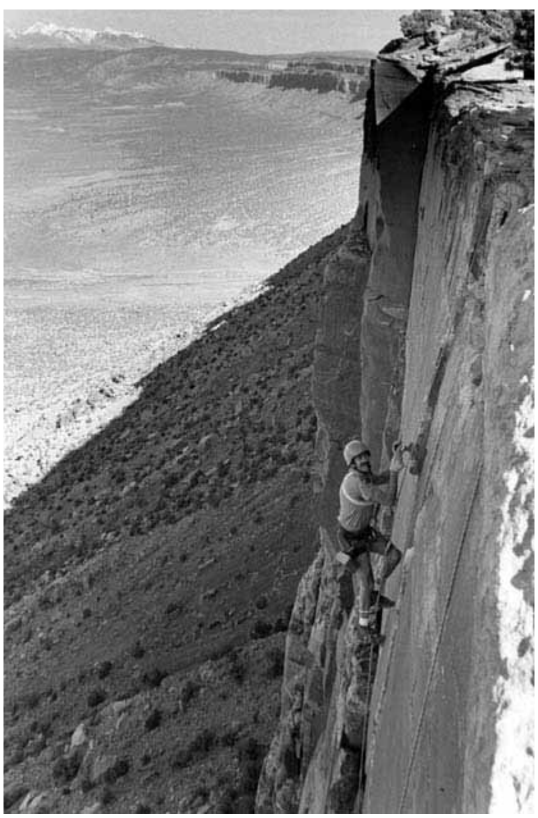

FIGURE 1. Dan Berger ascending with eggs.

Dan Berger had surveyed peregrines in the eastern U.S. and brought his expertise to the project. He became a critical partner with us. He devoted more than a decade assisting with field observations, climbing into nests (Fig. 1), and helped refine and implement our efforts to reverse the population decline.

We are especially appreciative of more than 100 individuals who were employed seasonally as a major part of the tedious field work (Appendix 1). It has been gratifying to learn that some among them became lawyers, physicians, professors, veterinarians, and professional wildlife biologists.

Mark Robert first came to work for us as an observer in 1983 and became a valuable asset to the project over the next 10 years. Mark standardized survey and observation methods and organized the field teams to more efficiently observe wild sites as the population expansion stretched our resources.

Terry Meyers worked up through the ranks and developed a wonderful insight into peregrines. His leadership and expertise permitted us to monitor an expanding list of sites as dwindling resources reduced the number of observers we could send into the field in the late 1990's.

We thank Steve Petersburg in particular. He made peregrine monitoring and recovery a priority in Dinosaur National Monument. He hired observers, ran hack sites and even insisted that we recycle new pairs of peregrines in Dinosaur to provide young for release on the east Slope where the population still lagged. Other important NPS participants are Joe Alston, Myron Chase, Jeff Connor, Steve King, George San Miguel, Pat Perotti, and Dave Price.

Dale Wills was member of the Rocky Mountain/Southwest Recovery Team and facilitated recovery efforts in Colorado on behalf of the USFS. Denny Bohon, Chris Schultz, Jim Sheppardson, and other USFS biologists monitored nesting pairs and implemented measures to protect nest sites.

Rod deWeese of the Biological Research Division of the U.S. Geological Survey helped with pesticide analysis of peregrine eggs and prey. Andrew Archuleta of the Colorado Field Office, Ecological Services, U.S. Fish and Wildlife Service (USFWS) arranged for the pesticide analysis of peregrine eggs.

Bob Tully, Wayne Sandfort and Judy Sheppard of the Colorado Division of Wildlife had the foresight to recognize the difficulties and issues facing the project and worked administratively to smooth the path to recovery of the species in Colorado.

The flying skill and dedication of Bert Metcalf, owner of Thunderbird Helicopters, got us onto remote cliffs without incident. He stretched our limited dollars by camping out and by ferrying his own fuel.

Ed Freienmuth provided our 'Durango headquarters.' He and his wife Charlotte housed and fed us while Ed managed hack sites, temporarily incubated eggs, and monitored nest sites.

We developed a close partnership with Bill Burnham of the Peregrine Fund in 1975 and enjoyed a cooperative relationship for over 20 years. Cal Sandfort, also of the Peregrine Fund, received our precious cargos of wild eggs at all hours and carefully nurtured them. His husbandry successfully produced chicks from cracked, thin-shelled eggs that would not have hatched in the wild.

Jim Gammonley, Tom Remington, Todd Sanders, and Karen Steenhof kindly reviewed the manuscript and provided valued criticisms for improvement. We thank them for their time and effort.

This project was intermittently funded through the Pittman-Robertson grant-in aid program. The Great Outdoors Colorado funds and citizen donations to Colorado's Wildlife Check-off were also important.

PEREGRINE BIOLOGY AND MANAGEMENT IN COLORADO

ABSTRACT

In the early 1970s nesting peregrine falcon (*Falco peregrinus anatum*) population in Colorado had declined due to the adverse effects of DDT in prey birds. By 1976 only five pairs could be found on territory at about 30 historical territories. At that time, we began nesting studies and management including fostering and release by hacking of captive bred young. With the cooperation of federal agencies and the Peregrine Fund, about 400 young were successfully released 1974-90. We report here on the expansion and performance of nesting peregrines in Colorado in the 35 years ending in 2001 at a time when more than 100 pairs were found on territory.

In the 1970's Colorado peregrines persisted on tall cliffs exceeding 60 m, and since population expansion in the 1990's they also have accepted cliffs as low as 30 m. About 39% of recent nests were on cliffs in the lower half of the range of cliff height and prominence. Nest ledges were found at all compass orientations at elevations up to 2300 m, but most faced southerly to easterly in the 2300-3200 m range. In about 60% of the cases at 34 long-studied sites, pairs selected ledges each year not known to have been used previously. The same ledge was used more than three years in 12% of the cases.

Five radio-tagged adults hunted over areas as large as 1,440 km2 and ranged up to 43 km from the eyrie. Twenty species of prey occurred more than 12 times in remains of 1,106 prey individuals found in nests. Most frequent were white-throated swift (*Acronautes sextalis*), mourning dove (*Zenaida macroura*), common nighthawk (*Chordeiles minor*), and rock dove (*Columbia livia*); collectively these remains comprised 45% of the top 20 species.

Egg-laying centered in mid-April. Clutches averaged about 3.5 eggs, and brood size was 2.9 chicks. Sex ratio of nestlings were 1.22 females to males (n = 577). We found a daily chick mortality rate of 0.01 using the Mayfield method. Natural productivity (young fledged per pair on territory) was about 1.2 (1973-80) and about 1.7 in 1995-2001. The overall rate was 1.67 young/attempt (n = 381). We estimated the productivity necessary for an equilibrium population based on mortality of age groups from band recoveries and re-sighted peregrines; if 50% of two-year-olds breed, about 1.2 young per pair would be required. We estimated that adult annual survivorship averaged about 80%.

Adults identified through photographs or colored markers occupied territories an average of 2.7 years and 25% were present at least 4 years. We found no change in productivity of males or females present up to 9 years on territory. Productivity was normal even when both adults were new on the territory. Recent productivity was similar at newly used sites compared to sites we studied before 1985; newly used sites were not poorer in terms of nest success.

In 65 cases, causes of mortality were known; golden eagles (*Aquila chrysaetos*) killed 11 peregrines (8 nestlings), and great horned owls (*Bubo virginianus*) killed 8 (7 nestlings). Collisions killed 13 peregrines (1 with a jet fighter).

DDE declined in the contents of eggs from 82 sets, 1973-90. The thickness of eggshells from whole eggs (n = 213) increased from about 0.300 ppm in 1973 to 0.330 ppm in 1998, the latter still below 0.359 ppm we took as normal for the species. We found wide within-clutch variation in the thickness of intact shells and shell fragments, and no direct correlation between shell thickness and nest productivity.

In fall, Colorado peregrines (n = 14) generally moved south to northern Mexico, but one juvenile was found in Panama. Birds fledged in Colorado (n = 15) were later found at nest sites; 10 were in Colorado, 3 in Utah, 1 in New Mexico, and 1 in Arizona.

We estimated that the known Colorado peregrine population has grown about 10-fold in the 35 years of this study. Before 1985, searches for new sites were mainly fruitless, then success improved. After 1996, searches were markedly productive. Occupancy and survey efforts were evaluated and protocols were recommended for future monitoring.

INTRODUCTION

Distribution

Peregrine falcons breed throughout the Colorado Plateau and Southern Rocky Mountain ecological provinces of Colorado (Fig. 2). However, nesting does not occur on the eastern plains. Prairie falcons (*Falco mexicanus*) nest widely there and to a limited extent in the mountains as well. Peregrine nest cliffs (n = 133) were distributed from 4,560 ft (1,390 m) to 10,800 ft (3,292 m) (Fig. 3). Seven nesting sites occurred above 10,000 ft (3,048 m) ranging from 10,100 ft (3,078 m) to 10,800 ft (3,292 m). Thus suitable nest situations apparently exist throughout all elevations in the western half of the state.

Inventories

The history of observations of peregrines nesting in Colorado is provided in Appendix 2.

In 1964, Enderson (1965) searched 15, 3, and 10 reported locations in Colorado, Wyoming and Montana, respectively. These locations were from the literature, reported by biologists and falconers, or those he discovered while studying prairie falcons. At least one adult was seen at 9 of the 28 locations, demonstrating the species was widely, but sparingly distributed in the region at the time. Informal observations by T. Smylie in New Mexico and by C. White in Utah supported this conclusion. At that time a large portion of reported sites were vacant, and the few pairs found appeared to reproduce poorly. These conditions had been reported elsewhere; in fact no pairs remained in the eastern United States (Berger et. al. 1969) and the species was also in decline in Britain and Europe. In North America, the cause of the population collapse was poor reproduction due to DDT/DDE induced eggshell thinning (Fyfe et al. 1988). After 1964, the peregrine became the subject of enormous systematic surveys throughout the western United States, and in Canada and Mexico (Cade et al. 1988).

In 1972, the Colorado Division of Wildlife (CDOW) established its first nongame biologist position and also hired J. Craig, the first raptor biologist employed by a U.S. government agency. The CDOW initiated inventories to determine the status of various raptors including peregrines. Enderson was funded to repeat the nesting survey work he had accomplished in 1964. Our first intensive inventory of 22 historical sites in 1973 yielded only 10 adult pairs, of which only two were known to have produced eggs. By 1976, we had discovered three other pairs, but in the meantime occupancy continued to decline and adult pairs then defended only five sites. It appeared that Colorado peregrines were experiencing the same difficulties that lead to the extinc-

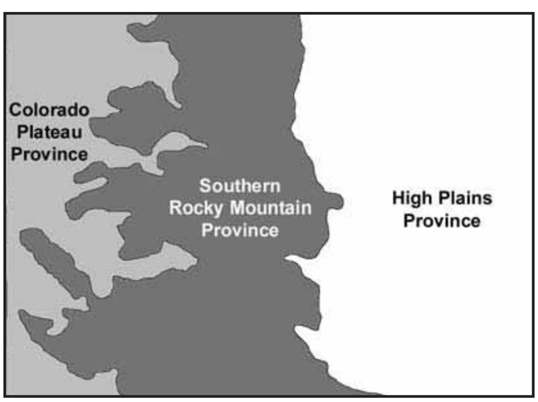

FIGURE 2. Distribution of breeding peregrines was limited to the Colorado Plateau and Southern Rocky Mountain ecological provinces within Colorado.

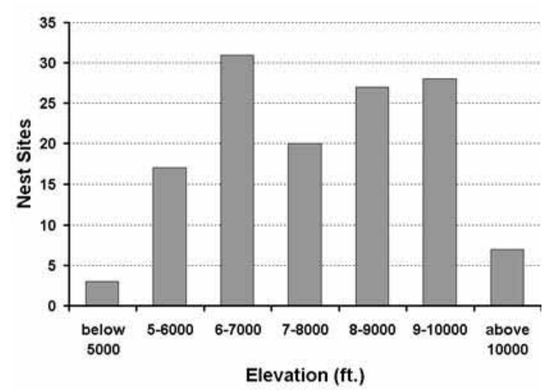

FIGURE 3. Elevations of peregrine nest sites throughout Colorado (n = 133). Elevations were taken from the most frequently used ledge.

tion of eastern U.S. peregrines, and it would be a matter of only a few years until our falcons also disappeared. As opportunities arose, we began to experiment with ways to maintain the few breeding pairs at their cliffs.

RECOVERY PROGRAM

Recovery Plan

Appendix 3 provides a chronology of recovery events. At the request of the FWS in 1974, the CDOW hosted a national meeting in Denver to discuss development of recovery teams and plans mandated by the Endangered Species Act (ESA). A prototype recovery plan was drafted and 4 recovery teams were recommended. In 1975, the USFWS appointed national recovery teams for the East, Alaska, the Pacific States, and the Rocky Mountain/Southwest region. J. Craig was appointed leader of the Rocky Mountain/Southwest group whose jurisdiction encompassed 13 states. The team published the first recovery plan in 1977 (Craig 1977). The Plan was revised and re-published in 1984 (Craig 1984). In addition to charting biological measures to halt the decline and reestablish peregrines, the plan provided an estimated budget and recognized the need to muster public support for the falcons.

Propagation

At the outset, it was apparent that artificial incubation of wild eggs and captive propagation was fundamental to the recovery effort, and the CDOW provided partial support for Enderson's peregrine captive propagation project. In 1973 Enderson hatched the first peregrine of the *anatum* subspecies ever produced in captivity and by 1975 his facilities housed 17 breeding adults and young.

In 1973, the CDOW responded to a request from the Peregrine Fund and shipped several dozen wild prairie falcon eggs to Cornell University for use in the development of incubation techniques for peregrines they were attempting to breed. This was the beginning of a partnership that would culminate in the establishment of The Peregrine Fund western propagation facility at the CDOW Wildlife Research Station at Fort Collins in 1974. Enderson transferred his breeding stock to Fort Collins and they provided the nucleus of The Fund's western program. Peregrines were soon produced for release throughout the Rocky Mountain States.

Falcon Management

While the Peregrine Fund concentrated on producing captive stock, the CDOW focused on monitoring nesting pairs and developing release protocols to augment wild production. A substantial portion of funding for these activities was supported through a cooperative agreement with the USFWS authorized through Section 6 of the ESA.

Recycling. - The technique of recycling (double clutching) was developed by falcon breeders in the early 1970s to induce captive falcons to produce second clutches of eggs. The process capitalizes on the tendency of wild raptors to renest if they lose their original eggs during incubation. Early in the project, we observed that 2 wild pairs also renested after their first clutch failed. We successfully recycled a pair in 1976 when we removed and artificially incubated their first clutch and induced them to produce a second clutch. Recycling became a routine process in conjunction with fostering to induce wild pairs to produce additional eggs to augment young available for release to the wild (Fig. 4).

We recycled the falcons early in incubation to avoid the possibility pairs may not renest if the clutches were taken late in incubation. We also wanted to acquire thin-shelled eggs as early as possible to avoid inadvertent breakage by adults and to ameliorate abnormal water loss. The Peregrine Fund discovered that hatchability improved if the eggs had a week to 10 days of natural incubation before they were placed in incubators (Weaver and Cade 1991). Optimally, we took eggs between 1 and 2 weeks after clutch completion. Invariably, pairs relocated to another ledge and initiated egg laying within 14 days after we removed their eggs.

Between 1974 and 1990, 84 sets of eggs were taken (Table 1). Fifty-two of the pairs had their sets replaced immediately with replicas. The remaining 32 pairs were not given replica eggs, inducing them to produce second clutches. Twenty-three of the 32 recycled pairs received foster young and yielded 72 eggs in second clutches (mean = 3.13 per set). Although the mean size of second clutches of 23 pairs with known clutches was smaller than first clutches, the difference between first clutches (3.61 eggs per set) and second clutches (3.13 eggs per set) was not significant (paired t test, $P = 0.0083$, 22 d.f., $P = 0.05$). The remaining 9 pairs were permitted to keep and incubate their second clutches and although the actual number of eggs produced was not determined, we estimated that they probably produced about 30 eggs.

FIGURE 4. Jerry Craig ascending from eyrie with eggs.

Recycling was also used to augment captive production of eggs. For example, in 1986, The Peregrine Fund experienced poor production by captive birds. To supplement the reduced captive production, we recycled 5 wild pairs without returning foster young and 2 other pairs received only 2 fostered young each. In all, 30 eggs were taken into captivity yielding 23 young of which 19 were released by The Peregrine Fund elsewhere in the Rocky Mountain region. Meanwhile, all of the pairs recycled in this work successfully fledged young.

In 1990, the Peregrine Fund did not provide captive produced young for release in Colorado, but continued to hatch eggs from Colorado and returned the resulting young to the state. That year, 6 sites on the West Slope of Colorado were recycled without placement of replica eggs or young. Eighteen eggs were obtained from those first clutches and 17 young were hatched from them and placed at hack sites on the East Slope of Colorado. All 6 pairs produced second clutches but they only fledged 5 young (0.83 young per pair). Four sites produced and fledged young, and 2 sites failed to hatch their second clutches. Although the pairs experienced poor fledgling success, their actual productivity was equivalent to 3.67 young per pair when the 17 hacked young produced from their first clutches are included. The important result was to augment the

TABLE 1. Eggs resulting from fostering of Colorado peregrines 1976-1989.

Pairs Subjected to Manipulation	84
Total First Clutch Eggs Obtained	300
Pairs Recycled	32
Second Clutch Eggs Known Produced	72
Second Clutch Eggs Estimated, Not Known	30
Total Wild Eggs Probably Produced	402

species on the East Slope where few pairs remained.

Recycling also was used to relocate pairs from inferior ledges. Peregrines selected ledges that were vulnerable to disturbance (n = 4), predation (n = 1), flooding (n = 1), or were too small for a brood of fledglings (n = 5). When we discovered a poor ledge early in incubation, we took advantage of the habit of laying second clutches on another ledge. Although there was always the chance that the pair might select another inferior site, pairs usually chose better ledges. When pairs could not be recycled, we upgraded the ledge by adding rock barriers to exclude predators or expanded the eyrie area with rock slabs and gravel. We limited the visits to under one hour to reduce disturbances.

Fostering. - Fostering involved replacement of wild eggs or young with eggs or young from the breeding facility. The first peregrines fostered were in Alberta and Colorado in 1974. In Canada, Richard Fyfe removed a set of eggs causing the pair to renest. He later replaced the 2 pipped eggs with 3, 3-week old young, that successfully fledged. The same year, we also experimented with fostering. The resident female at the Royal Gorge failed to hatch her eggs in 1972 and 1973. In 1973, she flew from her eggs, perched on a grassy ledge, and laid down and rubbed her breast against the grass. Her breast feathers appeared to be matted with the contents of a broken egg. In 1974, her eyrie contained 2 eggs; 1 was dented (Fig. 5), the other cracked. We replaced the eggs with 3 from a wild prairie falcon nest. Jim Weaver of The Peregrine Fund at Cornell University was contacted and brought 2 of their captive produced peregrine nestlings to Colorado. Upon arrival, 2 peregrines were exchanged for the 2 prairie falcon chicks that had hatched (Fig. 6). Both fostered peregrines successfully fledged. However, it was too little too late for the pair. The site was abandoned after that year and was not reoccupied until 1988.

The Peregrine Fund's Fort Collins facility enabled us to increase reproduction of wild pairs through fostering. Researchers incubated and hatched eggs brought in from wild nests. On occasion, young hatched from wild eggs were added to similar age captive young to maximize the broods returned to wild pairs (Fig. 7). The captive stock was composed entirely of birds from temperate western North America, genetically appropriate for release in the Colorado region. Further, young hatched from eggs taken from the wild were sometimes held as breeders, maintaining diversity in the captive stock. The process also benefited the local wild population genetically because genes from outlying regions were infused from the captive stock.

Fostering also had research benefits. Wild eggs brought into captivity in 1972-98

FIGURE 5. Dented egg recovered from a peregrine eyrie in 1974.

FIGURE 6. Jim Enderson with nestling prairie falcon at Royal Gorge.

produced a collection exceeding 300 eggshells and whole eggs for shell thickness evaluation and pesticide analysis of egg contents. Further, adults were usually aggressive during our visits and their close approaches made it possible for us to make photographic identification records and to look for bands. In that way, adult replacement rates could be determined.

Fostering did not ameliorate normal mortality expected in rearing a brood. But it assured a normal brood size at a time when nesting pairs experienced eggshell thinning and reduced broods. Indeed, we sought to deliver large broods of 3 or 4 young at foster sites. In 1973-90, pairs that laid eggs, but were not given foster young fledged 1.8 young per pair (n = 133). Pairs that laid eggs and were given foster young in that period fledged 2.7 young per pair (n = 69). In 1977-78 five pairs failed to fledge entire fostered broods, and other pairs lost individual nestlings. From 1974 to 1989 we experienced an 80% fostering success rate (183 fledged of 229 young fostered) (Table 2).

FIGURE 7. Adult female peregrine with fostered young. She refused to leave the eyrie when the young were exchanged for the replica eggs in the foreground.

Hacking. - This was the most common method used to reestablish peregrines throughout the United States and Canada (Barclay and Cade 1983). Hacking alone established breeding pairs throughout the East and Midwest. Hacking is a centuries-old technique developed by falconers to provide experience so young falcons develop flight and hunting skills. Young birds, taken from the wild, were released from an opened loft and maintained by an attendant, who placed food where the birds could find it. Prior to the point of complete independence, the young were trapped and trained. Release by hacking was used to establish pairs at abandoned cliffs. It differed from the falconry procedure mainly in that the young were simply allowed to gain full independence and then disperse from the hack site (Sherrod et al. 1987). Hacking differs from fostering in that the former did not require the presence of a laying pair. In fact, returning falcons hacked in a previous year, or other visitors, interfered with newly released young. Hack sites were not used if adults became established on the cliff.

Hack boxes were placed by hand or by helicopter. Most were situated on steep walls well up on cliffs overlooking vast valleys, but some were placed on top of cliffs in situations that prevented easy access by predators (Fig. 8). Three sites were used only once; all young falcons were killed by great horned owls before independence at 2 of these. The entire brood was lost at two other sites, and we did not use one of these again.

Most releases by hacking efforts in Colorado were at vacant historical cliffs. Hack sites were usually operated by The Peregrine Fund under the guidance of W. Heinrich and funded through the appropriate federal land

TABLE 2. Young released and success of hacking and fostering in Colorado, 1974-89.

Method	Attempts	Young Released	Young Succeeding*	Success Rate (%)	Young per Attempt
Hacking	64	279	221	79.2	4.4
Fostering	70	229	183	79.9	3.3
Combined	134	508	404	79.5	3.8

* Young were considered successful when they became independent and dispersed.
Fostered young were considered successful when they were capable of sustained flight.

management agency. The cost to operate and staff a hack site was about $10,000. The CDOW operated 4 of 7 sites in 1988, and all sites used in 1989-90. In all, 279 young were placed in hack boxes, and of these, 221 or about 79% reached independence (Table 2). These releases occurred at 20 localities, including 12 east of the Continental Divide.

Excluding the 3 sites used once, sites were operated on average between 3 and 4 times, and the maximum was 8 years in a 9 year span. Excluding 1978, when the first site was activated in Rocky Mountain National Park, an average of 5 sites was operated annually. Most of the hack boxes are at least 20 years old.

Ultimately, availability of young dictated the release techniques. Each season, early nestlings produced by The Peregrine Fund or those hatched from eggs that we obtained from the wild were used for fostering to wild peregrines. Young produced later in the season either in captivity, or as the result of recycling, were hacked.

FIGURE 8. Recently released young at hack box. The barred front of box has been removed.
Photo courtesy Mark Robert

Hack sites on buildings, bridges, and other structures were used routinely in the Midwest and eastern United States. Of the 20 Colorado hack locations, only the Denver site was urban. By 1987, the known peregrine population in Colorado had increased to 23 breeding pairs of which 3 were on the East Slope. Releases were then shifted to that region. In 1988, young falcons were released at 6 hack sites on cliffs. The office building at Colfax and Broadway in downtown Denver was selected as an additional release location to educate the public about an endangered species recovery effort (Fig 9). The falcons were an almost daily media event. A camera outside the hack box provided local television stations video material and a monitor at street level enabled the public to see the falcons. A display on the project was placed in the main atrium of the Denver Museum of Natural History. A corps of volunteers managed the releases which were maintained through public donations.

In 1988, all 5 falcons (3 females and 2 males) that were released in Denver achieved independence. Of the 5 released in 1989 (4 males and 1 female), 2 suffered injuries from collisions with buildings. One male lost vision in an eye, and a second male fractured a leg. Neither could be released to the wild.

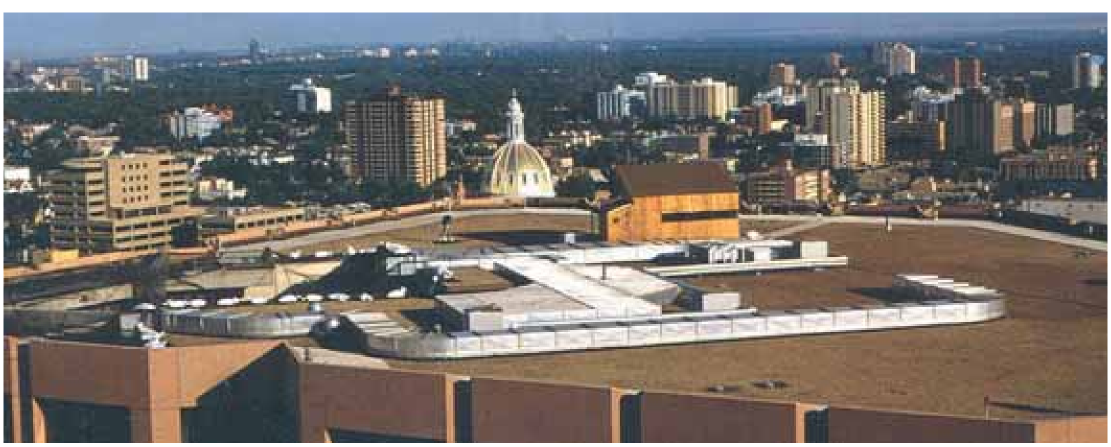

FIGURE 9. Hack site on a building in downtown Denver. The hack box is affixed to the left side of the wooden structure enclosing the roof access. Netting has been placed over the air conditioner bay to exclude the young falcons.

The Peregrine Fund estimated that 14-16 young, on average, had to be released to establish a pair of peregrines at a location. Only 8 young successfully achieved independence in Denver. At least 2 more years of hacking may have been required to establish a pair. Volunteers in Denver reported a number of peregrine sightings throughout the first half of May 1990 in the vicinity of the release site. These included 2 adults and a subadult. The 1990 metropolitan release was suspended because a female from the 1988 release was frequenting buildings adjacent to the hack site. The Peregrine Fund advised against attempts to release young in her presence because their experience suggested that she would interfere. By 1991, the East Slope population had increased to 17 occupied territories. All augmentation and release activities were discontinued statewide.

Falcons released in Denver have not been documented at other wild territories in Colorado. Although the public expected to have falcons breeding in Denver, the project was a success in other ways. It certainly increased public awareness of wildlife and in particular, peregrines. The effort demonstrated that technical biological tasks could be assigned to the public with professional guidance. The Denver project served as a prototype for other volunteer efforts undertaken by the Division.

Cross-fostering. - This technique involved replacing broods of one species with broods from another species. The young were adopted by their foster parents and reared and fledged. One concern was that the young might imprint upon the foster species and years later attempt to mate with others of that species. Cross fostering to prairie falcons was used in 1981-92 to reintroduce peregrines in California (Kirven and Walton 1992). In Colorado, the logical species to serve as foster parents for peregrines was also the prairie falcon.

E. Freienmuth attempted cross fostering at the 2 prairie falcon eyries in 1979. Three young peregrines were placed in each eyrie and were adopted by their foster parents. The first site was a pothole with a sloping ledge in front and the young were vulnerable as they scrambled across the ledge when prey was delivered. Two young fell from the eyrie and 1 survived the fall. The remaining chick was removed and replaced with 2 prairie falcon young. Both prairie falcons also fell or were frightened from the site, and we abandoned the effort. The second pair of prairie falcons initially received 3 young. The brood was augmented with the 2 survivors from the other cross-foster attempt. Two nestlings succumbed to a blood parasite (*Leucocytozoon sp.*) carried by black flies (*Simulium sp.*). The other 3 fledged successfully. No subsequent sightings or band recoveries were obtained from the 3 cross-fostered peregrines.

A prairie falcon formed a mixed pair with a peregrine in north-central Colorado. The site had been occupied by adult peregrines that successfully fledged young from 1983 through 1987. In 1988 the female peregrine was replaced by an adult female prairie falcon. The male peregrine continued to court and maintain a pair bond with the prairie falcon and she successfully defended her territory over 4 years although no young were produced. The prairie falcon was replaced by an adult peregrine in 1992 and the pair fledged 3 young. Although the prairie falcon was not trapped and examined for bands or markers, we speculate that she may have been produced in captivity in Utah. In 1987, a female prairie falcon drove away the resident female of a pair of incubating peregrines at a hack tower in Ogden Bay. The falconer's marker on her leg confirmed that she had been reared in captivity with peregrines (cross-fostered). After her capture, the resident female peregrine returned and continued to occupy the site. The prairie falcon was transported and released in Nebraska that same summer. It is possible that this aggressive prairie falcon moved westward into Colorado and displaced the female peregrine in 1988.

A captive produced gyrfalcon/peregrine hybrid successfully drove away an adult female peregrine at a central Colorado territory in 1996. The hybrid laid 2 infertile eggs. Soon after a climber caught her on her eggs and removed her, the resident female peregrine returned and was courted by her original mate. The pair laid 2 eggs and hatched 1 young. The hybrid had belonged to a falconer who originally lived in the vicinity, then moved to California. He alleged she escaped there. If so, she found her way back to Colorado.

Results of Fostering and Hacking

Size of the releases. - Although the first fostering was done in Colorado in 1974, the program began in earnest in1976, 2 years prior to the initiation of hacking. Both types of release were essentially concurrent (Fig. 10), and both used young that were captive bred, or hatched in captivity from eggs taken from wild pairs early in incubation in an effort to circumvent egg breakage in eyries.

Four hundred and four young were released successfully by fostering and hacking. The success rate was about 80% for either method, but hacked young were considered successful when they reached independence about 4 weeks after fledge (Table 2). Fostered young were considered successful when they reached flying age at 40-43 days.

From 1973-81, site occupancy continued to decline until all East Slope sites were vacant by 1982. Fostered young were used to augment the remaining West Slope sites while hacking attempted to restore falcons to vacant cliffs on the East Slope. Fostering occurred at 21 territories, only 6 of which were east of the Continental Divide. Out of 64 total attempts, East Slope sites received fostered young only 16 times. About 32 fostered young fledged east of the Continental Divide, compared to about 152 young successfully hacked in the same region.

Fostering (Appendix 2) began in 1976 and continued through l989 in Colorado (Fig. 10), and 183 young were fledged as a result (Table 2). Of those, 90 young were fledged by 10 females for whom we have information about tenure on territory. Those females were present mainly from 1 to 4 successive years, but one female was present for 7 years and fledged 21 fostered young.

None of the 10 females given broods in this subset failed to fledge some of the young in any of the 32 attempts. In all, 2.8 young were fledged per attempt. In contrast, females not fostered in the 1980-89 period fledged 1.8 young per attempt. Fostering

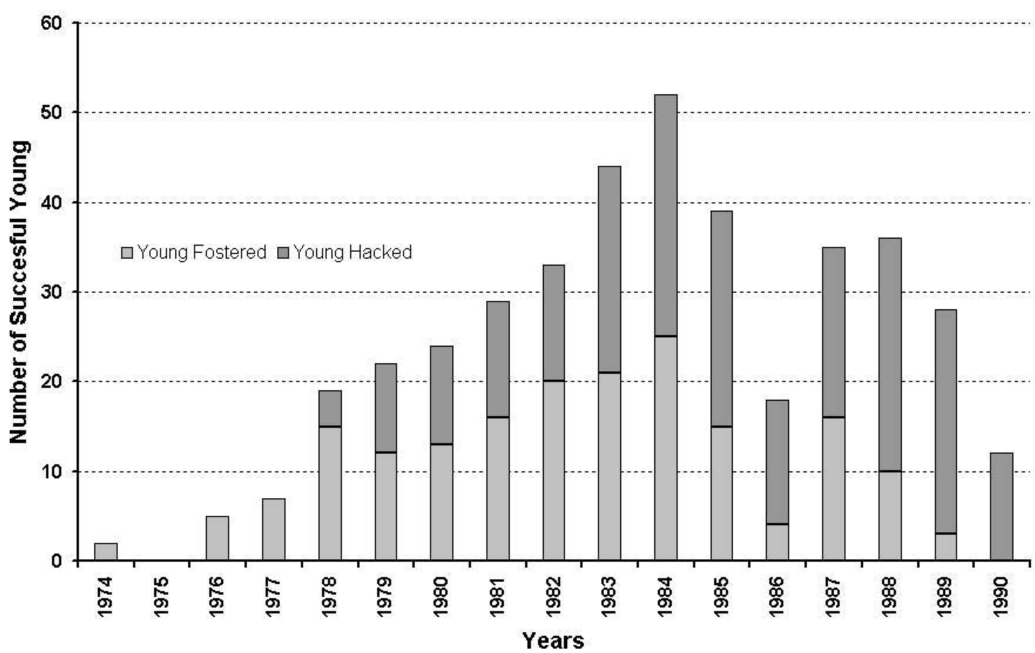

FIGURE 10. Number of young peregrine falcons successfully released to the wild. Fostered young were considered successful when they attained sustained flight. Hacked young were successful when they dispersed from the hack site.

apparently resulted in a net gain of about one young per female attempt.

From the perspective of males, 5 peregrines in the subset fledged 56 young in 19 attempts, or 2.9 young per attempt. As in the case of females, the net gain for those males averaged about one young. No male failed to fledge young in any attempt.

These gains in productivity through fostering may seem modest, but they represent a gain of over 50%. Gains may well have been even greater in 1976-79, a time when natural reproduction was spotty because of eggshell thinning. This gain probably created an excess of young beyond replacement needs.

Population Increase. - Most releases of peregrines in Colorado preceded the increase in known individuals on territory (Fig. 11). Prior to 1978 the releases were mainly of an experimental nature and were too few to have measurably affected the population. From 1978 onward releases increased until the mid-1980s.

The presence of banded released birds among the pairs on territory became substantial in the mid-1980s (Fig. 12). A few banded birds appearing on territory were yearlings, but most were at least 2 years old. Prior to the mid-1980s most of the banded peregrines appearing on territory must have been released birds because fostering and hacking had been well underway since 1979, and only 14 wild young and 3 adults were banded by 1985.

Two questions arise in regard to the effects of releases which totaled 339 by 1986. First, why was no upward trend in breeding population apparent until the end of the period? Second, why did banded adults not appear on territory in any numbers until 1986? In regard to the first question, perhaps we failed to detect an increase despite a moderate level of annual surveys. Although all potential habitats were not rigorously surveyed during this period, all previously occupied sites on record were checked annually. For example, in 1986 only 19 out of 38 sites on record were occupied and we investigated 37 other potential nest cliffs all of which were occupied in subsequent years (1987-2001). If peregrines were breeding at unknown locations around the state at the time, a significant portion of them should have been discovered. In fact, only one new pair was found at the potential sites that

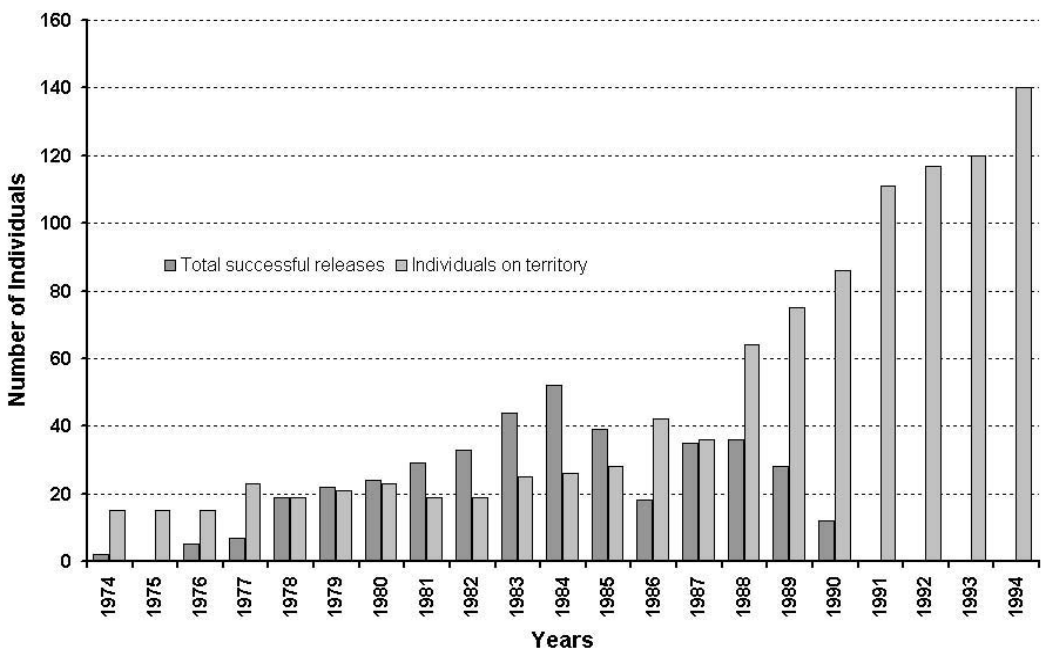

FIGURE 11. Young peregrines successfully released by hacking and fostering combined compared to individuals found on territory.

were surveyed. Low survivorship of released birds was not likely since fostered young were reared by wild pairs and would have similar opportunities as other wild young. Prompt assimilation of hacked young into the wild was evident in the reestablishment of the eastern peregrine population. We suspect dispersal to other regions is the most likely answer to the second question. On their spring migration, Colorado falcons must have passed through territories of resident birds and may have filled vacancies south of Colorado. The lack of banded released birds at eyries prior to 1986 could also be the result of this. Population expansion undoubtedly occurred in adjacent states at about the same time and immigration into Colorado would increase the proportion of unbanded birds.

Discovery of Peregrine Eyries. - At the onset of systematic surveys and management of peregrines in Colorado in 1976 about 26 nesting locations were on record, of which about 18 were known from the mid-1960s (Enderson 1965). In the decade prior to 1976, historical sites were visited in most years, but searches of other potential peregrine cliffs were few. In 1976 the CDOW initiated systematic visits to known sites and as time permitted, visits to other likely cliffs. That pattern of survey continued right through to 2000 without interruption, and the number of locations known to have been used by pairs of peregrines grew to 136.

The searches of likely cliffs, in hopes of discovery of peregrines, were called surveys, as opposed to visits to cliffs known to have been used before by a pair. In this analysis a pair might have been, uncommonly, a mixed pair including an adult and a yearling, or usually a pair of adults. In any case, a pair on territory resulted in an occupied cliff, even though an outsider could displace yearlings or adults.

The number of territories used by pairs annually depended on 1) the number of pairs returning to territories that were occupied the previous year, 2) the disappearance without replacement, of one or both members of the pair from the previous year, 3) the number of pairs re-establishing territories at cliffs known to have been vacant the previous year, and 4) the discovery of pairs at survey cliffs where peregrines had not been known. Pairs in the latter two situations were collec-

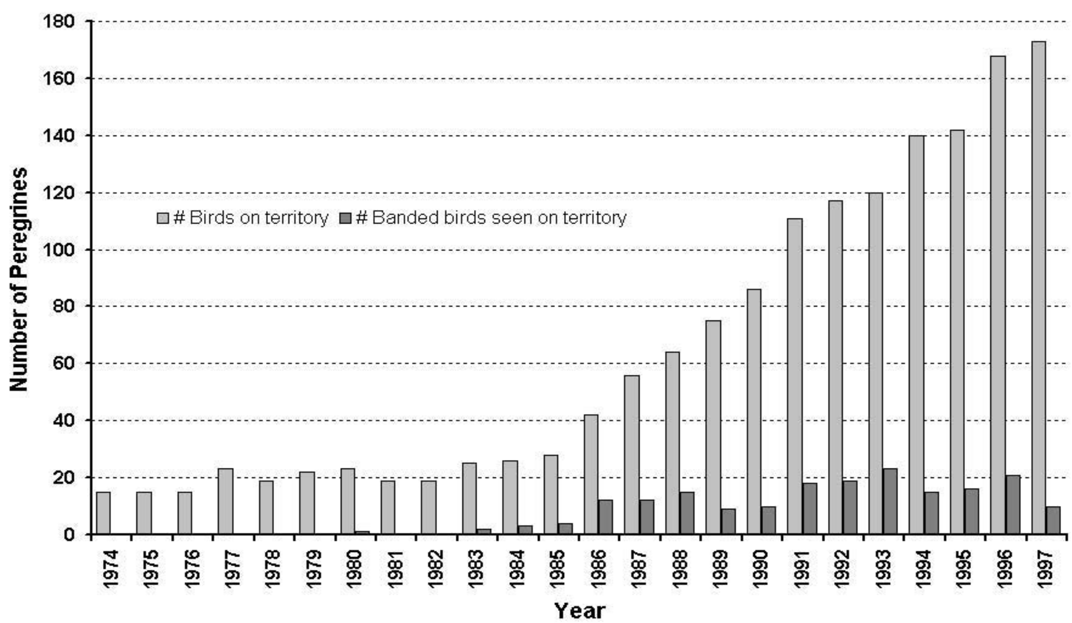

FIGURE 12. Banded peregrines seen on territory compared to all birds seen on territory.

tively called new pairs. The identity of individual pair members was not considered, and was poorly known in later years.

Surveys of likely cliffs were not systematic. Potential peregrine eyries came to light as our experience grew in the mountainous western one-half of the State. A number of territories were confirmed after cooperating agencies (BLM, USFS and NPS) reported sightings of peregrines. Known territories, occupied or not, were given priority not just in regard to nesting success, but also concerning the timing of nesting to facilitate fostering of additional young. Field teams (Appendix 4), usually of 2 people, visited survey cliffs when logistics, weather, and work load permitted. Further, the effort made at each survey cliff varied because of similar constraints, the presence of excrement marks ("whitewash"), and the overall impression of the observers. Over the years, some survey cliffs were visited from one to 16 times (Table 3). Peregrines were not found at many seemingly suitable cliffs, but sometimes pairs were found on the first visit. Although 41 sites were found occupied on the first survey, 16 sites received 8 or more annual visits before occupancy was discovered. None of the potential territories was visited each year without break, although one site was surveyed 16 times over a 19-year span before it was found occupied. The actual year of reoccupancy could not be established for many of the survey sites.

From 1976-2001, the number of cliffs surveyed annually varied between 6 and 122 (Fig. 13). Generally, these searches resulted in little discovery prior to the mid-1980s. From 1996 to 2001 when field crews were busy visiting the many known territories, relatively few survey cliffs were visited. Nevertheless, the success rate in that period was much higher than in any other comparable period. Apparently many cliffs were newly used in that period. An alternate view of reoccupancy is provided in Figure 14 which traces occupancy of 40 sites that were unknown prior to 1980. Although peregrines were not discovered on initial surveys, cliff features suggested that they could be occupied at a future date. These sites were revisited intermittently from 1980 through 2001 as schedules permitted. However, 2 sites were visited annually for 12 years before occupancy was confirmed and 2 other sites received 10 and 9 annual visits, respectively, before pairs were found. Overall, 192 search visits were made to the 40 sites over the 22 year span (0.4 visits per site year). The pattern of colonization of these potential sites confirms that population expansion truly occurred and was not created by discovering previously existing pairs.

Increases in known pairs. - The total number of pairs on territory, and pairs on territory used the previous year increased steadily after the mid-1980s. The latter event signifies mainly the reestablishment of adult pairs linked to a cliff, a reliable measure of population growth (Fig. 15). Equally impressive in the mid-1980s was the decline in the loss of pairs from territories occupied the previous year (Fig. 16). The decline of loss rate may have been due to an increasing supply of peregrines reaching breeding age or because of a non-breeding adult component in the population called "floaters" (Hunt 1998) so that when individuals died or relocated elsewhere, they were immediately replaced by "floaters".

Table 3. Number of visits made to survey potential nest cliffs in Colorado 1973-2001. All cliffs were either occupied on the first visit or in subsequent years.

Years Visited	Cliffs Visited
1	41
2	18
3	19
4	9
5	3
6	4
7	3
8	1
9	2
10	3
11	5
12	3
13	1
14	1
15	0
16	1
Total	114

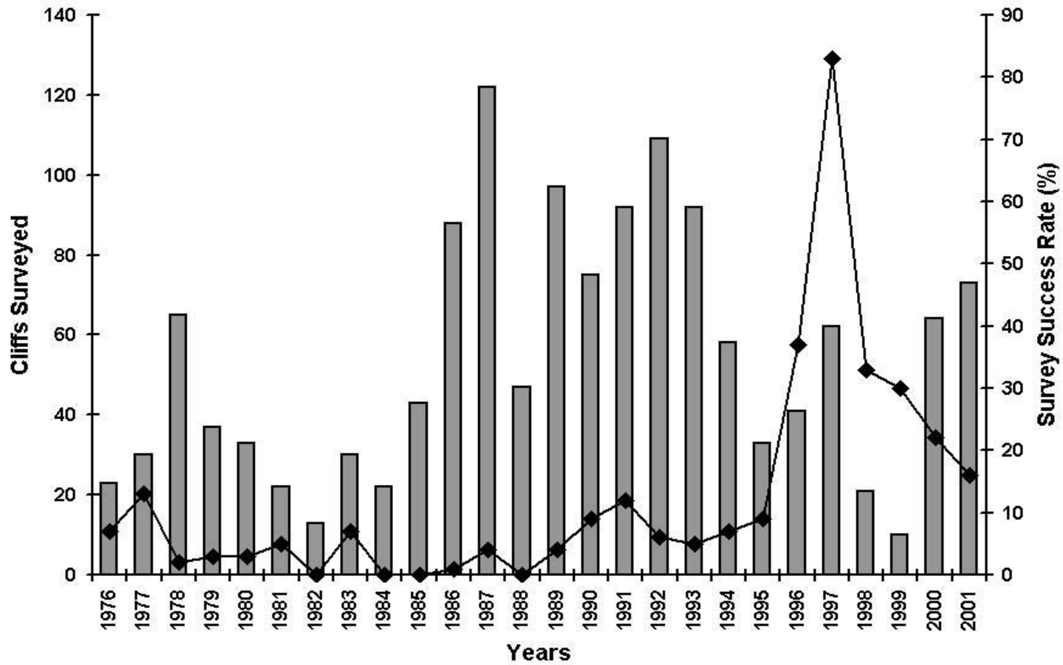

FIGURE 13. Number of potential nest cliffs surveyed in Colorado.

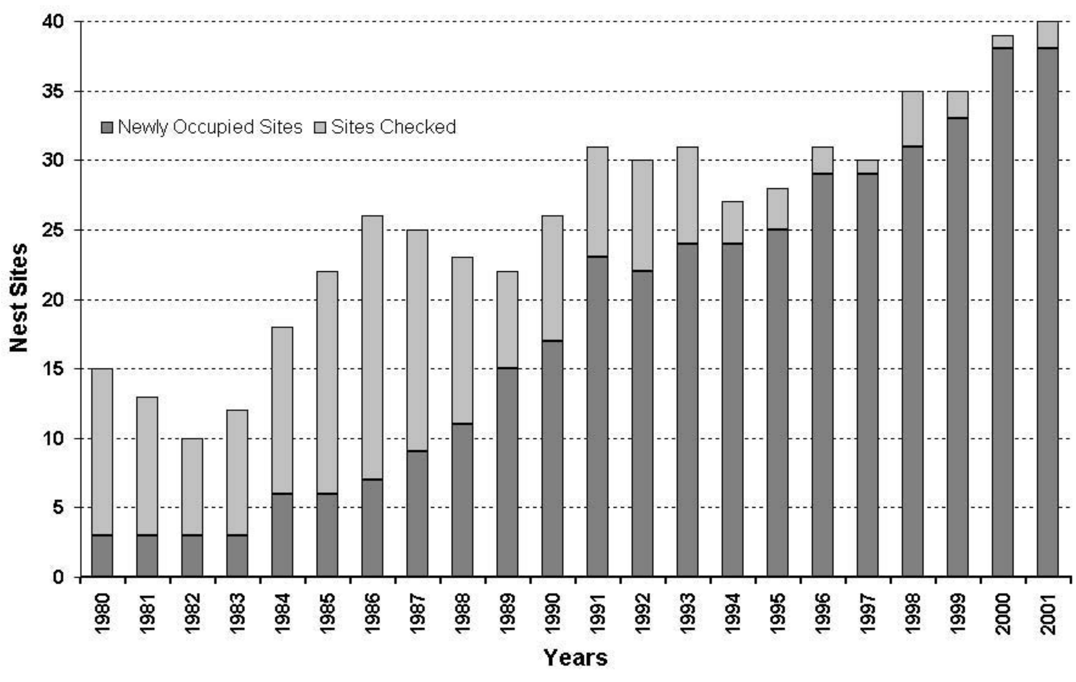

FIGURE 14. Occupancy of 40 nest sites unknown prior to 1980 and discovered in subsequent years. Surveys were intermittent and accomplished as schedules permitted.

The number of pairs seen on territory sharply increased after 1985 (Fig. 15). The potential for further increase is good. No peregrines have been observed at 380 survey cliffs visited. Some were perhaps not suitable because of small size or lack of suitable nest ledges. Some may be vacant because they are within territories of other pairs. Further, prairie falcons and golden eagles were found at 25 and 21 of these cliffs, respectively. Peregrines may displace the former, but perhaps not the latter. No doubt other cliffs occur in places where our access was poor. It seems clear at least 250-300 potential peregrine cliffs occur in Colorado far enough away from existing pairs. Many of these have not been examined in the last few years; some may already be in use. In any event, there is opportunity for the discovery of new territories in Colorado.

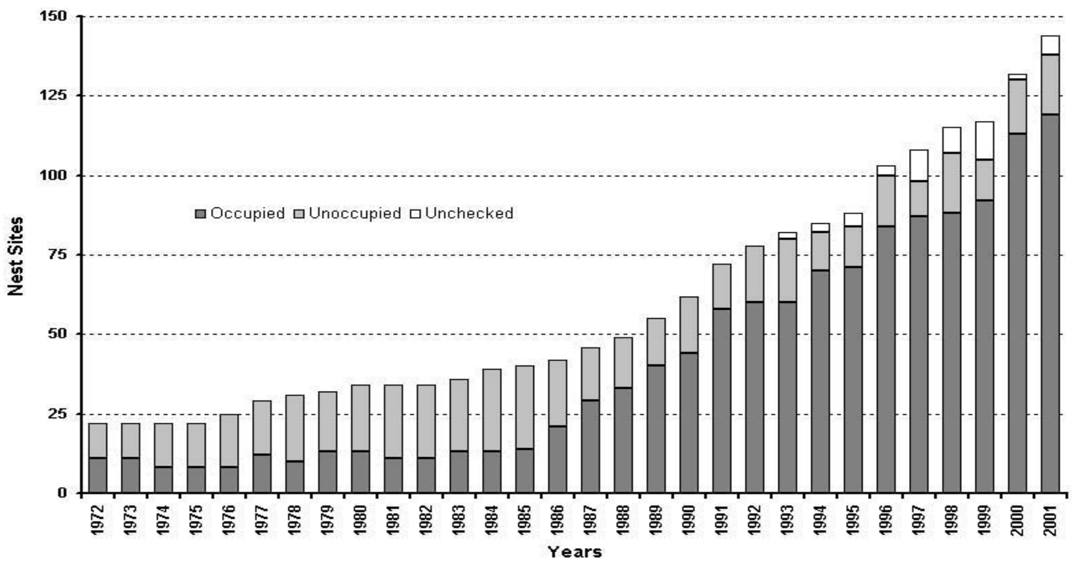

FIGURE 15. Peregrine falcon population expansion in Colorado.

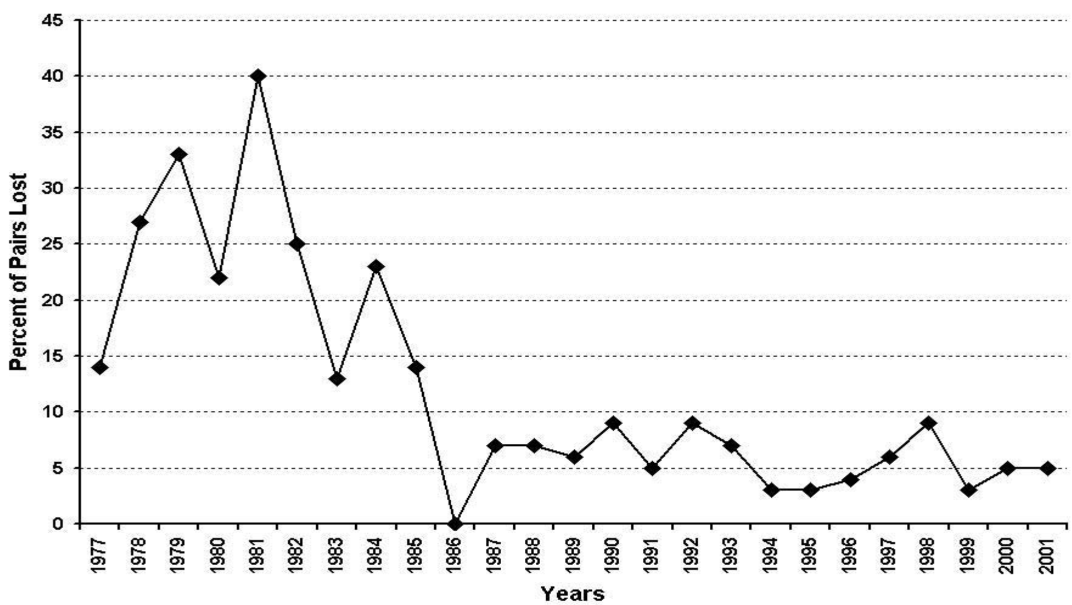

FIGURE 16. Annual loss rate of pairs from territories used the previous year. A pair was considered lost when a site held one or no adult after a year when a pair was present.

NATURAL HISTORY

Breeding Chronology

Although actual initiation of egg laying was infrequently observed in the field, we were often able to back-date by estimating chick age. In most cases the chicks were aged to within a day or two from a photographic guide (Cade et al. 1966). In this manner, initiation of egg laying in first clutches was determined in 620 cases in the period 1991-2001 (Fig. 17). Although known renestings were eliminated from consideration, some late nesting recorded as first attempts may have actually been second attempts. However, a number of sites under regular observation did initiate first clutches in late April and early May. Generally, eggs hatch after 33 days of incubation, and nestlings fledge at 42 - 44 days of age, so we also generated similar curves for hatch and fledge dates (Fig. 18).

Nesting Habitat

Cliff prominence. - Peregrines frequent imposing cliffs. Newton (1988) thought cliffs overlooking surrounding lowlands (dominant cliffs) were preferred because of the height advantage when hunting, pursuing

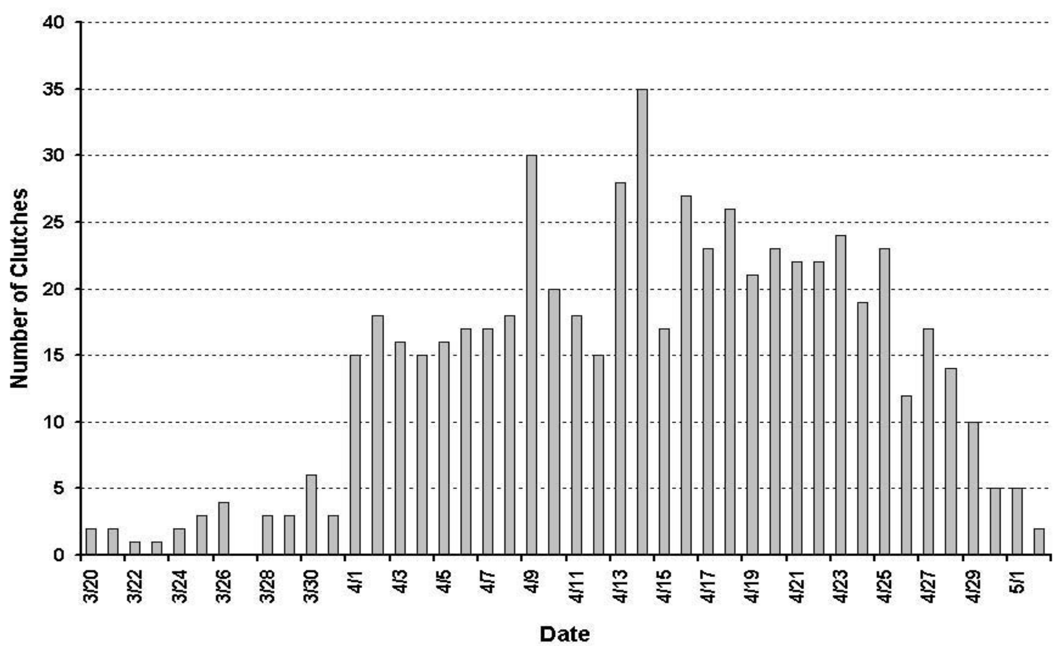

FIGURE 17. Initiation dates of first clutches for Colorado peregrines (n = 620).

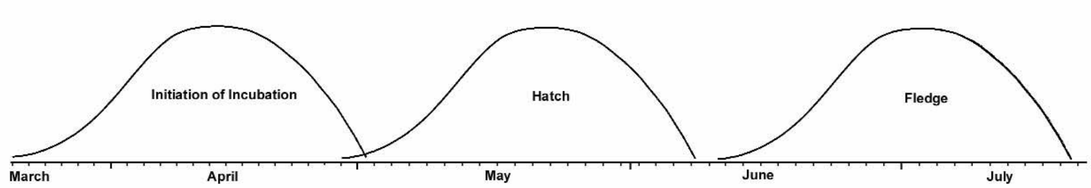

FIGURE 18. General breeding sequence of Colorado peregrines.

prey, defending against interlopers, and courting prospective mates. Hickey (1942) called cliffs "ecological magnets" and ranked them in 3 classes. First class cliffs were "extremely high, often rather long, usually overlooking water, and generally dominating the surrounding countryside." These cliffs were rarely vacant. Second class cliffs "differ merely in their (lesser) dimensions" and may be abandoned indefinitely if both adults are lost. Third class cliffs were marginal "small, not very high" and would be permanently abandoned with loss of one member of the pair. Hagar (1969) and Rice (1969) used a similar classification.

We subjectively ranked Colorado nest cliffs according to prominence over the surrounding terrain (a rank of 1 was the most prominent). Figure 19 shows examples. In general, highly ranked cliffs possessed faces

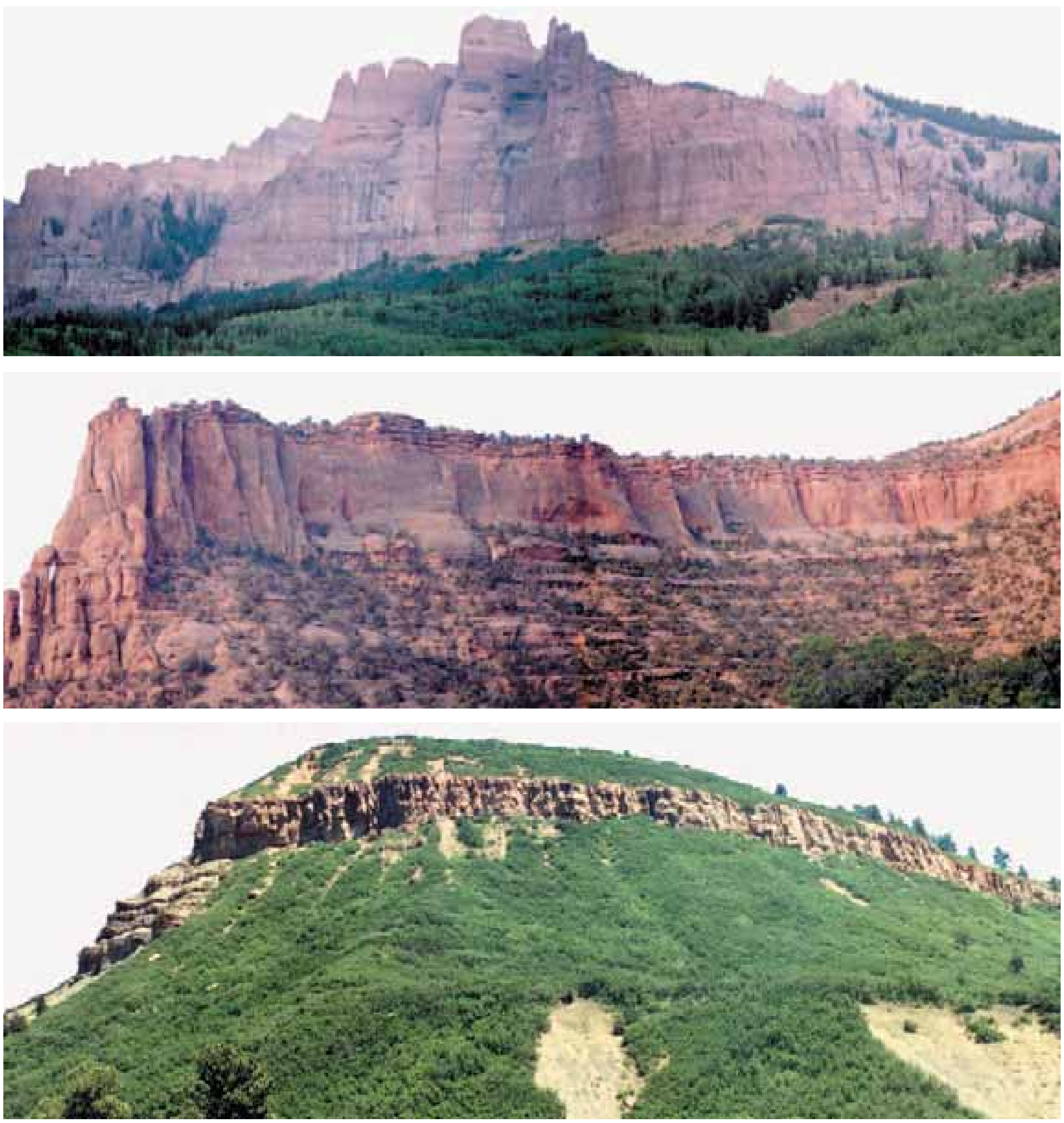

FIGURE 19. Examples of peregrine nest cliff dominance. Tall first class site in montane region(*top photo*). Sixth class cliff in piñon-juniper habitat (*middle photo*). Eighth class cliff on low mesa in brushland habitat (*bottom photo*).

Top two photos courtesy Terry Meyers

exceeding 425 feet (130m), offered an extensive panorama and tended to dominate surrounding topographic features. Length of the cliffs was not an important factor. Cliffs lining a gorge 1,300 feet (400 m) deep may not project above the surrounding terrain, but are dominant features and may serve to concentrate and expose prey. Therefore the walls of gorges and deep canyons often received high ranks. Mid-ranked cliffs were 100–200 feet (30-60m) with limited panoramas. Lowest ranked cliffs were not tall (usually less than 30m) with little or no panorama.

We ranked nest cliffs (n = 138) and tabulated tenure of use for each rank. In Colorado the abundance of cliffs are inversely related to rank. Large cliff faces that dominate the terrain are relatively rare while small cliffs in less prominent locations are abundant. Peregrine occupancy was directly related to prominence (Fig. 20). We cannot discount completely a bias due to searches of high ranking cliffs, especially in the early years of this study. Low ranking cliffs probably received less survey attention throughout the study, so discoveries of nesting pairs on low cliffs might have been biased downwards.

During the extirpation of eastern peregrines, Hagar (1969) noted that superior cliffs were last to be abandoned. When we began our investigations in the 1970s, the Colorado population had already declined, so we could not detect a pattern of desertion. In the late stages of decline (1973-80) only 64 occupancy-years accumulated over a 7 year period. Peregrines were limited to sites ranked above 5, with about 87% of the occupancy on truly dominant cliffs. The relationship shifted during re-occupancy (1990-2001). We examined the pattern of preference for cliffs by comparing the frequency of occupancy of ranked cliffs (n = 23) during the period of population depression (1973-80) with the period of re-occupancy (1990-2001) (Fig.21). Occupancy-years totaled 942 in this 12-year interval with 19% of the pairs at sites ranked 6 or lower. Dominant cliffs (rank 3 or above) still accounted for two-thirds (67%) of the sites occupied. Occupancy included more small cliffs in later years.

Settings of cliffs. - Landforms of nest cliffs and surrounding areas fell into 4 somewhat overlapping categories (Fig. 22). 1) *Rampart and Mesa:* These were dominant mountain masses that rose above the surrounding terrain within several miles, whose cliffs were often visible from tens of miles away. Ramparts are associated with foothills or mountain sides while mesas are independent landforms. 2) *Canyon:* These were U-shaped in cross-section, usually less than 0.75 miles (1.2 km) across and typically less than 1,000 feet (300 m) deep. Cliffs may be individual, or continuous along one or both sides. Canyons tend to interconnect into sys-

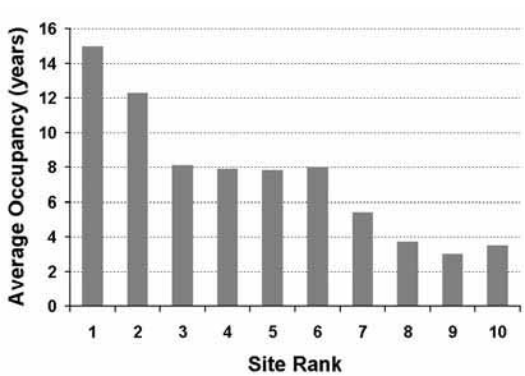

FIGURE 20. Occupancy of peregrine nest sites ranked by cliff dominance. Ranking proceeds from one (highest) to ten (lowest).

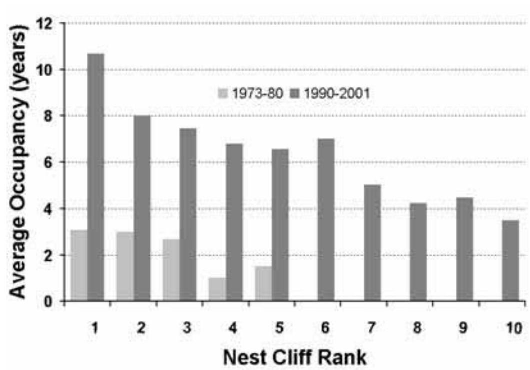

FIGURE 21. Occupancy of cliffs (n = 23) during period of low population (1973-80) compared to period of reoccupancy (1990-2001) in relation to cliff dominance rank. Ranking proceeds from one (highest) to ten (lowest).

tems. 3) *Gorge:* Steep, narrow V-shaped cross-section, these chasms were usually less than 0.75 mile (1.2 km) across with depths exceeding 1,000 feet (300 m). Gorges may interconnect with canyons, but were singular and generally did not exceed 1 to 2 miles (1.6–3.2 km) in length. 4) *Valley:* The broad U-shaped profile was usually over 1 mile (1.6 km) across, depth varied from several hundred to several thousand feet.

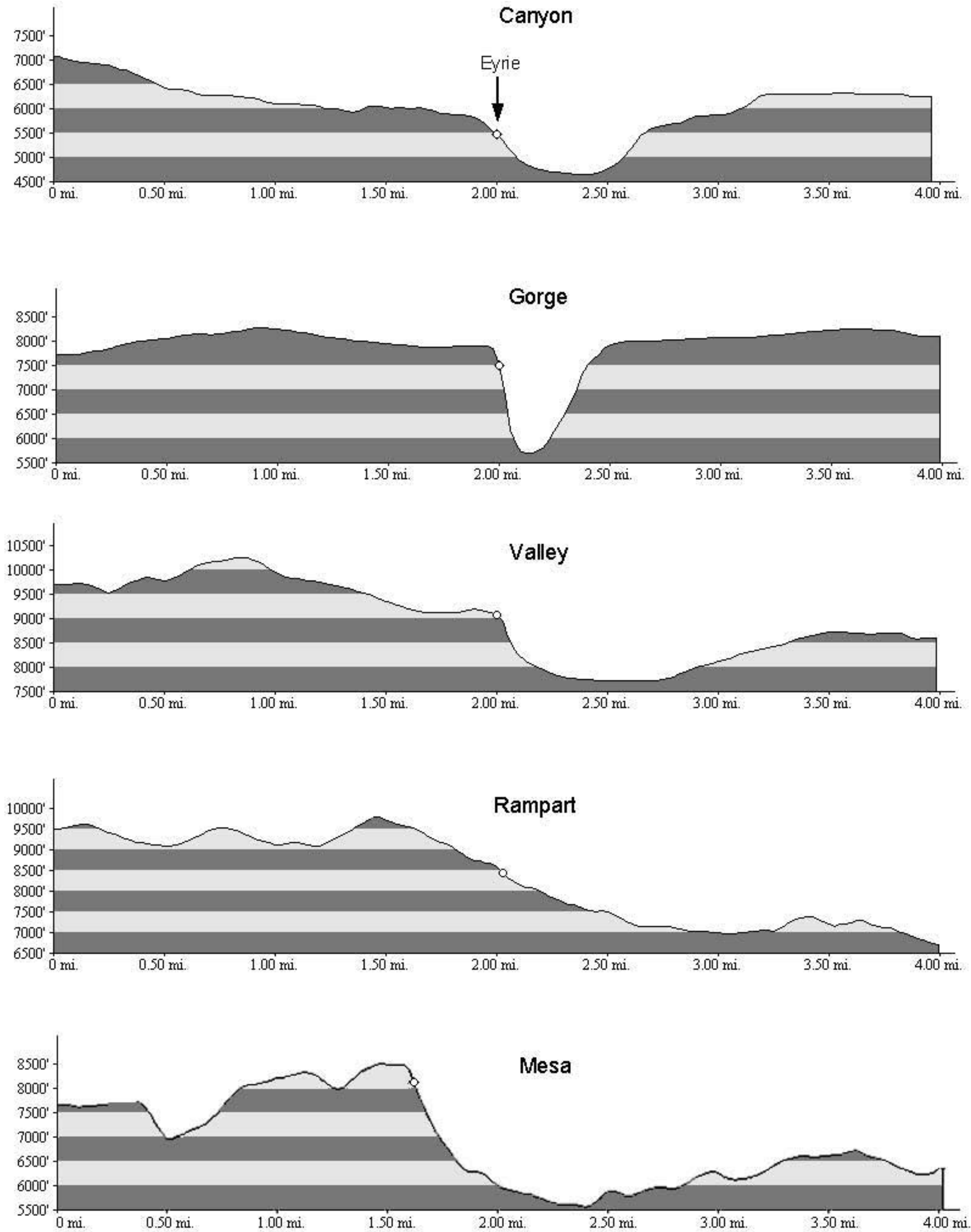

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FIGURE 22. Typical relief profiles of nest cliffs.

Cliffs were outcrops, intermittent or continuous. Average occupancy of cliffs on the 6 landforms used throughout the investigation (1973-2001) was similar and is compared in Figure 23. Gorges were the least abundant landform (8) but had the longest average tenure (9.9 years) followed by canyons (9.8 years). Valley sites were most abundant (59) but tenure was similar to mesas and ramparts (7.6, 7.8 and 7.7 years respectively).

Grebence and White (1989) examined physiographic characteristics of peregrine nesting habitat along the Colorado River in Utah and could not detect significant differences in any features but nest exposure (azimuth). This is not surprising since their sample was limited to a relatively small elevation range and all cliffs had similar geology in a canyon setting. Our experiences with nests (n = 139) over a wider range of landforms, geology and elevations suggest Colorado peregrines nest with greater fidelity in gorges and canyons (Fig. 23).

Cliff orientation. - Several investigators have evaluated the influence of cliff orientation on nest selection. Grebence and White (1989) observed a preference for Utah cliffs facing in the eastern quadrant (45-135º) and hypothesized ledge selection ameliorated solar radiation in a desert environment. Cade (1960) observed that Alaskan nests had exposures protecting them from storms from the north. Kuyt (1980) theorized that Northwest Territory peregrines selected southern and western exposures where those ledges were free of snow early in the nesting season.

In 1979 we examined the orientation of nesting cliffs and found no pattern in regard to exposure (Enderson and Craig 1979). However, at the time, the sample was relatively small (32 sites were on record). We revisited the question and examined the orientation of 411 cliffs used by peregrines in Colorado from 1973-2001. Cliff locations were plotted on 7.5′ topographic maps and orientations were determined by taking a bearing (cliff azimuth) 90 degrees from an axis parallel to the face of the nest cliff. Where a ledge was located in an alcove or on a cliff facet, the bearing was adjusted to reflect the orientation of the alcove or facet.

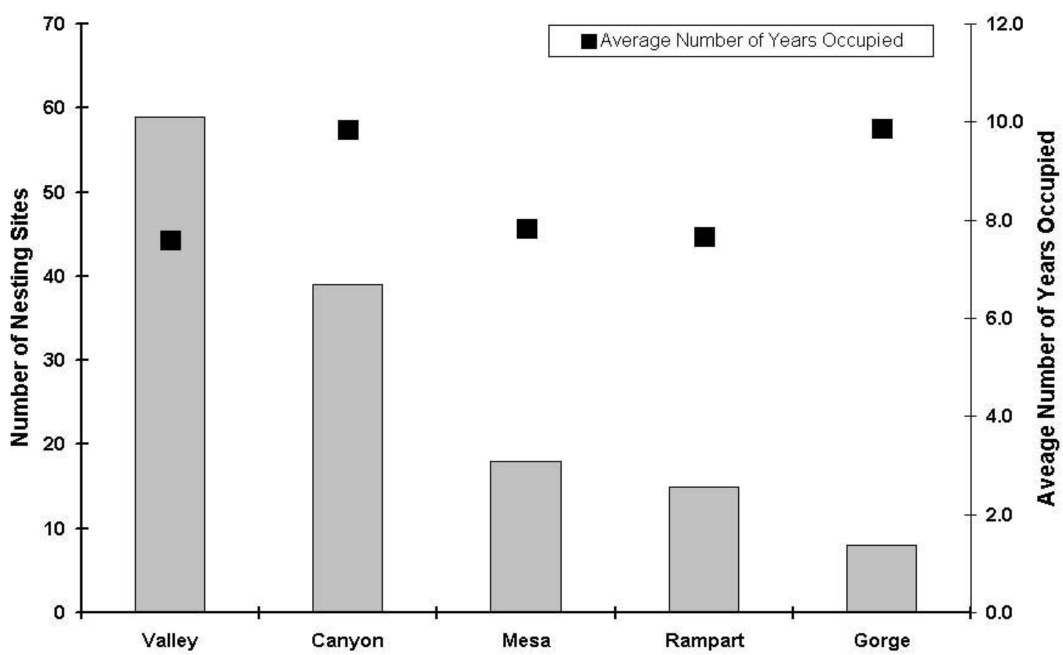

FIGURE 23. Peregrine occupancy of nesting sites in five different land forms.

Overall, peregrines tended to use ledges with southern exposures (Fig. 24). However, when cliff orientations were stratified by elevation, a pattern emerged (Fig. 25). At the lowest altitudinal range of 4,500 - 6,000 feet. (1,371-1,828 m) northern exposures were prominent. Exposures were in nearly all aspects in the 6,000-7,500 feet (1,828-2,286 m) range but in the 7,000 - 10,500 feet (2,286 - 3,200 m) elevations, aspects were mainly southerly to easterly. Perhaps the latter is explained by protection from adverse temperature and wind in a region where prevailing weather flows from the northwest. At higher elevation, ledges with a southeastern exposure also offer the advantage of solar heating.

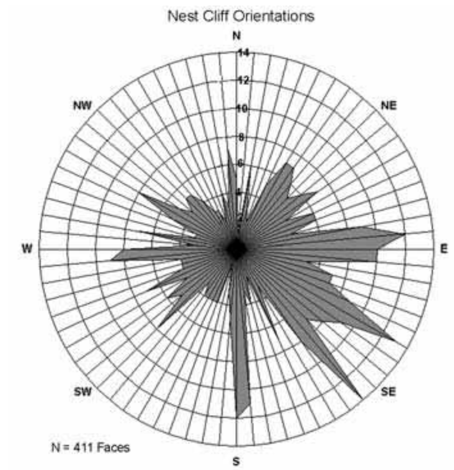

FIGURE 24. Orientation of all peregrine nest cliffs in Colorado. Most sites offered more than one cliff face and pairs selected multiple orientations during their tenure.

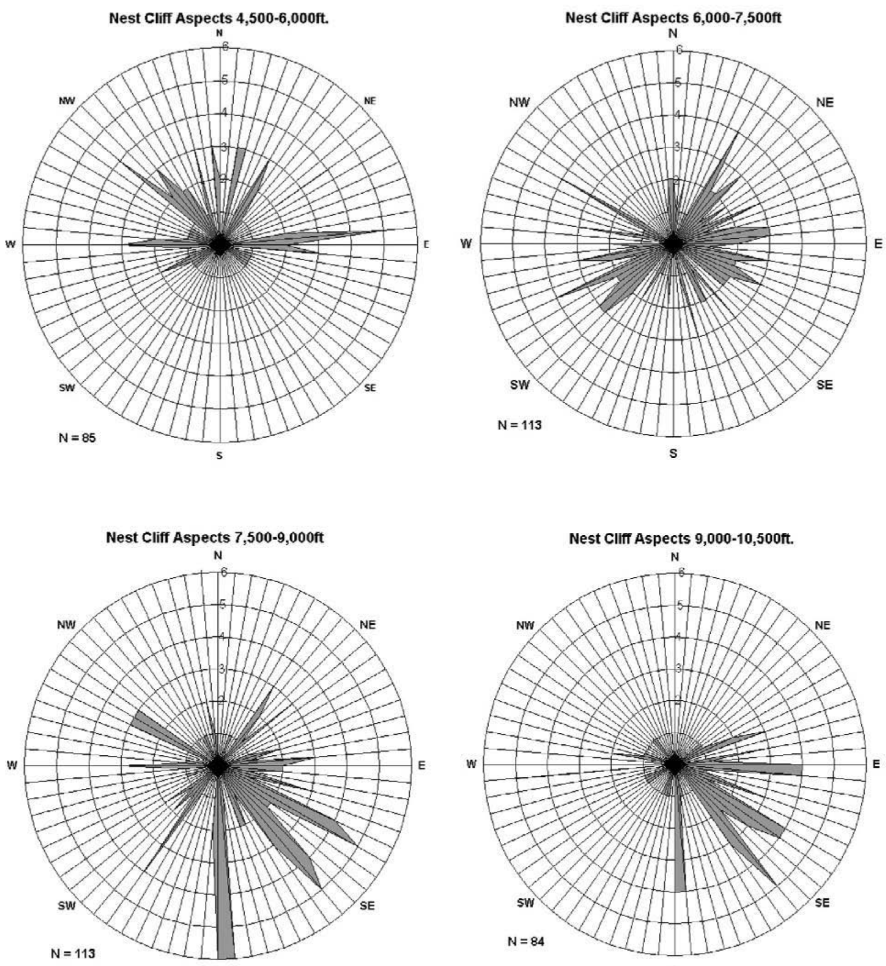

FIGURE 25. Orientations of peregrine nest cliffs stratified by elevation intervals.

Nest ledges. Although peregrines had a high fidelity for the same nest cliffs throughout their lives they may occupy several eyrie ledges on the cliff complex (Hickey and Anderson 1969, Ratcliffe 1993). We encountered a variety of nesting situations including potholes, overhangs, exposed ledges and abandoned nests of golden eagles and ravens (Fig. 26). Abandoned cliff nests of ravens and golden eagles were used on 16 of 922 nesting attempts during 1981-2001. Eleven abandoned golden eagle nests were used on 29 occasions while 5 common raven nests were used 10 times. Two pairs of falcons occupied eagle nests for 8 and 7 consecutive years, respectively. At both sites, it appeared that there were few nest ledges.

Eyrie ledges may be selected that provide protection from the elements and terrestrial predators, and possess a substrate for the falcons to scrape a depression for their eggs. Therefore among the various ledges that were available on an escarpment, it was not surprising that the number of suitable ledges would be limited. Certain ledges were reused over subsequent years, but many pairs seemed to shift annually to different ledges. We investigated the use pattern by selecting 34 sites that were occupied for at least 10 years (Fig 27). Sites with at minimum 10 year occupancy history were selected to avoid a bias toward brief ledge use that would occur with recently established pairs. Cumulatively, the sites averaged 14.5 years of occupancy. One site had hosted a nesting pair for 25 years. Previously unoccupied ledges were selected 60% of the time (153 cases), and ledges were reused a second time in 46 instances (19%).

FIGURE 26. Examples of nest ledges used by peregrines (*clockwise from top*). Pothole (*Photo courtesy Terry Meyers)*. Abandoned golden eagle nest. Abandoned common raven nest. Open ledge without ceiling. Ledge with ceiling.

Repeated use of the same ledge beyond 3 years occurred only 32 times.

The 34 sites with at least 10 years of nesting history averaged 8 eyrie ledges per site which was identical to the British Isles (Ratcliffe 1993). The number of nest ledges per site varied from 2 to 19. Pairs present at the site with only 2 eyrie ledges used 1 ledge 12 times over a 15 year span. The site with 19 different nest ledges used over 20 years had numerous potholes and ledges.

We suspected that as the term of occupancy increased, certain ledges might become favorites and receive disproportionate use. We examined the pattern of ledge use at 8 cliffs that had been occupied by nesting pairs for at least 19 years. The pattern that emerged showed 63% (52) of the 82 ledges were used once while 13% (11) were used twice. As in Great Britain (Ratcliffe 1993), there was no discernable tendency for a successful pair to return to the same ledge the next year.

Horizontal separation of ledges seemed to be constrained by the amount of cliff available. Nest ledges on single mesas and lone outcrops were limited to the immediate vicinity. Canyons and continuous escarpments permitted lateral movement and ledges used were sometimes separated by several kilometers. Among the above 34 sites, the average distance between the most extant nest ledges was 0.7 mi (1.17 km). The greatest separation of eyrie ledges at a site was 2.1 mi (3.42 km).

As the population rebounded and we visited previously unknown ledges at long-vacant sites, we often found evidence of previous occupancy, usually excrement from former broods. Over the millennia, most suitable nest ledges were probably used at some time.

Hunting Range

In 1994 we tagged 5 breeding peregrines (2 males, 3 females) nesting along the Front Range by attaching transmitters to the 2 central rectrices. The transmitters were ultimately lost at the time of molt in midsummer. Three or 4 stationary receiver stations on promontories were operated in most the daylight hours, 5 days per week, from 7 April to 4 June. The positions of the hunting birds were determined by triangulation using bearings obtained simultaneously by

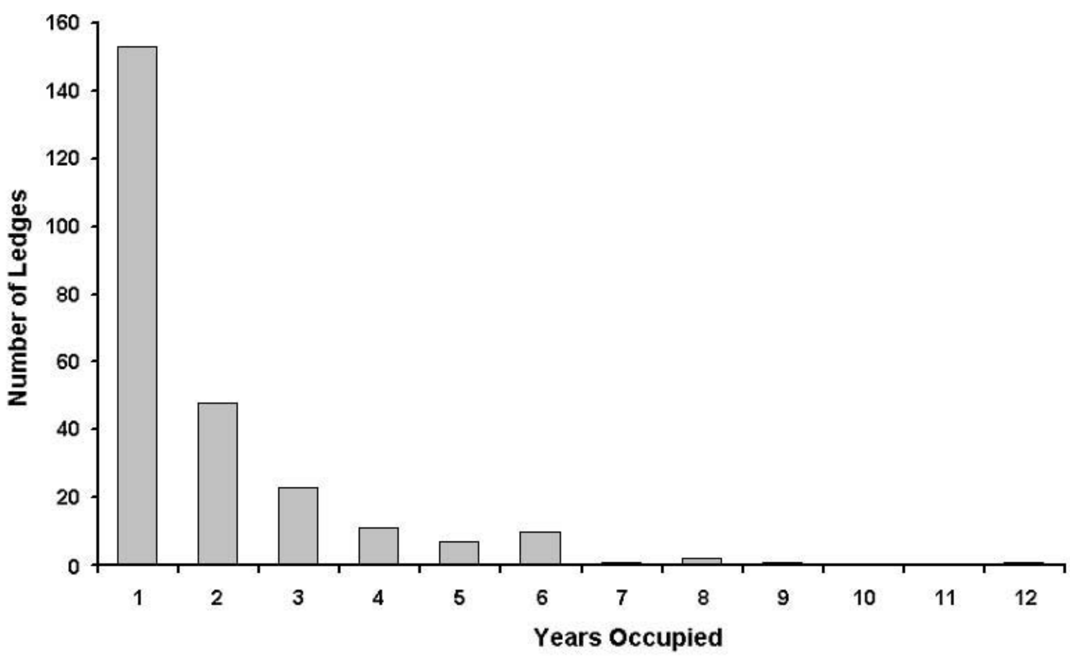

FIGURE 27. Frequency of occupancy for nest ledges (n = 257) at 34 sites that were occupied at least 10 years. Ledges are grouped by the number of years they were used. The majority (60%) of ledges were used only one year).

2-4 tracking stations. Actual locations of the peregrines were estimated using LOCATE II software as described in Enderson and Craig (1997). We arbitrarily rejected locations for which error ellipses exceeded 12,300 acres (5000 ha), and those obtained at intersections of only 2 bearings converging at less than 20 degrees. Only locations obtained an hour or more apart were accepted to avoid autocorrelation.

The 5 adults in this work nested within 20 km of each other and their harmonic mean 95% contour home ranges overlapped greatly. The areas of these ranges varied between 138 mi^2 (358 km^2) and 582 mi^2 (1,508 km^2). We also estimated home range based on minimum convex polygons. Those varied between 313 mi^2 (811 km^2) and 556 mi^2 (1,440 km^2). Females tended to have larger ranges than males. About 60 % of the foraging by males was done less than 5 mi (8 km) from the eyrie, and males rarely moved 15 mi (24 km) from the site; about 25% of female flights ranged beyond 15 mi (24 km) (Enderson and Craig 1997). We used an aircraft to verify the greater distances. One female was found in riparian habitat on 3 different days 12.4–13.7 mi (20-22km) from its eyrie, and the other female was found twice in the same drainage 37 and 43 km from its eyrie. The latter distance was the maximum we found.

Hunting trips (n = 21) of males lasted an average of 102 minutes; those (n = 35) of females had a duration averaging 97 minutes. Sometimes we recorded swift outbound or inbound flights, the latter were presumably with prey for the young. Outbound flights were apparently to foraging areas, in one case a reservoir 13 mi (21 km) from the eyrie. Twice the female was estimated to have flown the distance in no more than 10 minutes (71mi/hr or 115 km/hr). The male was detected once on its way to the same reservoir and traveled 11 mi (17.6 km) in 10 minutes (65 mi/hr or 105 km/hr). These speeds were the extremes, but peregrines in general showed great mobility; almost half of the 41 long distance runs we timed covered more than 6.2mi (10 km) in 10 minutes.

The 3 eyries with radio marked falcons overlooked great expanses of lowland 656 yd (600 m) or more below the elevation of the nests. Riparian and other habitats, presumably rich in prey, were widely scattered. That setting may have contributed to the extensive ranges we found. In Scotland, a female ranged over only 45mi^2 (117 km^2) in a 2-month period, less than half that of our lowest value (Mearns 1985). Our results imply that peregrines are capable of routinely moving great distances to take advantage of hunting opportunities. This finding suggests in turn that several different kinds of habitats (plant communities) are used opportunistically within the foraging ranges of most peregrine eyries in Colorado, and that no single local hunting area is likely to be critical to the existence of any one pair of peregrines.

Prey

Prey remains were obtained opportunistically in the course of visits to eyries to band nestlings. In all, remains were found in visits to 229 eyries between 1973-81 and 1985-96 (Table 4). Collections were made about equally among the Southern Rocky Mountain and Colorado Plateau provinces

TABLE 4. Number of nesting territories where prey remains were collected in the Southern Rocky Mountain (SRM) or Colorado Plateau (CP) provinces by year.

Year	SRM	CP	Total
1996	15	10	25
1995	8	10	18
1994	11	8	19
1993	11	13	24
1992	16	12	28
1991	10	12	22
1990	8	9	17
1989	5	10	15
1988	4	10	14
1987	3	9	12
1986	4	6	10
1985	3	4	7
1981	1	5	6
1973-1980	7	5	12
Totals	106	123	229

(Fig.2) and were fewer in the first period because few pairs were present.

Remains of about 1,106 prey individuals were found, including 1,002 identified to species; 104 items, mainly small birds, were not separated by species. In all, 83 species of birds were identified as prey, usually on the basis of flight feathers, but sometimes from skulls or feet. We did not examine regurgitated pellets. In all, only 20 species were identified more than 12 times. Except for the 3 most common species, the others were found fairly uniformly (Table 5). The ranking was surely subject to biases. Remains of small birds, especially feathers, were probably less likely to remain on wind-blown ledges and less likely to be seen by the collectors who were also involved with other tasks. About 80% of all remains not identified to species were feathers from small birds whose body weight was less than 1 oz (35 g). Violet-green swallows (*Tachycineta thalassina*) and pine siskins (*Carduelis pinus*) appear in Table 5. The latter have brightly colored flight feathers and may have been more conspicuous to the collectors. Violet-green swallows are very common near cliffs throughout Colorado and may be caught by peregrines far more frequently than our data suggest. Other small birds, identified only a few times, were mountain chickadees (*Parus gambelli*) (3), plain titmice (*Parus inornatus*) (3), warblers (*Dendroica sp.*) (4), and trochlodytid wrens (3).

White-throated swifts (*Aeronautes saxitalis*) were prevalent near cliffs throughout the range of the peregrine in Colorado, and their remains were the most common found, both in the mountains and on the Plateau. However, based on body weight (Steenhof 1983), the frequencies of the remains we analyzed suggest rock doves (*Columba livia*) and mourning doves (*Zenaida macroura*) were equally as important as the swift as food sources. The common nighthawk (*Chordeiles minor*) was about half as important as the swift and the two doves, but equivalent to several other species (Table 5).

TABLE 5. The 20 most common species of birds identified from remains found in peregrine eyries 1973-81, 1985-96, divided among the Southern Rocky Mountain (SRM) and Colorado Plateau (CP) provinces, and ranked by frequency.

Species	Number of Individuals		
	SRM	CP	Total
White-throated Swift (*Aeronautes saxitalis*)	57	92	149
Mourning Dove (*Zenaida macroura*)	40	71	111
Common Nighthawk (*Chordeiles minor*)	28	44	72
Rock Dove (*Columba livia*)	15	30	45
American Robin (*Turdus migratorius*)	23	21	44
Red-winged Blackbird (*Agelaius phoeniceus*)	29	15	44
Brewer's Blackbird (*Euphagus cyanocephalus*)	24	20	44
Western Tanager (*Piranga ludoviciana*)	18	26	44
European Starling (*Sturnus vulgaris*)	18	23	41
Brown-headed Cowbird (*Moluthrus ater*)	18	23	41
Clark's Nutcracker (*Nucifrara columbiana*)	19	14	33
Mountain Bluebird (*Sailia curricoides*)	15	17	32
Western Meadowlark (*Stumella neglecta*)	13	17	30
Black-billed Magpie (*Pica pica*)	9	15	34
Pinyon Jay (*Gymnorhinus cyanocephalus*)	1	23	24
Pine Siskin (*Carduelis pinus*)	17	6	23
Violet-green Swallow (*Tachycineta thalassina*)	9	10	19
Killdeer (*Charadrius vociferus*)	3	13	16
Red Crossbill (*Loxia curvirostra*)	11	5	16
Common Grackle (*Quiscalus guiscula*)	12	2	14
Total			865

Other studies of raptor diets have shown that prey remains may not reflect the actual diets determined from items brought to the nest (Marti 1987, Bielfeldt et al. 1992). However, in western Greenland where the diet was predominantly small passerines, prey remains gathered on nest ledges agreed with actual observations made during prey delivery (Rosenfield et al. 1995). Several prey items fell outside the general pattern of a diversity of medium-sized birds comprising the diet of peregrines. We found the fresh remains of 4 chipmunks (*Tamias sp.*), 3 rock squirrels (*Spermophilus sp.*), 3 unidentified bats, and 1 cottontail (*Sylvilagus sp.*). Two reptiles were also recovered. Remains of a collared lizard (*Crotaphytis collaris*) were found in an eyrie in western Colorado. In the same region, a bull snake (*Pituophis catenifers*) was delivered by a male to female with young. She rejected and abandoned the snake. Although arthropod remains were not encountered, an incubating female repeatedly consumed Mormon crickets (*Anabrus simplex*). As the cricket band crossed the top of the escarpment and down the cliff face into the river below, the falcon reached out and ate those that ventured within her reach.

The absence or rarity of the remains of scrub jays (*Aphelocoma coerulescens*), horned larks (*Eremophila alpestris*), and band-tailed pigeons (*Patagioenas fasciata*) was noteworthy. These species are widely distributed in Colorado. One specimen each of American kestrel (*Falco sparverius*), and black swift (*Cypseloides niger*) were found. Two belted kingfishers (*Ceryle alcon*) were found.

Heavy prey items were seldom recorded from nests. Exceptions to this included part of a northern pintail (*Anus acuta*) and a long-billed curlew (*Numenius americanus*). We found the partially eaten wing of a common raven (*Corvus corax*) and observers photographed a raven being consumed at another site.

The diet of peregrines in the Southern Rocky Mountains overlapped broadly with that of peregrines on the Colorado Plateau. This may be due to the ability of wide-ranging males to hunt in habitats at great altitudinal extremes many miles from their eyries. Further, several important prey species are not habitat specific.

Pinyon jays (*Gymnorhinus cyanocephalus*) were found almost exclusively in Plateau eyries (Table 2). Killdeers (*Charadriius vociferous*) showed the same tendency although the sample size was small. Common grackles (*Quiscalus guiscula*) appeared mainly in mountain sites.

An analysis of prey from 5 mountain eyries (including one in pinyon-juniper habitat on the East Slope), and 8 on the Plateau, showed 3 of the top 12 commonly found prey were encountered more in one region than the other. White-throated swifts and common nighthawks were found more often in eyries on the Plateau, and Brewer's blackbirds (*Euphagus cyanocephalus*) more commonly in the mountains (Mann-Whitney U tests; P = 0.003, 0.005, and 0.016, respectively). Mourning doves were somewhat more common from nests on the Plateau, but not significantly so (P = 0.067).

REPRODUCTION

Clutch Size

One hundred seventy-two clutches of eggs from first clutches encountered in 1973-2001 averaged 3.52 eggs per clutch (Table 6). Four egg clutches were in the majority (62%) and only a single clutch of 5 eggs was encountered. In the course of augmenting production we removed clutches from 23 pairs. Once we found an egg well away from the scrape (Fig. 28). All renested and laid second clutches. The recycled pairs averaged first clutches of 3.61 eggs and 3.13

eggs in their second clutches, the means were significantly different (P = 0.0008, 22d.f., paired t-test).

Brood Size

There is little information available on brood sizes in the literature. Hickey and Anderson (1969:25) provide a table of brood counts for peregrines from several countries, but do not state when in the nestling period the counts were made. It is possible that these brood counts included nestlings varying widely in age. The means vary from 1.87 young per brood (n = 92, SE = 0.91) in Great Britain in the DDT period, 1945 - 61, to 3.05 (n = 282; SE = 0.80) in the eastern United States prior to 1942.

Ideally, brood size is the number of chicks that hatch from a set of eggs. The best estimate of average brood size would include only observations made early in the nestling period before chick loss. The mean size of 20 recently hatched (1 to 5 days old) broods was 2.95. However our information on actual brood size is sparse due to difficult viewing conditions. Newly hatched chicks are usually obscured by brooding adults. Further, we seldom predicted the date of hatching; most visits occurred later. Some undetected mortality may have occurred prior to the count so that estimates of original brood size were probably biased downwards.

For the period 1998-2001, we compared the means of counts of chicks made 1-5 and 6-10 days after hatching to see if mortality reduced the latter mean. The average brood size in the 1-5 day counts was 2.95 young per brood (n = 20), and 2.94 (n = 28) in the later period. Because the means were essentially the same, we combined the data for the 2 periods. The resulting mean brood size was 2.94 chicks per brood (n = 48, SE = 0.93).

TABLE 6. Clutches of eggs encountered in Colorado peregrine eyries, 1973-2001 (n = 172).

Eggs Per Clutch	Clutches	Total Eggs
2	15	30
3	50	150
4	106	424
5	1	5

FIGURE 28. Completed clutch with displaced, non-viable egg.

Fledgling Rate

For our purposes, fledged brood size of successful pairs is the number of fledged age young divided by the number of pairs fledgling at least 1 young. This measure permits comparison between regions.

Throughout the period 1973-2001, 664 fledged broods were counted and averaged 2.33 young per brood. Broods of 2 and 3 were most prevalent (Table 7). Broods of 4 were observed least frequently, but accounted for 15 % of the total young fledged. We compared the fledged brood sizes for the period (1973-90) with a later population growth period (1991-2001) and found no significant difference (P<0.001) in fledged brood sizes (2.23 and 2.36 per pair respectively). Sixty-four instances where pairs received fostered young were excluded.

When young were large enough to be counted from a distance, some mortality may have already occurred. Large broods might sometimes exceed the ability of adults to feed and care for all the young. However, we never saw malnourished nestlings. Although 58 broods of 4 fledged, other broods had undoubtedly suffered losses resulting in 1, 2 or 3 young near fledgling age. The timing of attrition or their causes usually could not be documented.

We examined the loss rate of broods that were fostered to wild pairs. Young were usually placed into wild nests at 18-21 days of age. When available, the augmented pairs received 4 young. Of 64 foster attempts, 37 pairs received broods of 4 young.

Pairs with fostered young made an immediate adjustment from incubation of replica eggs to caring for large broods. If large brood size adversely influences fledgling success, pairs that received large broods of half-grown young should have fledged fewer young on average than those receiving fewer young. However this was not the case (Table 8). Although the fledgling rate of pairs with 3 young was greatest, pairs with broods of 4 were nearly as successful. Of the 37 pairs that received 4 young, about half (18) successfully fledged all the young, while 30% fledged 3 and 16% fledged 2. There was no evidence that broods of 4 compromised the ability of adults to rear the entire brood. Peregrines typically laid 3 or 4 eggs and adequately cared for all the young from those sets.

Nest Success

Nest success (the percentage of pairs that successfully fledge at least one young), fledged brood size (average number young fledged per successful pair), and proportion of breeding (egg producing) pairs are measures of output of young. The relationship between these factors is displayed in Figure 29. In recent years, the proportion of breeding pairs (including pairs with a yearling) remained above 80%, within the range associated with eastern populations prior to decline (Enderson and Craig 1974) and the recovering British population (Ratcliffe 1993).

Nestling Attrition

Estimation of fledgling success was made difficult because young were within a few days of fledgling. If young were counted after fledgling, some may not have been seen. If young were overlooked, the estimate of nest productivity was biased downward.

We developed a simple coefficient of nestling mortality that can be used to estimate the number of young likely to be fledged, on average, when a count was made prior to fledgling. The coefficient is based on observed attrition of nestlings in 174 broods in the period 1998-2001. Usually counts were made where chicks could be seen from a distance, or during banding activities. Mayfield (1975) estimated hatch success based upon egg loss between laying and hatch. We applied the same process to determine loss of chicks from hatching to fledgling.

The exposure of a chick to possible loss was tallied by chick-days. For example, if a

Table 7. Frequency of fledged brood sizes of peregrines in Colorado 1973-2001.

Fledged Brood Size	Number of Broods	Total Young Fledged	Percent of Broods	Percent of All Young Fledged
1	137	137	20.6	8.7
2	229	458	34.5	29.7
3	240	720	36.1	46.6
4	58	232	8.7	15.0
Total	664	1547	100	100

Table 8. Success of fostered young peregrines compared to initial fostered brood size in Colorado 1974-1989.

Initial Fostered Brood Size	Number of Broods	Total Young Placed in Nest	Total Young Fledged	Success Rate %
4	37	148	118	79.7
3	17	51	44	86.3
2	10	20	13	65.0
			Average	79.9

chick was present on the first visit, and also on the second visit 22 days later, 22 chick-days were recorded. If 4 chicks were present on both visits in the above example, 88 chick-days were recorded. However, if 4 chicks were present on the first visit, and only 2 on the second visit, 44 chick-days were recorded for the 2 survivors, and 11 chick-days for each of the 2 chicks lost; 66 chick-days were recorded in all. As described by Mayfield (1975), we assumed the loss of chicks took place halfway, on average, in the interim. In actuality, losses surely occurred variously in the period between counts.

The interim between the first and last count of the nestlings in the 174 broods varied from as little as 2 days to as great as 44 days. About 21 % of the periods between counts were in the 1-10 day category, 48% were in the 11-20 day category, 19% were in 21-30 day, and 12% included a span of 31-44 days. No count of broods was included after day 44, when all chicks would have fledged.

In all, 7,867 chick-days were tallied for the 457 nestlings counted on first visits. Of these nestlings, 80 disappeared between the first and last counts resulting in an average loss of 0.0102 chicks per chick-day. This value may be taken as the mean probability of the loss of 1 chick per day of exposure in the eyrie and was termed the daily mortality rate by Mayfield (1975).

In general, our daily annual mortality rate of about 0.0102 can be used to estimate how many chicks will likely be lost, on average, if the days remaining until fledgling can be judged. For example, if 3 chicks, 20 days old, are seen on a visit to an eyrie, the loss for the brood by time of fledgling (day 44) can be calculated. The loss rate for the 3 chicks is: 3 chicks x 24 exposure days remaining x 0.0102 chicks lost per day exposed = 0.734 chicks lost. So, on average, about 2.27 chicks could be expected to fledge.

Productivity

Productivity is defined as the total number of young fledged by all pairs on territory, breeding or not. It was difficult to document the reproductive results at every known site throughout the state, and pro-

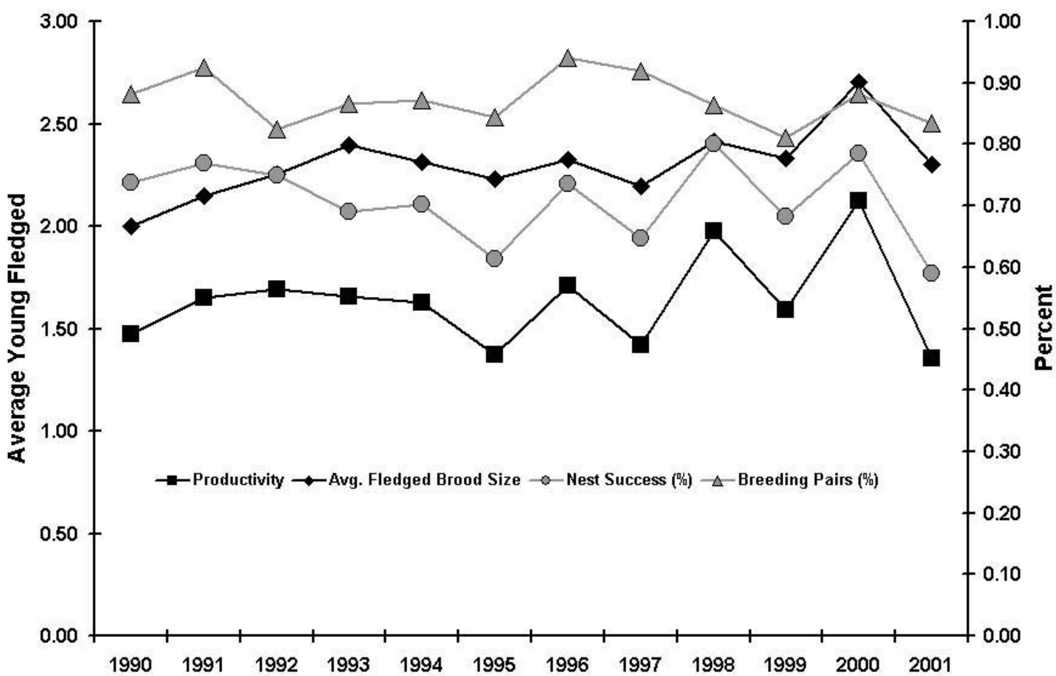

FIGURE 29. Relationship of nest success, fledged brood size, and proportion of breeding pairs.

ductivity estimates were restricted to those pairs with known outcomes. Figure 30 summarizes productivity observed between 1972-2001. The years of intensive fostering (1978-85) masked natural productivity since all or most wild pairs had their eggs removed and replaced with captive hatched young. Manipulated pairs received 3-4 young of 18-21 days of age which elevated their brood sizes over natural brood sizes that had experienced natural attrition by that age. Productivity of 22 non-manipulated pairs was only 1.23 during 1973-80. By 1985 natural productivity had improved to 1.44. Beginning in 1995, productivity exhibited an annual cycle of seemingly increasing fluctuation that cannot be explained. The mean 1995-2001 productivity was 1.72 (SD = 1.33). Future monitoring schedules should address trends over several years since productivity varied as much as 0.76 between high and low years. If inventories occurred on alternate years, another oddity emerged. Even year counts beginning in 1990 depict a significant (P = 0.001) upward trend while odd year counts beginning in 1991 exhibit a slight, uncorrelated decline (Fig. 31). Neither of the alternate year counts represents the actual productivity trend experienced over the 12-year period (Fig. 30). This illustrates the importance of long-term monitoring over years.

Sex Ratio of Nestlings

We used size of the tarsus at banding to determine sex of nestlings. Banding was scheduled when chicks were at least 3 weeks of age to avoid misidentifying sexes. By that age, the chicks had developed sufficiently so that differences in leg size were evident. A large female band placed on a male may be a hazard if a foreign object, such as a twig should become lodged between the leg and the band. A smaller male band placed on a female nestling could constrict the blood supply. At the time of banding, the bander made a judgment of sex and affixed the proper sized band. If there was doubt of the sex, the bird was not banded. The sex ratios that follow are for 3-4 week old young and may not represent the actual ratio at hatch.

We placed 577 bands on wild peregrine

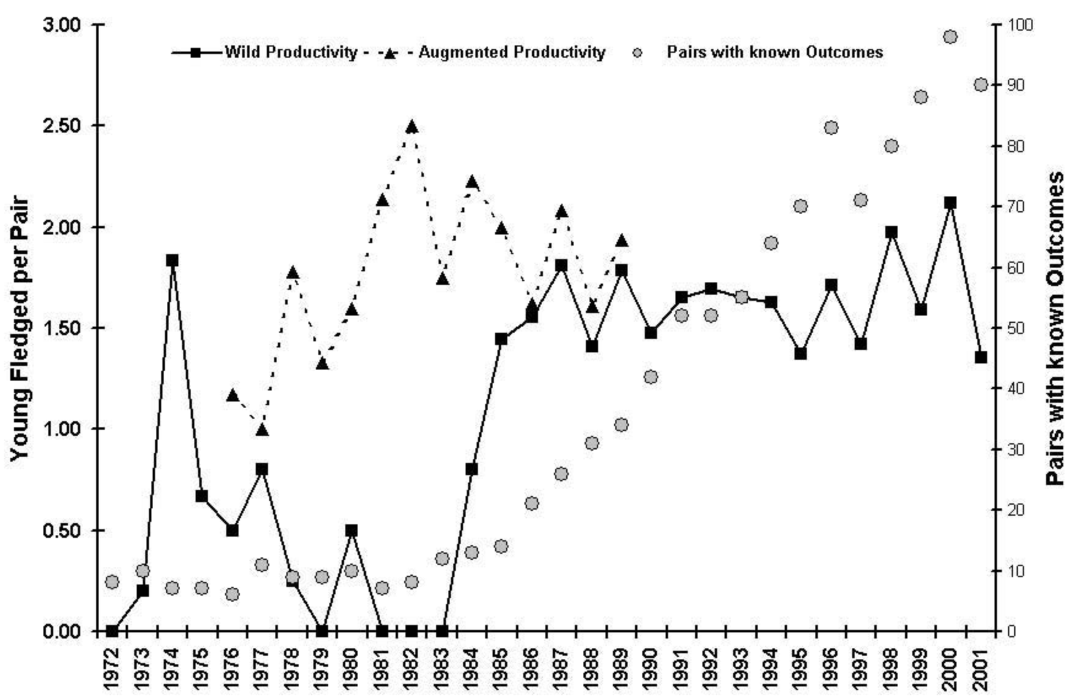

FIGURE 30. Annual productivity of peregrines in Colorado, 1972-2001

nestlings. Of these, 317 size 7a bands were affixed to females and 260 males received size 6 bands. This is an overall ratio of 1.22 females to males (Table 9). Significantly more females were present in eyries than males at 3 weeks of age (P = 0.02, Multinomial Test). About twice as many females as males were present in 1987 and 1988 (a third more in 1993) while males outnumbered females only in 1996. We cannot explain these disparities from a 1 to 1 ratio.

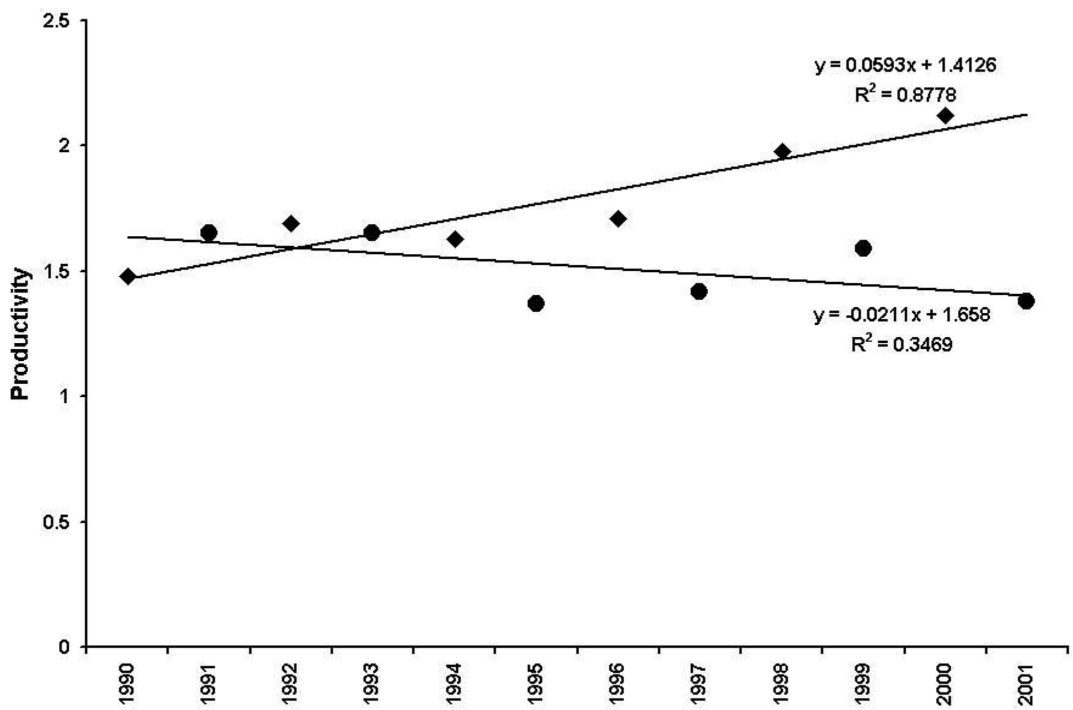

FIGURE 31. Productivity trends of data collected on alternate years beginning in 1990 (diamonds) compared to data collected on alternate years beginning in 1991 (circles).

Table 9. Ratio of male to female peregrine nestlings at about 3 weeks of age in Colorado.

Year	Males	Females	Total	Ratio
1987	12	28	40	1:2.33
1988	15	31	46	1:2.06
1989	21	22	43	1:1.05
1990	15	22	37	1:1.47
1991	21	22	43	1:1.05
1992	28	26	54	1:0.93
1993	28	46	74	1:1.64
1994	23	24	47	1:1.04
1995	16	22	38	1:1.38
1996	39	29	68	1:0.74
1997	24	24	48	1:1.00
1998	18	21	39	1:1.17
Total	260	317	577	1:1.22

SHELL THICKNESS, DDE, AND REPRODUCTION

Eggshell Thickness

Whole shells. - We accepted the value of 0.359 mm as "normal" eggshell thickness for peregrines prior to the advent of DDT /DDE from this region (Anderson and Hickey 1972). The same authors reported a value of 0.365 mm for peregrines in California, and that value has often been generalized to other regions. It is also important to mention that Ratcliffe's (1967) initial report of eggshell thinning in peregrines also revealed large variation in thickness between peregrine clutches in a region before and after the use of DDT. Others have reported large within-clutch variation in thickness (Enderson et al. 1982, Burnham et al. 1984, and Monk et al. 1988). The latter report involving large numbers of clutches found within-clutch standard deviations of 0.020-0.024 mm.

Whole eggshells were obtained from 1973 to 1998. Figure 32 is a plot of thickness against years where each datum is the value for a single egg. The least-squares regression suggests an increase in thickness from about 0.300 mm in 1973 to about 0.330 mm in 1998. However, the correlation coefficient (r^2) value is small (r^2 = 0.1525, P = 0.000). In other words, a single datum for a given year in Figure 32 is a poor predictor of shell thickness in the population.

Whole eggshell thickness appears to have improved from about 17% thinner than the pre-DDT value in the mid-1970s to about 8% thinner than normal in the mid-1990s. The former value corresponds to that found in several declining peregrine populations after the advent of DDT (Peakall and Kiff 1988). They reported no decline in populations suffering average eggshell thinning less than about 15%.

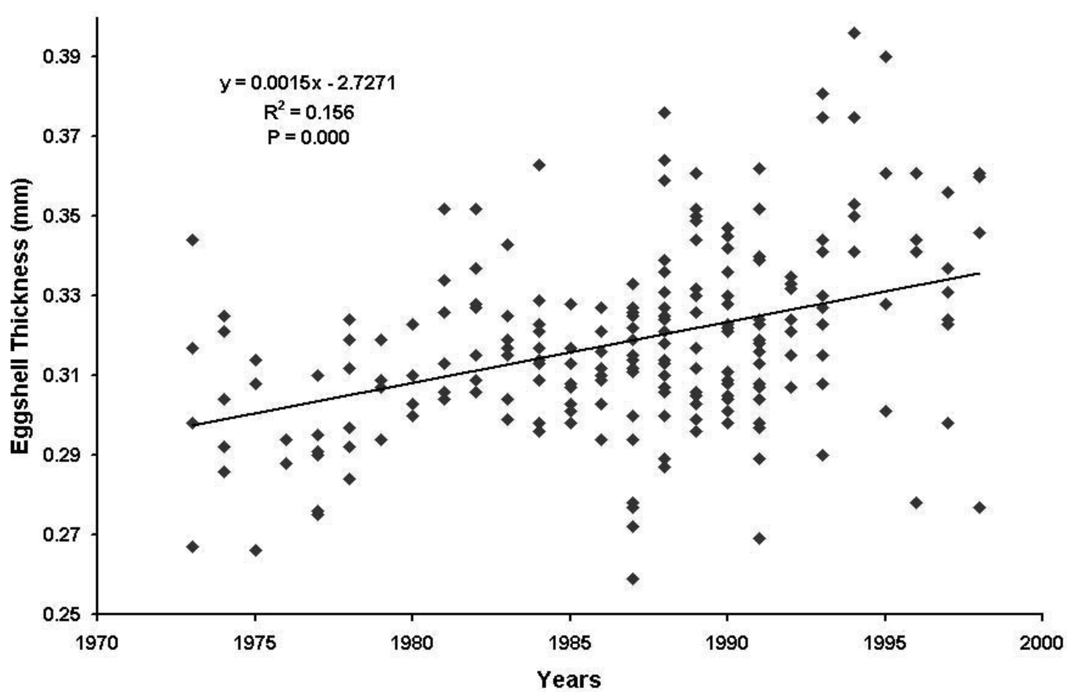

FIGURE 32. Thickness of whole eggs (n = 374).

Shell fragments. - All fragments from each eyrie were averaged. The mean thicknesses of fragments (n = 179) show wide variation between eyries within years (1987-98) and no apparent trend (Fig. 33). Further, in instances where we had both whole eggshells and fragments from the same set (n = 45), fragments tended to be thicker in sets where whole shells were thicker, but the correlation is very weak ($r^2 = 0.122$, $P = 0.02$) (Fig. 34).

Shell thickness and hatching. - We found no obvious association between whole shell thickness and the number of young hatched from remaining eggs in each set (n = 70) (Fig. 35). Nearly all the data are from the period 1985-98. Hatched young included the greatest number observed on each ledge in one or more visits prior to fledgling. This suggested that even in eyries where whole eggshells measuring less than 0.310 mm are found, 2 or 3 young were not uncommon. A similar result has been reported from Washington (Hayes and Buchanan 2002).

DDE Relationships 1973-90

DDE in eggs, 1973-90. - Laboratory methodology and analysis are described in Appendix 5. In the period 1973-90 we were able to obtain egg content analyses of DDE from 82 sets of eggs (Fig. 36). Usually only one egg was available from a set, if more than one was tested, the single egg values were averaged. Rarely did DDE levels from eggs in the same clutch differ by more that a few parts per million (ppm) (Enderson et al. 1988). DDE values for 1988-90 are clearly much lower than those for the 1970s. Only 3 of 19 eggs in 1988-90 exceeded 10 ppm DDE wet basis, and 12 of 19 had about 5 ppm or less. As little as 2-3 ppm DDE (wet basis) may be enough to cause detectable shell thinning, but serious reduction in thickness would not be expected in peregrines at DDE levels much below 20 ppm (Fyfe et al. 1988).

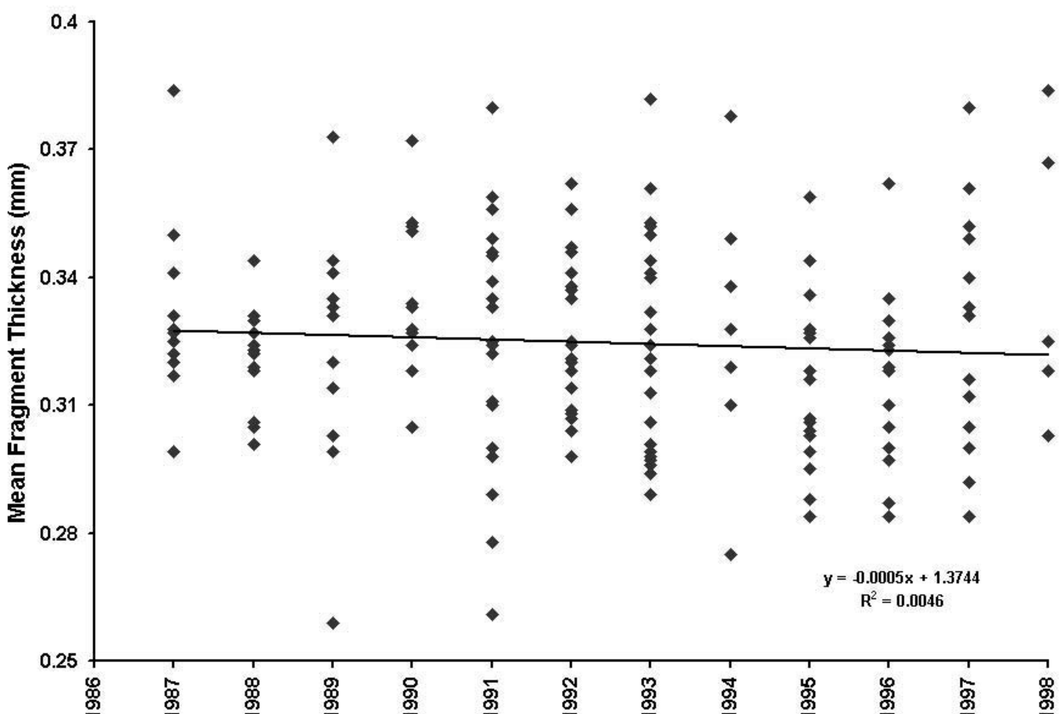

FIGURE 33. Fragment thickness vs year (n = 180).

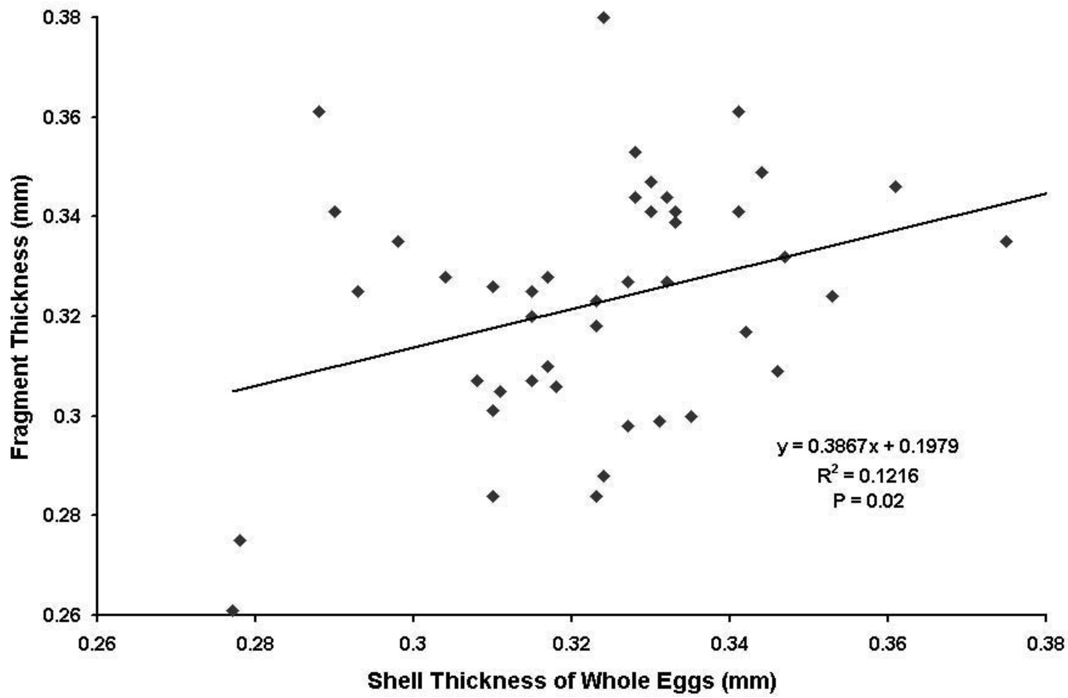

FIGURE 34. Thickness of whole eggs vs fragments from the same clutch (n = 45).

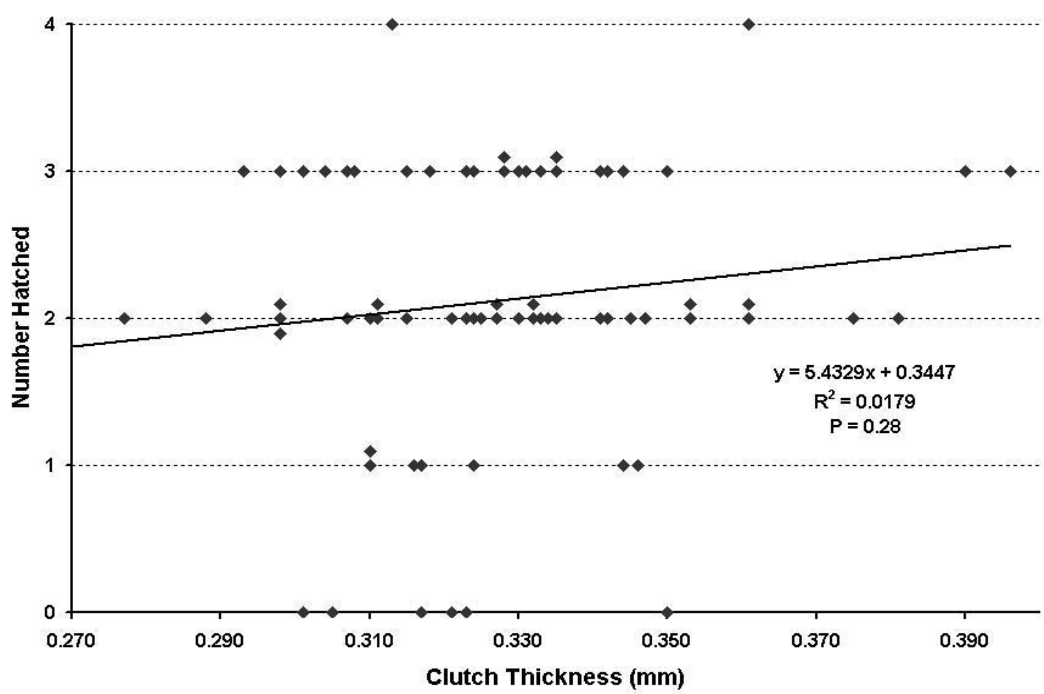

FIGURE 35. Young hatched vs average shell thickness of clutches (n = 70).

DDE and shell thickness. - Figure 37 shows the regression of shell thickness against log DDE in egg contents. The inverse relationship (r2 0.213, t = -3.31, P = 0.0014) is similar to that shown earlier in North America (Cade et al. 1971, Peakall et al. 1975). The extreme large DDE values we found equate to an eggshell thickness of about 0.295 mm, or about 18% thinner than the pre-DDT mean of 0.359 mm thought to be normal for peregrines in this region (Anderson and Hickey 1972). In the 1970s, eggshells averaged about 0.310 mm when log DDE was roughly 1.5 (30 ppm). In the period 1988-90, when average shell thickness was about 0.320 mm, log DDE was roughly 1.0 (10 ppm). A population-wide thinning of over about 18-20% is usually associated with reproductive failure at the population level (Peakall and Kiff 1988).

The correlation of eggshell thinning with DDE might have been tighter if the DDE in the yolk directly affected the performance of the shell gland. Instead, DDE in the yolk may better represent general body burden over the period egg yolk is formed. Actual shell thickness may relate more directly to levels of DDE in circulation at the time the shell is formed (Miller et al. 1976). Circulating DDE may be proportional to the degree of contamination of the prey being digested at the time.

Regional Comparison of DDE levels. - Between 1980 and 1986, only 1 or 2 territories were intermittently occupied by adult pairs on the east side of the Continental Divide in Colorado. To the west, several pairs remained, including those adjacent to the Colorado Plateau. These conditions caused speculation that DDE may have been more important east of the Divide. The arithmetic means of DDE in egg contents (east = 15.5 ppm, n = 22; west = 15.7 ppm, n = 60; P = 0.94) and the log DDE means (east = 1.11 ppm, west = 1.09 ppm; P = 0.80) did not differ significantly east and west of the Divide.

DDE Overview

The eggshell and DDE residue measurements presented here for the period 1973-98 were from samples collected non-systemati-

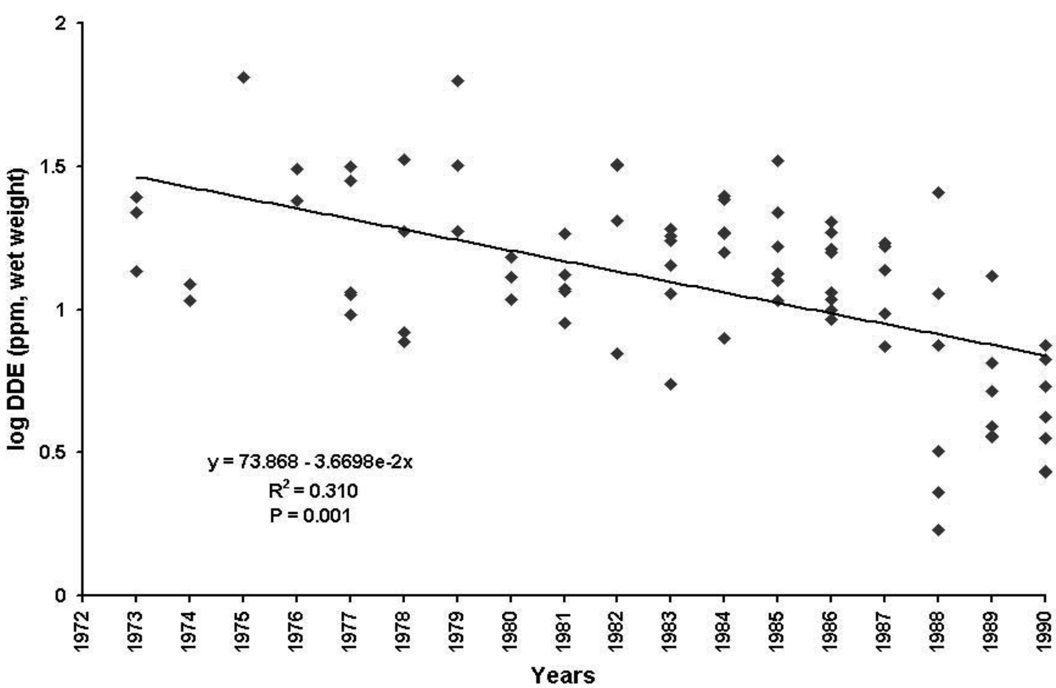

FIGURE 36. DDE residue in egg contents (n = 82).

cally incidental to fostering and banding work. Whole shell measurements were mainly from wild eggs that hatched in captivity, or from eggs found unhatched on the cliffs. The sample of unhatched eggs may not have had shells representative of the population in general. Eggs could be collected one from each set, but within clutch thickness variation is large in our experience. Ideally entire sets should be taken and the impact reduced by removing them early in incubation to assure re-laying by the pairs.

Because of great between-egg variation in shell thickness in a clutch, and variation in thickness in different parts of the shell, fragments of shells found on the ledge seem to have no value in revealing average shell thickness of the clutch. Further, substantial numbers of whole shells must be collected over many years to show thickness trends population-wide.

DDE, although declining, is still present and its effect on shell thickness has ameliorated only very slowly. From 1988 onward, most eggs held less than 10 ppm DDE wet weight, whereas in 1977 and before, nearly all held more than 10 ppm. Our data show mean peregrine eggshell thickness in Colorado was reduced by about 17% in the 1970s, a degree of average thinning that surely caused some nest failures. If the Colorado population had exceeded the critical threshold of thinning sufficient to cause significant population decline, as we believe, then a relatively small improvement in thickness above the threshold value could have resulted in near normal reproduction (Fyfe et al. 1988). Productivity was about "normal" at un-manipulated eyries by the mid-1980s when shell thinning was about 14%. Studies on DDE in potential prey of peregrines in the Rocky Mountain region have recently been summarized (Kennedy et al. 1995). Despite the apparent decline of DDE in peregrine eggs, some favored prey species such as white-throated swift, American robin, European starling (*Sturnus vulgaris*) and Brewer's blackbird have been shown to have significant DDE in local collections compared to early analyses from Colorado (Enderson et al. 1988).

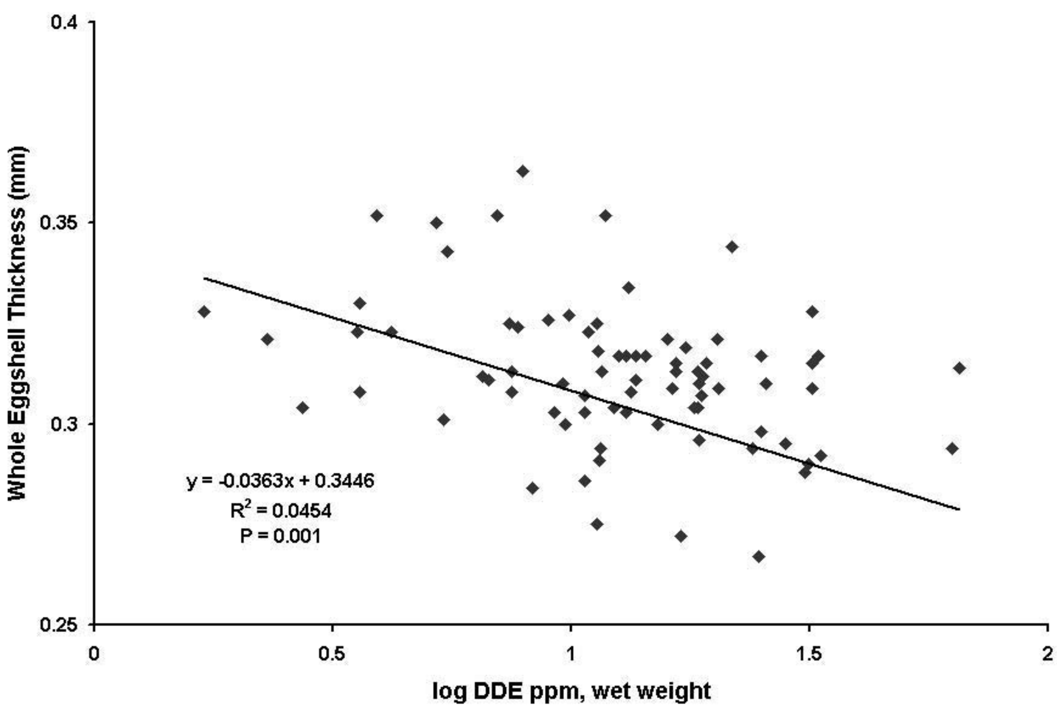

FIGURE 37. Eggshell thickness vs DDE residues (n = 80).

REPRODUCTIVITY AND MORTALITY

Minimum Productivity to Sustain the Population

When the peregrine was listed under the Endangered Species Act of 1973, basic population data, including mortality and productivity were few (Craig 1977). It was clear, however, that peregrine extirpation east of the Mississippi and severe decline in the western United States were pesticide induced. All 4 of the national peregrine falcon recovery plans included productivity among the parameters that were to be monitored during population recovery.

Predictions from population models are useful to the degree the data used are realistic representations. Models should be employed to simulate changes in population performance when one or more parameters are changed. Models do not predict when or how wild populations will change, but instead reveal the interaction of the demographic variables.

Using Mebs' (1971) formula $f = \frac{2m}{(1q)1m)}$ where f = adult mortality and q = first year mortality, a minimum productivity could be projected that was required to offset estimated mortality and assure population stability. The Rocky Mountain Southwest Peregrine Recovery Team assumed 60% mortality for the first year and 20% for subsequent years and recommended an 'equilibrium' productivity of 1.25 young per breeding pair per annum to sustain the population.

Information collected over the intervening 3 decades provides insight into Colorado peregrine mortality and recruitment. Between 1974 and 2000, 938 peregrines were banded in Colorado that yielded 53 dead recoveries and 11 re-sightings of live birds. Using the program Mark (White and Burnham 1999), mortality estimates were generated for ages 0-1, 1-2 and 2+ which are 0.46, 0.33, and 0.20, respectively. If these rates are representative of Colorado peregrines, in order to achieve a population lambda of 1.00 (equilibrium) productivity must average 1.22 young fledged per occupied territory if half the 2-year-olds were to breed (Fig. 38) (Craig et al. in press). Although in 1995 and 2001, the productivity dipped to 1.37 and 1.36 respectively, the mean rate over 1995-2001 was 1.72.

Adult Tenure and Productivity on Territory

After a historical territory became occupied, or a new territory was discovered, we

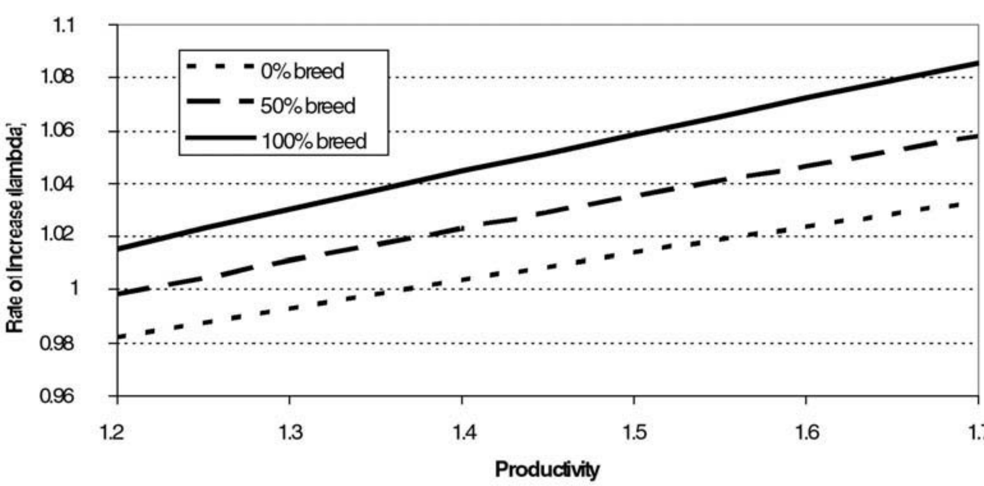

FIGURE 38. Critical productivity required to maintain population equilibrium (λ = 1) for the Colorado peregrine falcon population. Three levels of participation by 2-year-old birds are shown. (From Craig, White and Enderson in press).

returned each year and hence had a chance to identify individuals and to record returning adults. In some cases we were able to determine both the year an adult first appeared on a territory and the last year it was present. These cases were relatively rare compared to instances in which an individual was recognized one or more years without our knowing whether the first year we recognized it was indeed the first year the bird was present on territory or if the last year we saw it was indeed its last year on territory. Similarly, sometimes we failed to be in a position to see identifying characters, and were therefore unable to verify if an individual remained present in a later year. Sometimes, we were able to tell when an adult was replaced by another, one breeding season to the next, but had no further information in regard to the tenure of either bird.

One banded female was known to be on territory 14 years, the maximum recorded, and although her identity was not confirmed after that, she may have been present 17 years based upon her poor production in subsequent years. A 14-year old male originally produced on the Dolores River died in a collision with a power line below a cliff during the nesting season in northern New Mexico. It is probable he was a resident at the site.

Adults (n = 147) occupied territories as long as 8 years (Fig. 39), excepting the case of a female known to be on territory 14 years. The sexes were similar in their longevity and taken together, were present an average of 2.7 years. This is a minimum estimate because an individual could have been on the territory one or more years before we established its identity. Further, an individual might have returned to the territory one or more years after the last year we were able to verify its identity. Sixty adults were present a minimum of 1 year and fully 25% of that number (15) were present at least 4 years. The data in Figure 39 suggest a decline in disappearance rate with increasing years on territory. Perhaps older adults have learned to better cope with the demands associated with holding a nesting territory, or with demands at other times of the year.

From about 1980 onwards, we annually visited nearly all occupied territories to record reproduction, collect eggshells, band nestlings, and to estimate adult turnover by band pattern, sketches, photographs, unusu-

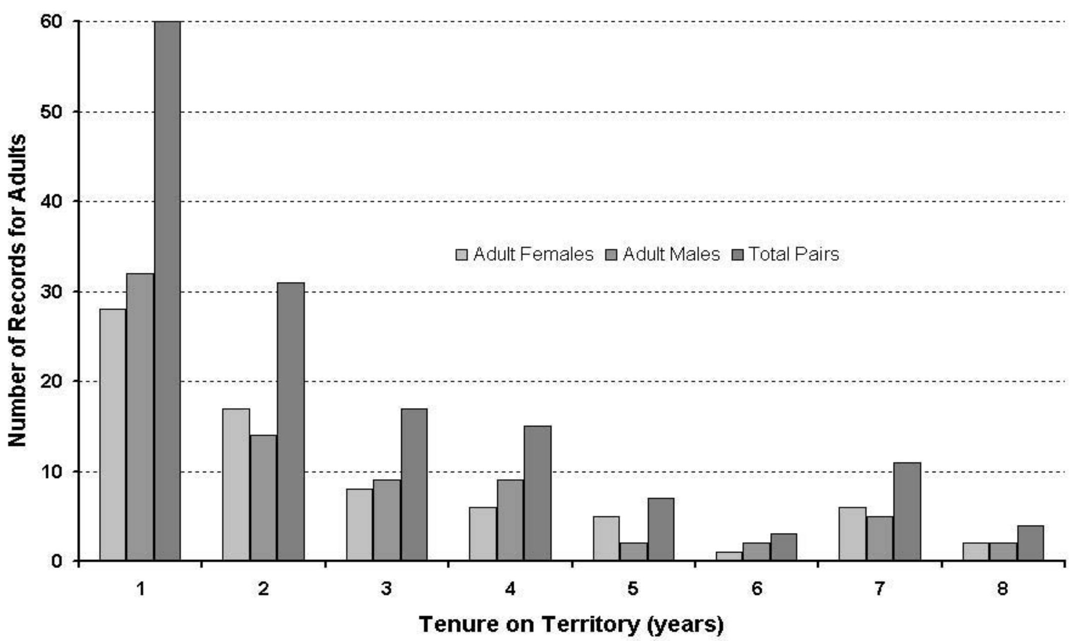

FIGURE 39. Minimum tenure of adults on territory, excluding one peregrine known to be present 14 years. Individuals were identified by markers or unique plumage markings.

al behavior, or other characters. Often 2 or 3 visits to the top of the cliff, or to the nest ledge, were necessary. The number of young fledged at sites in use by a pair was nearly always determined.

The data set analyzed here are for 36 adult females observed a minimum of 2 consecutive years (30 different territories) and 36 adult males observed at least two consecutive years (31 territories) in the period 1980 to 2000. Each of 4 other males and 4 other females replaced an adult for 1 year, and in turn were replaced themselves after only 1 year. These 8 birds comprise the data for birds present only 1 year. For the other adults, present 2 years or longer, we can only be sure these were the minimum number of years of residence because of the limitations described above. There was probably no bias in identification of adults of long tenure or of short tenure. Therefore, we expect our distribution of adults by length of minimum tenure was proportional to the distribution of actual tenures among these birds. The exception is the set of 8 adults known to have been present only 1 year; it is surely under-represented because of the difficulty in detecting such birds.

From 1980-1988 some of the adults for which there are tenure data were augmented reproductively by fostering. Those adults are kept distinct here from adults not augmented. Further, we kept the sexes separate in this analysis because they have different roles in the breeding period and could be expected to have different tenure and lifetime reproduction potentials. This is based on the finding that average age at death of males and females are apparently different in a recently studied population in the Midwest U.S. (Tordoff and Redig 1997).

Reproductive Performance by Females

The 36 females in the sample of non-fostered breeders on territory 2 or more years, collectively attempted to breed a minimum of 134 times (Table 10). The sample sizes for birds with longer tenures were understandably smaller. The average reproductive rate per attempt for birds of all tenures combined was 1.7 young. In the Midwest females had an average tenure of only 2.7 years (Tordoff and Redig 1997).

The cumulative number of young generally increased with age. On average, 4 females present only 1 year fledged 1.8 young. For females present at least 2 years or more, the cumulative average of young increased from 3.5 young (2 years) to 13.0 (7 years). The increase in cumulative number of young seemed constant, at least up to a minimum of 7 years on territory (Fig. 40).

The longest tenure for any female was 14 years. She first appeared as a yearling in 1980 and was extremely aggressive. In 1982 she was caught on the nest ledge by hand and fitted with a single aluminum band. Most peregrines banded then were given a marker band as well. Her broods were not augmented in the last 9 of the 13 years she was present (Table 10).

In 13 cases we saw the replacement of a female, present one or more years, by another adult female the subsequent year. Both the old females in their final year, and their replacements in their first year had the same average fledgling rate of 1.5 young. Apparently females are not disadvantaged at the end or the beginning of their tenure. We detected no reduction in productivity among females with up to 9 years of tenure. The female with 14 years of tenure had fledged 23 young (including 11 fostered

Table 10. Productivity of non-fostered female peregrines on territory in Colorado.

	Minimum Years Present								Totals
	2	3	4	5	6	7	8	9	
Number adult females	15	6	3	3	6	2	-	1	36
Breeding attempts	30	18	12	15	36	14	-	9	134
Cumulative young fledged	52	27	20	27	65	26	-	12	229
Young per attempt	1.7	1.5	1.7	1.8	1.8	1.9	-	1.3	-
Cumulative young per adult	3.5	4.5	6.6	9.0	10.8	13.0	-	12.0	-

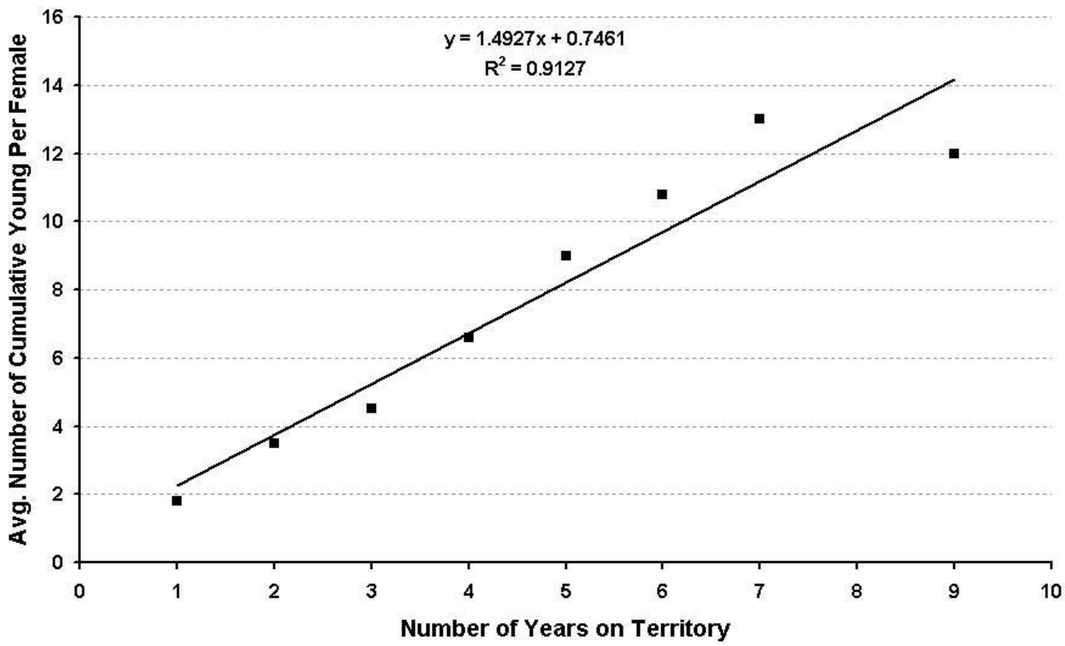

FIGURE 40. Cumulative number of young produced by females vs number of years on territory.

young) when she reached her eleventh year, but failed to produce young when she was aged 12-14 years. The most prolific female we encountered was on territory in the upper Arkansas River drainage for 7 seasons. She fledged 18 young. Although most females present several years seldom failed more than 2 years, a female on the northern Front Range failed to fledge any young in 6 successive attempts.

Reproductive Performance by Males

We treated the tenure and productivity data for males in the same way as for females. The 36 males present a minimum of 2 years, whose broods were not augmented by fostering, were on territory collectively 143 times (Table 11). The mean annual fledgling rate for these males was 1.8, nearly the same as for females. Four other males, known to be present for 1 year averaged 1.8 young per attempt, the same as the parallel subset of females. Similar to females, the cumulative number of young realized by males increased in direct proportion with years on territory, and to a very similar degree (Fig. 41).

The worst record of productivity was for a male on the central Front Range who fledged 2 young in each of only 2 years of the 7 years on territory. The best rate of productivity was by a male on the Yampa River drainage who fledged 16 young in 5 seasons. The greatest total production by any non-augmented adult, male or female, was for a male on the central Front Range who in 8 years

TABLE 11. Productivity of non- fostered male peregrines on territory in Colorado.

	Minimum Years Present							Totals
	2	3	4	5	6	7	8	
Number adult males	11	8	5	3	2	6	1	36
Breeding attempts	22	24	20	15	12	42	8	134
Cumulative young fledged	36	35	39	38	19	67	18	229
Young per attempt	1.6	1.5	2.0	2.5	1.6	1.6	2.3	-
Cumulative young per adult	3.2	4.4	7.8	12.7	9.5	11.2	18	-

fledged 18 young. This record was especially noteworthy because he had only one foot.

The Effect of Adult Turnover on Productivity

We often were able to verify on the basis of bands, or through photos (Enderson and Craig 1988) (Fig. 42), whether adults on territory from the previous year returned to breed the following year, or if they were replaced by an adult new to the site. Also data on fledgling success was often available. We wondered if fledgling success is as high when either adult is new to the territory as when either adult returned from the previous year?

We compared the productivity of new adult males (n = 30) with that of returning adult males (n = 28) using t-tests and found the mean number of young fledged in both cases was 2.0. For females, the mean number of young/attempt was actually lower (1.67; n = 21) for returning birds than for new birds (2.16, n=32), but the difference was not significant (P = 0.16).

In 8 instances we verified that both adults were new at a territory. They fledged a mean of 1.75 young per attempt. The sample size is too small for meaningful testing, but their performance was similar to that for the population in general over the years of our study (1.67 young/attempt, n = 381).

Biases of Reproductive Estimates

Success at historical eyries compared to recently found sites. - By 1975, about 27 historical eyries were known for Colorado. Some of these were known from published records, but most were not published, and in a few cases historical occupancy was uncertain. Most of these sites were re-occupied by the mid-1980s, along with "new" sites found in use in the preceding decade. All these sites either remained in use through the period of depressed population in the 1960's-70s, or were occupied early in the post-depression growth. It might be argued that peregrines in the 1990s expanded into "marginal" sites, and if so reproduction of these recently occupied sites might be lower.

Because we carried out extensive searches for new pairs each year, beyond those we had already recorded, newly occupied cliffs

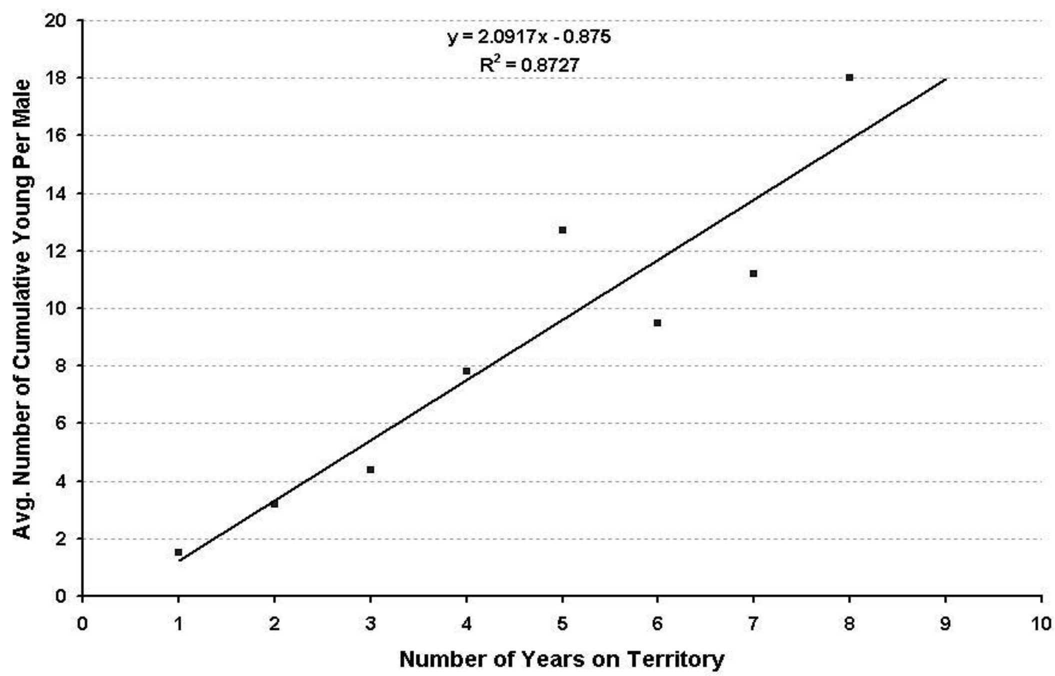

FIGURE 41. Cumulative number of young produced by males vs number of years on territory.

were probably unlikely to remain undiscovered for many years unless they were remote. We believe most of the pairs newly found after the early 1990s were not present prior to 1985. We compared the 1994-96 fledgling rate per pair for 23 sites that were in use in 1986 or before with the 1994-96 fledgling rate for 39 sites found after 1990 even if they were occupied only 1 year in the 1994-96 period. The fledgling successes were not averaged by site for the 3-year period; each attempt was considered independent. The mean of 1.55 young per attempt (n = 66) for old sites did not significantly differ from the 1.46 young per attempt (n = 79) for sites found after 1990 (t = 0.42, P = 0.67).

In a second analysis we used sites in use all 3 years 1994-96, and averaged the production by site. Old sites produced a mean of means of 1.50 young per attempt, new sites 1.48 young per attempt, the difference was not significant (P = 0.95, t = 0.006).

Potential for bias caused by using data from year of discovery. - Falcon pairs may be easier to discover late in the reproductive season when mature young are present. Inclusion of fledgling data from these sites may bias the overview upwards, because newly occupied, but failed eyries tend to remain undiscovered (Steenhof and Kochert 1982). We compared the success recorded in the year of discovery with that recorded the following year at 34 sites. Excluded were sites visited regularly prior to the first year a pair was found, and sites where a lone adult or mixed pair had been seen the year before an adult pair was found. In the year of discovery 1.97 young per attempt were recorded versus 1.74 the following year (P = 0.42, t = 0.81). Although not significant, the difference was substantial and owed importantly to complete failures the second year. In year of discovery there were only 3 total failures, but 10 occurred the year after. We cannot discount a bias resulting from using data from "new" sites, with those from sites known to be occupied by pairs in previous years.

If newly discovered sites inflate the productivity estimates, then productivity

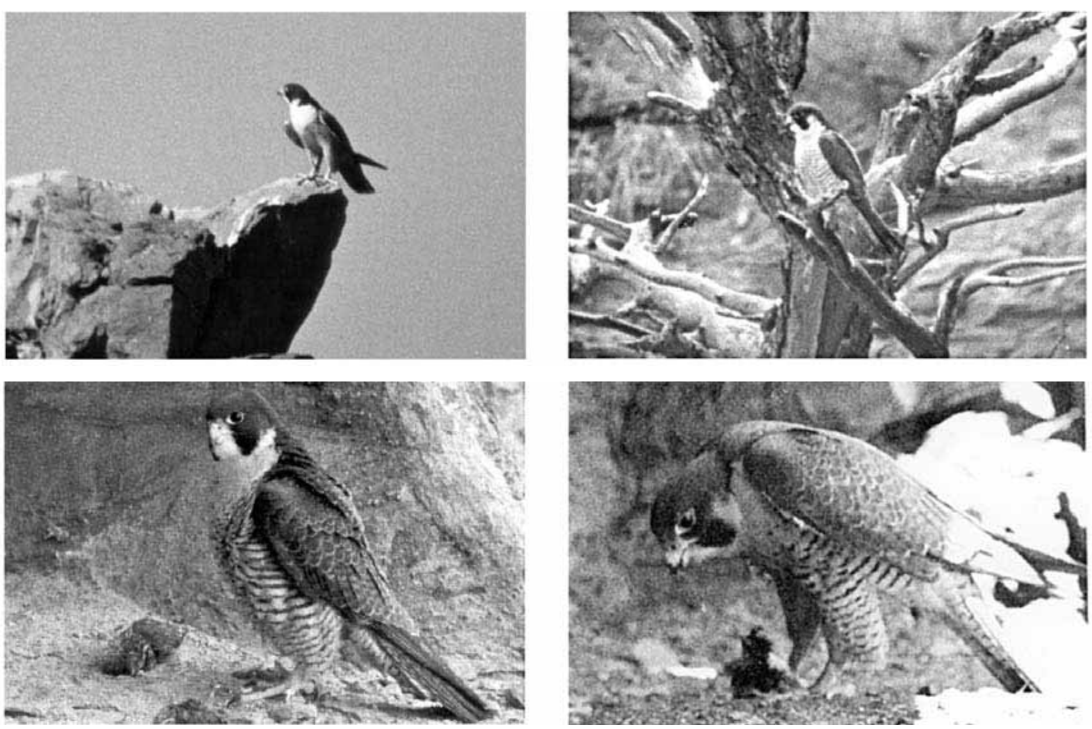

FIGURE 42. Examples of auricular patches of adult peregrines. Males with nearly full helmet (*top left*) and large auricular patch (*top right*). Females with nearly full helmet (*bottom left*) and large auricular patch (*bottom right*).

should decline if the newly discovered sites are discounted. To test this, we compared the productivity of all sites inventoried in 1991-2001 with productivity that would have resulted if only those sites on record from the previous year were counted ("new" sites were deducted) (Table 12). Eliminating sites discovered in the same field season caused annual productivity to fluctuate slightly, but there was no bias toward overestimating productivity. In fact, productivity was reduced slightly in 2 high discovery years (1996 and 2000) when 14 and 12 new pairs were reported. In the combined years 1991-2001, productivity remained unchanged (1.66 for both groups). Hence, the influence of including new sites was insignificant.

In Colorado, discovery of new pairs of peregrines occurred throughout the breeding season. Detection of the 34 sites included 1 found during courtship, 12 during incubation, 12 during brood rearing and 9 during or after fledge. At the time they were found, 9 pairs were not breeding or had failed and 3 of the failed pairs were located in mid-June, before the normal time of fledgling. Peregrines tend to remain at the cliffs throughout the breeding season after nest failure and therefore may be encountered. This is not the case in some other raptors. Any newly discovered site can be included in the season's results without significant bias.

Mortality

Mortalities suffered by 65 Colorado peregrines were recorded over the period 1974-2001 (Table 13). The information was compiled from band recoveries (46 cases) and direct observation (19 cases) in the course of monitoring eyrie sites.

Predation. Predation accounted for 45% of the deaths, most of which were documented while observers monitored nesting pairs. Of the 29 cases of probable predation, 10 appeared to be avian caused, but the predator could not be confirmed. Of the remainder, golden eagles were observed to capture 11 peregrines, and great horned owls accounted for 8 other mortalities. Because golden eagles and great horned owls were the only species confirmed to have killed peregrines, it is possible that they also accounted for other losses in the unknown category. Eagles were seen by our observers to kill 8 nestlings at 3 nest sites. A brood of 3 nestlings was taken just prior to fledgling in 1978. They had been equipped with telemetry and signals indicated 2 were in an eagle nest on the same cliff approximately 330 yd (300 m) away. The remains of the third were recovered on the talus below the eagle nest. In 1981, one member of a brood was caught as the brood competed over a prey item. The nestling was taken by an eagle which was nesting approximately 2 mi (3 km) downstream. The attack occurred in spite of aggressive defense by the adult. Nestlings appear to be most vulnerable to attack at the time of fledgling when they advertise their presence with frequent wing exercising or are preoccupied competing for prey. During this period, the adults are hunting for their hungry brood and are often not present to defend their nests. During two attacks, eagles snatched the falcon off its perch, flew toward a cliff face, and hurled the falcon against the rocks, and returned to retrieve it when it fell to the ground.

Eagles also attacked more experienced peregrines. A yearling that visited a site when the young had recently fledged was

Table 12. Productivity of all nest sites compared only those sites known the previous year in Colorado 1991-2001.

		1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	Cum
New Pairs Discovered		6	2	1	3	3	14	2	4	1	12	4	52
Total Pairs	All Pairs	52	54	55	64	68	83	71	81	88	98	90	804
	Previous Pairs	46	52	54	61	65	69	69	77	87	86	86	752
Productivity	All Pairs	1.65	1.63	1.65	1.63	1.37	1.71	1.42	1.95	1.59	2.12	1.36	1.66
	Previous Pairs	1.65	1.65	1.63	1.61	1.32	1.72	1.46	1.99	1.60	2.16	1.31	1.66

Previous Pairs are total pairs minus newly discovered pairs.

Table 13. Causes of peregrine mortality in Colorado, 1974-2001 reported by observers, the public, and from band recoveries.

Cause	Number	Percent
Predation	29	45.5%
Collision	13	19.7%
Unknown	12	18.2%
Starvation	8	12.1%
Gunshot	2	3.0%
Poisoned	1	1.5%
Total	65	

captured during an inattentive moment when it landed and was preening. This bird was also dashed against a cliff. It was retrieved and taken to the eagle's nest about 2 mi (3 km) away. In another case, a dead adult male was photographed among other prey in a golden eagle nest near Lyons, Colorado. A telemetered adult male from a Front Range site appeared to have been killed by a raptor while on a hunting foray. An adult female near Rifle, Colorado was attacked and killed by an adjacent nesting pair of eagles. The pair of falcons at this site had defended daily against intrusions into their airspace by a pair of eagles nesting on an adjacent cliff. After the adult female was relieved of incubation duties, she perched in a dead snag at the top of the cliff and was preening when caught and killed.

Great horned owls killed 1 adult and 7 nestlings. A Front Range site suffered greatest with loss of 1 young in 1993, 1 in 1994 and 3 in 1995. Owl kills were usually represented by feathers or a complete wing, although the fledgling killed in 1994 was identified by the bones of a leg and a transmitter in an owl casting. Disappearance of a single nestling near Boulder, Colorado and subsequent discovery of a leg also was attributed to owls. A horned owl killed an adult in Dinosaur National Monument in 1981. Observers camped nearby heard peregrine defense calls in the middle of the night and when they investigated the next morning they found the adult female missing and a chick dead on a ledge approximately 20 feet below the eyrie. Owl feathers were in the eyrie along with several from the adult peregrine. The remaining 3 chicks were unharmed. By supplementing Coturnix quail, the attendants ensured that the male successfully fledged the remaining young without benefit of a mate.

Two gray foxes (*Urocyon cinereoargenteus*) stalked a male fledgling that landed at the base of a nest cliff. Repeated stoops by the pair successfully drove the foxes away. Presence of droppings and tracks of packrats (*Neotoma sp.*) and ringtails (*Bassdariscus astutus*) in the immediate vicinity of eyrie scrapes suggest that peregrines tolerate these nocturnal visitors.

Collisions. - Considering the falcon's fast flight speeds and hunting methods, it is not surprising that collisions with objects accounted for 20% of the known mortalities. Power line and guy wire strikes contributed to deaths of 6 individuals, and collision with the limb of a pine tree caused another death. Vehicle strikes killed 3, and a jet aircraft claimed another.

Collision losses were evenly distributed among juveniles and adults (6 each). Several adults struck wires that crossed their hunting areas. The 7-year old male that struck a distribution line within a mile of his nest cliff probably had occupied the site for at least 5 years. The accident occurred in the spring at a meadow that had recently cleared of snow and attracted migrant robins and black birds. Another male was 5 years of age when he struck a distribution line within a housing development approximately 2 mi (3 km) from his eyrie. An immature falcon was killed when it struck satellite dish guy wires near a stock pond at Marathon, Texas, during fall migration. Circumstances surrounding several of the wire collisions suggest the falcons may have been in pursuit of prey and did not see the wires.

Vehicle strikes killed 3 peregrines, 2 were immature but 1 was a 7-year old adult male that was struck by a vehicle during the breeding season. The falcons may have been perched on fence posts and were struck when they flushed in front of passing vehicles or they may have been in pursuit of birds flushed by the vehicles. The automobile strikes of a 2-month old juvenile was witnessed by a highway patrol officer. He reported that the falcon dove in front of a vehicle he was following and was struck. Even more bizarre was a yearling male that was struck by a jet aircraft on Buckley Air Base runway 50 mi (80 km) from where he was fledged.

Starvation. - Starvation was the cause of death for 1 adult and 7 nestlings. The adult male originally had been hacked on the Front Range in 1984 and was recovered in September of 1986 near the outskirts of Colorado Springs. The necropsy suggested starvation as the cause of death. In other instances, a brood of 3 and a brood of 4 starved when the adults seemingly disappeared.

Gunshot and poison. - Yearling male peregrines suffering from small caliber gunshot wounds were encountered near Grand Junction, Mesa County and Barr Lake, Adams County. A single poisoning case involved an immature female fledged near Montrose, Colorado, that was wintering in Chandler, Arizona. In December, she was encountered covered with pigeon Stickum®, a compound that is usually spread on pigeon roosts to cause them to relocate. The falcon had ingested a sufficient amount to be poisoned.

Rock Climbing. - Rock climbers caused the failure of at least 2 nesting attempts, but the number of young lost was not known. Productivity also may have been affected by climbers at a site in 1993 and 1994 because of the popularity of the cliffs and the extended time required for many of the climbs. These mortalities have not been tabulated because actual numbers of nestlings were unknown.

Mortality Rates

Estimates from band recoveries. - Between 1974 and 1998, 938 peregrines were banded in Colorado. We received 53 band recoveries of dead birds and 11 re-sightings of live birds. Because sufficient time had not elapsed to account for all the 1998 bandings (our oldest peregrine lived 14 years) , a conditional, time-specific reporting rate was applied. Using the program Mark (White and Burnham 1999), mortality estimates were obtained for ages 0-1, 1-2 and 2+. The mortality rates of the 0-1 and 1-2 age classes were 0.46 and 0.33 respectively. The mortality rate of adults over 2 years of age was 0.20 which is identical to the turnover rate documented through plumage changes of territorial adults (Enderson and Craig 1988).

Estimates from Adult Turnover. - Adult peregrines show strong fidelity to their breeding territories. Individuals rarely change territories in subsequent years; only 2 individuals shifted to adjacent territories. Because of this, the return rate of adults is a measure of survivorship, taking into account the few that nest elsewhere or those that do not nest at all. Estimates of annual adult survival for North American peregrines include 75% for the eastern U.S. prior to 1953 (Enderson 1969), 68% for British Columbia (Nelson 1988), and 86% for the Midwest U.S. (Tordoff and Redig 1997).

We examined turnover at Colorado sites in 1980-85, based on photos of the head plumage (Fig. 42) and other characters, and found 48 of 57 (84%) of the adults returned to breed in a subsequent year, including three accounted for at another site. Since then, we kept track of identifying characters such as the pattern of leg bands and markers, and photos or sketches of head plumage. For territories on which occupants were seen well enough to ascertain facial patterns or bands in consecutive years, we examined whether the bird in the second year was the same as the year before. An individual not identified in the second year, but in some subsequent year, was assumed to have been present through the period.

From 1986 to 2000, return from one year to the next was determined in 136 instances for males and in 134 instances for females, and of these, 97 (71%) and 97 (72%), respectively, were returning birds. Some individuals failing to return were perhaps on territory elsewhere and could have easily escaped notice. In 1980-85 we did find several birds that had relocated, and they comprised about 5% of the observed sample. On this adjusted basis, at least 76% of our more recent sample was still alive at the end of the year.

The sources of bias in this estimate are several. All released falcons and many wild nestlings received a USFWS aluminum band on one leg and an anodized marker band on the other. The neutral color of the Service band was more difficult to detect than the dark marker band. If the former were overlooked in the subsequent year, a new bird would be recorded which would bias return rate downwards. Further, if the same bird returned yet a third year and the aluminum band were then detected, another instance of failure to return would be tallied. Accidental transposition of the color pattern of bands between legs would have had a similar result. Colored bands fade in time. Colored tape placed on bands at hack sites to facilitate identification sometimes persisted variously into adulthood. Finally, through the years we recorded band combinations, there was some unknown chance, thought to be small, that a bird could be replaced in a subsequent year with an identical band pattern or head plumage pattern.

In view of these sources of error, our estimate of survivorship of about 76% is probably too low. The actual value is perhaps close to 80%. This is still less than the 89% survivorship found in peregrines in Scotland where banded birds were actually retrapped so the bands could be read (Mearns and Newton 1984). However, this high return rate resulted only after a correction factor of about 10% allowing for birds not returning but found on another territory. Without that correction the value from Scotland would have been close to 80%. In any case, adult survivorship would be expected to vary by region and through time. The Colorado population was expanding rapidly during the time of our study. The presence of vacant cliffs may have caused some adults to move so that they fell missing in former haunts.

MOVEMENTS AND WINTERING AREAS

Movements of Juveniles

We learned little about post fledgling movements of Colorado peregrines. On several occasions, nestlings were equipped with transmitters to follow movements but the results were poor. All 3 radio-tagged young on the Dolores River in 1978 were killed by eagles. On the Front Range, several telemetered broods succumbed to owl predation, and the fledglings at another site disappeared within 2 weeks after leaving the nest. A wide area around the site was searched from aircraft, but none was found. Efforts to track telemetered fledglings in 1996 at 3 adjacent sites also failed.

A banded young that fledged on 6 July 1983 was discovered with a fractured wing within the immediate vicinity of the eyrie on 15 September. Another juvenile that fledged in central Colorado on 25 June 1994 struck a wire 9.5 miles (5.9 km) away on 16 August. Observers said the falcon was in the company of 3 other falcons that could have been a family group.

Migration

Band recoveries were reported for 6 juveniles encountered on their first southward migration (Fig. 43). Two were trapped at banding stations near Albuquerque, New Mexico and another was trapped on the Texas Coast. Two others produced in central Colorado died of collisions in southwest Texas. The greatest distance traveled was a male produced in northwest Colorado that was hand caught on the coast of Panama.

FIGURE 43. Locations of banded peregrines encountered during their first fall migration.

FIGURE 44. Locations of peregrine band recoveries encountered during winter months.

Wintering Areas

We received band recoveries that identified wintering areas of Colorado peregrines in Mexico, Arizona, and New Mexico (Fig. 44). One female fledged in southwest Colorado wintered in metropolitan Phoenix.

Winter observations within the state historically occurred in December and January along the Front Range from Fort Collins to Colorado Springs (Bailey and Niedrach 1965). These are assumed to be regionally produced birds because the northern subspecies winters well south of Colorado. Several peregrines wintering in Colorado were associated with pigeons in metropolitan areas and waterfowl concentrations in the wild. A staff member at the Monte Vista National Wildlife Refuge in the San Luis Valley related a story about a flock of teal that regularly frequented the open water near an irrigation headgate. As he made his rounds to adjust water flows, the teal would flush, and a peregrine would appear overhead and dive on the teal as they took flight. As the winter wore on, only 1 or 2 teal remained. They refused to fly. Unfortunately, over the past decade waterfowl concentrations have been reduced at the refuge to avoid fowl cholera outbreaks and recent peregrine sightings have been scarce.

Another winter encounter involved an adult female that wintered at the railroad yards in Grand Junction in 1985 and 1986. She probably fed upon pigeons from flocks in the vicinity. Early in the spring of 1987, she was discovered with a fractured wing and was rehabilitated and released nearby at Colorado National Monument in the fall of 1987. Subsequently in 1988 and 1989, she successfully produced young in Dinosaur National Monument.

Another female produced near Rocky Mountain National Park wintered her first year at the Rocky Mountain Arsenal. She was observed preying upon pigeons. The adult female peregrine wintering in downtown Denver in 1992-93 may have been the same individual.

Dispersal to Breeding Sites

The dispersal of juveniles from their nest or release sites and eventual settlement at breeding sites was documented for 15 individuals over the course of the investigation (Table 14, Fig. 45). Sexes were nearly evenly distributed among the young that dispersed. The average distance males moved from their natal areas to breeding sites was 24 mi (39 km), significantly less (Students' t-test, $P = 0.001$) than dispersal distances for females which averaged 159 mi (256 km). The mini-

Table 14. Dispersal of juvenile Colorado peregrines to sites where they eventually nested.

Natal Region	Status	Sex	Band Date	Recovery Date	Age (yr.)	Recovery Location	Distance (km)
East Slope	wild	male	24 Jun 89	14 May 94	5	East Slope	60.4
East Slope	foster	male	19 May 87	4 Oct 94	7	East Slope	11.7
East Slope	hack	male	14 Jun 89	5 Jan 94	5	East Slope	10.5
East Slope	hack	male	7 Jul 89	31 May 96	7	East Slope	22.1
East Slope	hack	female	3 Aug 89	13 Jul 94	5	East Slope	42.6
West Slope	foster	male	7 Jun 84	15 Jun 86	2	West Slope	91.7
East Slope	wild	female	21 Jun 88	19 jun 92	4	East slope	185
West Slope	wild	female	22 Jun 91	4 Jun 96	5	West Slope	22.5
West Slope	foster	male	24 Jun 76	20 May 83	7	West Slope	32.2
West Slope	hack	male	29 Jun 81	1983,84,85	2,3,4	West Slope	46.7
East Slope	hack	female	4 Aug 82	May 83	1	Questa, NM	405.6
West Slope	wild	female	16 Jun 88	13 Jul 95	7	Grand Can., AZ	474.75
West Slope	wild	female	18 Jun 97	20 May 95	8	Capitol Reef, UT	275.2
West Slope	foster	female	24 May 85	22 Jun 95	10	Lake Powell, UT	437.75
West Slope	wild	male	13 May 89	31 May 01	12	Denver, CO	347.6

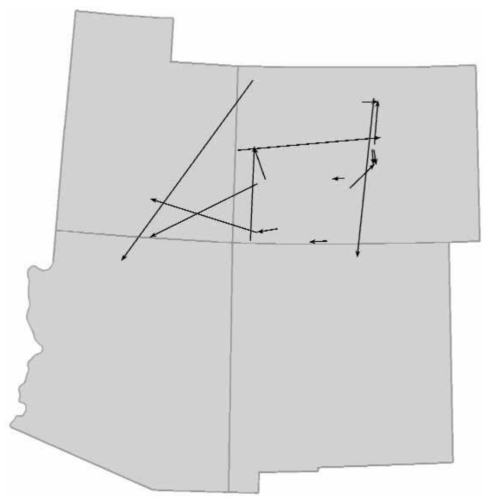

FIGURE 45. Dispersal of peregrines from natal area to breeding site.

mum distance that males relocated was 6.5 mi (10.5 km) and the maximum was 57 mi (91.7 km). A male produced on the West Slope in 1989 was observed on a Denver building in June of 2001. His behavior suggested that he may not have been breeding in the area. If he was, the movement of 216 mi (348 km) from his natal areas is extreme. Female movements were 26.7 mi (43 km) (minimum) and 295mi (475 km) (maximum), respectively. A differential movement of sexes from natal areas to breeding grounds was also observed by Mearns and Newton (1984) in Britain where 15 males and 24 females averaged 12.4 mi (20 km) and 42 mi (68 km) respectively.

FUTURE FIELD WORK

Monitoring

Inventory of nesting pairs is probably the only effective method of monitoring such a mobile, wide ranging species and should continue at least on an intermittent basis. DDT was responsible for catastrophic declines in productivity in the past and it may be a problem in the future. Although DDT application for most uses in the United States was banned in 1972, several proponents have urged its use to control agricultural pests and arthropod-borne diseases. Regular inventories may provide an early warning of an impending population decline. For example, vacancies at nest sites may be the only clue if West Nile Virus were to cause direct mortality range-wide.

A recent example is the poisoning of several thousand wintering Swainson's hawks (*Buteo swainsonii*) in Argentina (Goldstein et al. 1999). If researchers had not been at winter roosts to document the die offs, the only indication of trouble in the United States would have been the sudden reduction of nesting Swainson's hawks the following spring. There would be no clues to their disappearance. In fact, the disappearance might have been unnoticed for several years since we do not monitor the status of this relatively common summer resident.

The recent appearance of West Nile Virus decimated corvids in some regions and caused the deaths of hundreds of raptors (Saito et al. 2003). Birds suffering from WNV that are most frequently encountered are associated with urban habitats, perhaps because people are present to notice them. The high incidence of infected red-tailed hawks (*Buteo jamiasensis*) and great horned owls may be due to their association with suburban locales. However, it is unlikely that raptors such as goshawks and peregrines will be encountered in substantial numbers since they inhabit remote, unpopulated regions. The only effective way of determining the effects of WNV or other agents that cause adult or embryonic mortality is to monitor the birds when they are sedentary during the nesting season. We recommend the establishment of long-term, standardized monitoring protocols.

Field investigations can assess population expansion by monitoring occupancy of nest sites and periodically surveying potential habitats. Catastrophic loss of adults from environmental toxicants or disease would be reflected immediately by nest site vacancies. However, if population decline results from poor recruitment, site occupancy might not be easily detected because breeding birds would be initially replaced by non territorial "floaters" delaying site vacancy. Should chemical contamination occur, periodic collection of whole eggs may yield insight of relative pesticide loading. Periodic collection of an egg from a sample of clutches would assess contaminant loading.

Occupancy Level

An 80% occupancy rate of useful nest sites was a reference value based on pre-DDT populations suggested in the Rocky Mountain/Southwest Peregrine Falcon Recovery Plan. That level was achieved in 1991 and exceeded 1994-2001 (Fig. 46). A markedly low occupancy rate would be the ultimate indication of population decline, resulting from adult mortality not countered by recruitment when nonbreeding replacements are unavailable. If adult mortality were accelerated, increase in nest vacancy would be rapid. If a population decline was caused by reproductive failure, the time lag could be greater as breeders died and were not adequately replaced. Occupancy would decline only after all the non-breeding replacements (floaters) were recruited and eventually died.

Occupancy surveys should also include visits to potential cliffs as well as documented sites. Otherwise, the effort will be biased because attrition inevitably occurs as some sites are no longer suitable or pairs relocate elsewhere in the vicinity. Occupancy of previously surveyed, potential sites might also indicate continued population expansion if pairs are discovered. We also expect lower class (less dominant cliffs) to be occupied as the nesting population approaches equilibrium. Vacancy of less dominant sites should be expected and may occur intermittently as pairs fail and relocate to more substantial cliffs. However, accumulating abandonment of the lower class sites may be an early warning of a more extensive region-wide population decline.

Measures of Productivity

We have found that productivity (mean number of young fledged per pair) in

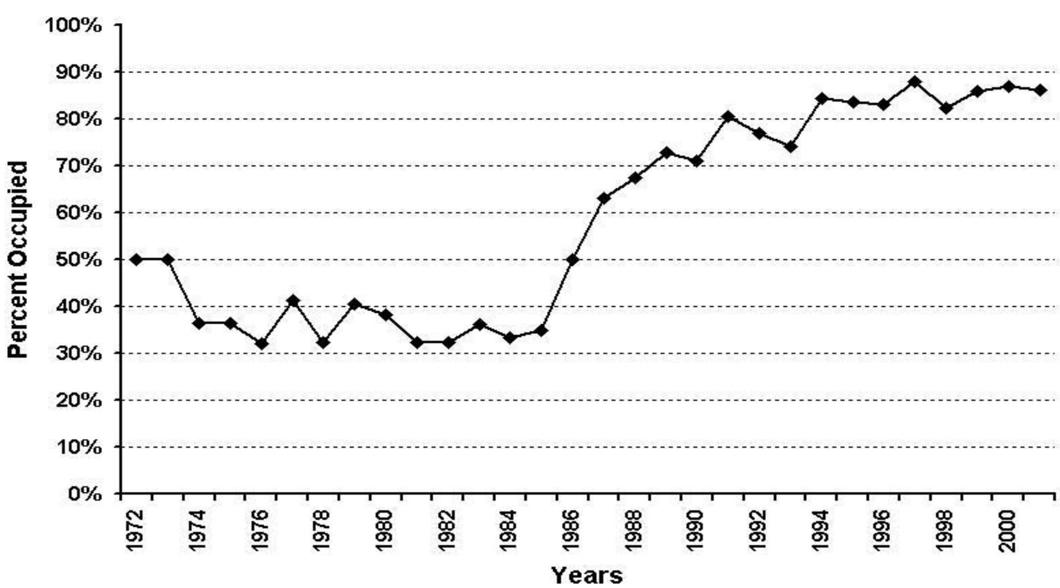

FIGURE 46. Occupancy rate of monitored peregrine nest sites in Colorado.

Colorado is markedly variable among years, and may fluctuate by almost 0.8 young on average (Table 15, Fig. 47). We urge the establishment of annual or biennial inventories to evaluate long-term trends in occupancy, breeding, and productivity.

Through 1992, all known peregrine nesting territories were surveyed annually to acquire occupancy, productivity and nest success data, but by 1993, the number of known territories had increased to 82 and survey teams could not visit all the sites. Funding constraints reduced the number of teams that could be fielded and a sampling protocol was investigated. When sampling peregrine productivity, only 5 outcomes can occur ranging from no young to a maximum of 4 fledged in a brood. This variation results in large variance of the mean. Figure 47 depicts the 95% confidence intervals around the mean productivity for each year 1986-2001. In all years except for 2001, confidence intervals overlapped. As the sample size (pairs) increased, the variability decreased, but even with a sample of 98, the confidence interval is large enough (±0.27) to cause uncertainty regarding reproductive trends. The purpose of monitoring productivity is to detect actual change and a confidence interval of ±0.30 includes a range of 1.5 young per pair which is associated with a stable or expanding population to and a pro-

Table 15. Productivity of indicator nest sites compared to all sites checked in Colorado. Indicator sites are a subset of 44 nest sites that reasonably reflect occupancy and reproductive performance statewide.

	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
Indicator Sites	2.14	1.16	1.73	1.85	1.90	1.69	1.60	1.95	1.60	2.17	1.76	2.15	1.43
All Sites	2.06	1.48	1.65	1.69	1.65	1.63	1.37	1.71	1.42	1.88	1.56	2.04	1.44

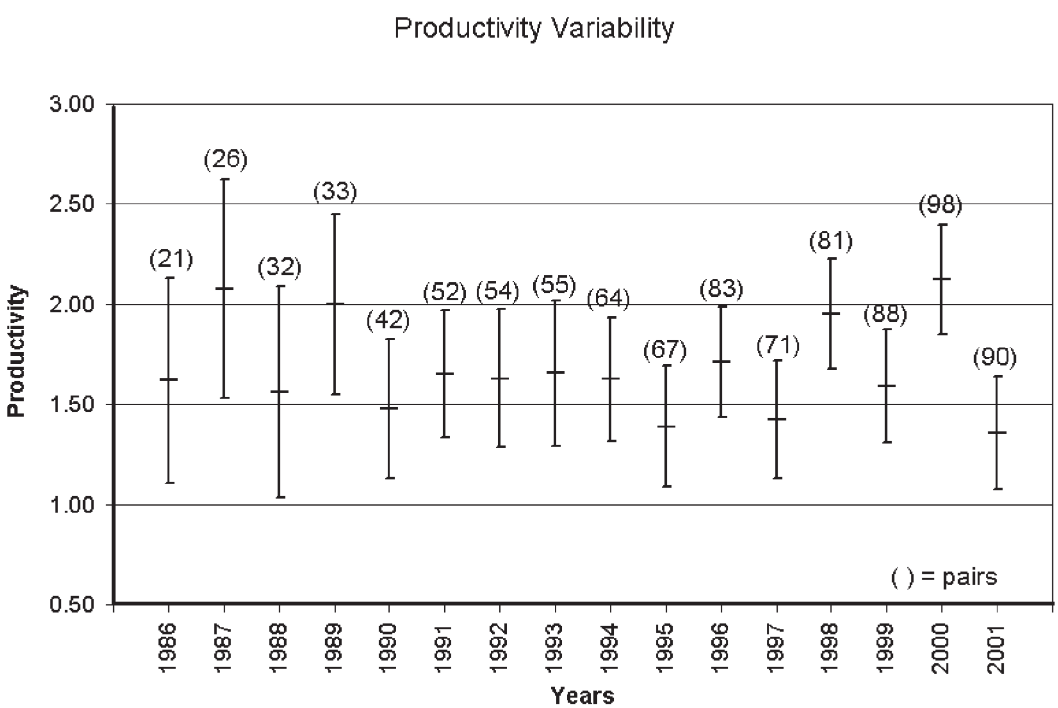

FIGURE 47. Annual estimates of mean productivity of Colorado peregrines. Augmented pairs are not included. Bars are 95% confidence intervals.

ductivity of 1.2 (Fig. 38), which may represent a declining population.

An alternate approach that circumvents the variability of sampling was to select a subset of the statewide population and monitor them annually instead of the entire population. Productivity obtained directly from the indicator subset provided data of the same quality that can be assessed for trends. The assumption was that any changes in annual productivity occurring on the population level also would be reflected by the subset. If occupancy and productivity of the subset declined sufficiently, the investigators would make an informed judgment and expand the monitoring effort, if necessary.

In Colorado, we chose 42 sites as indicators plus 2 alternate sites if sites were rendered unsuitable for occupancy. Selection was not random; in fact an effort was made to select a subset that reasonably reflected occupancy and reproductive performance statewide. In order to monitor trends, the selection was made from the pool of 82 sites on record in 1993. The list was refined to 42 sites by dropping those with long histories of vacancy (14 sites) or access difficulty (10 sites) and those that were not known prior to 1989. The proportion of indicator sites in relation to all has decreased in recent years as new locations are added to the record (Fig. 48). Inventories of productivity at 42 sites require approximately 4 visits to each site from April through July which totals 160 visits. This can be accomplished by 2 teams comprised of 2 experienced observers.

The subset approach appears to be an efficient means of monitoring Colorado peregrines with the least expenditure of funds. It would assure long-term continuity of productivity data since information on the majority of sites in the subset has been collected since at least 1989. Surveys of indicator sites will also reveal site occupancy and other reproductive parameters. If a downward trend in productivity or occupancy in the indicator subset were revealed, then a more expansive investigation of the population could be implemented.

To test the usefulness of the indicator subset in predicting the performance of the entire population, we monitored most of the

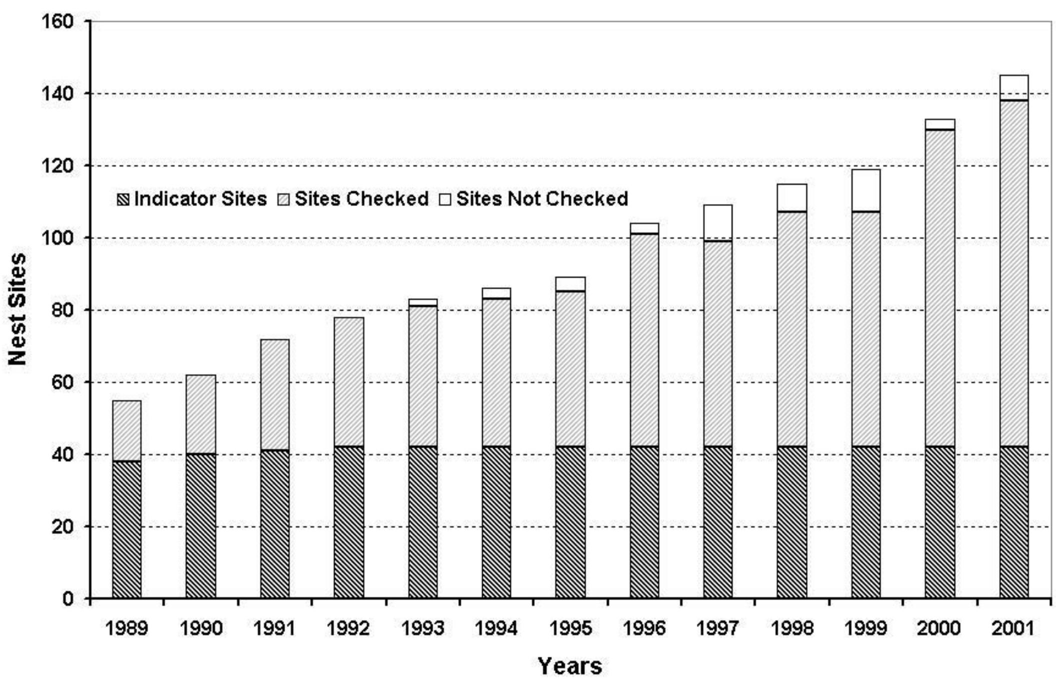

FIGURE 48. Relation of indicator sites to all sites on record. Indicator sites are 42 nests sites that were selected to be representative of the statewide peregrine population.

other known territories throughout the state and compared them to the 42 selected sites (Fig. 49). The subset generally mirrored the productivity of the statewide total, although subset productivity was consistently higher than the total in all years except 2001 when productivity was lowest (Table 15). This bias may result from more intensive monitoring of the subset to determine the outcome of each. However, some of the non-indicator sites were visited only once or twice and outcomes were not known. If a non-indicator site received a single visit when the pair had unfledged young, an unknown outcome was recorded even though young might have fledged. However, if a non-indicator site received a single visit after the adults had failed, but were still present, a known outcome (failure) was recorded. This process tended to under represent actual productivity among the all sites.

We examined the possibility that discovery of new nest sites might inflate productivity (Steenhof and Kochert 1982), but found use of data from new sites had little effect (see Reproduction Biases). We also considered the possibility of bias resulting from more intent observation at indicator sites. The subset approach was first implemented in 2000, and the 1989 - 99 observations were drawn from an unbiased statewide monitoring program. We cannot explain the disparity in productivity between the indicator subset and the total statewide sample. Occupancy and breeding attempts may be evaluated statistically, but due to variability, productivity may best be assessed by monitoring a number of representative sites and then make an informed judgment.

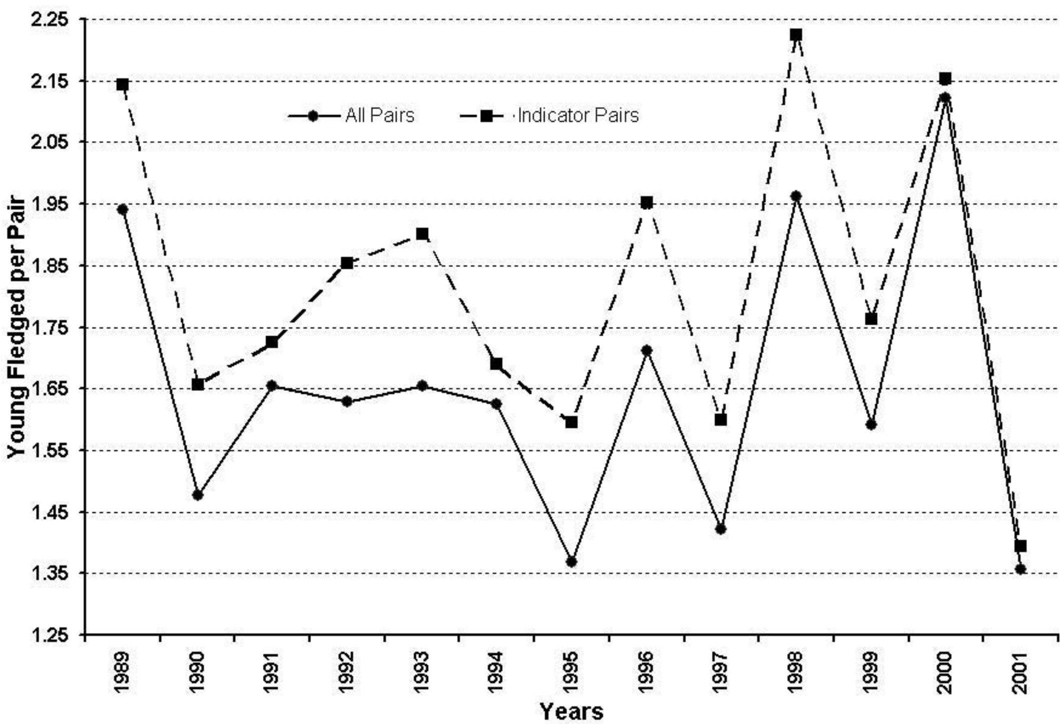

FIGURE 49. Productivity of all pairs compared to indicator pairs. Indicator sites are 42 nests sites that were selected to be representative of the statewide peregrine population.

OVERVIEW

Over the past 3 decades, Colorado's peregrine falcons have rebounded from near extirpation with only 8 known pairs in 1982 to a robust population of 115 known pairs in 2001. As pesticide contamination diminished, expensive and aggressive intervention infused 500 captive hatched young and helped to sustain and augment the wild birds in the critical period. It is possible that Colorado's peregrine population could continue to expand to as many as 180 to 200 nesting pairs. The species has been de-listed both on the state and federal level, but will probably always remain of special concern given the relatively small population and high public interest.

Peregrines have proven resilient and can adjust to some disturbance and habitat loss as evidenced by their continued presence near human activity in Colorado. Elsewhere, they have colonized metropolitan areas. Locally however, increasing urbanization, mineral extraction and water development will alter historical breeding and foraging areas. The potential of environmental chemicals also need to be considered as exemplified by deaths of tens of thousands of Swainson's hawks brought on by use of insecticides in Argentina (Goldstein et al. 1999). Because of greatly increased human mobility, wildlife is being exposed to foreign diseases beyond our control. The recent West Nile virus epidemic and the outbreaks of avian flue in Asia demonstrate the profound effects of exotic diseases that may directly or indirectly affect falcon survivorship (McLean 2002). The West Nile virus has spread across the continent in less than 5 years and long term effects upon our avifauna are as yet unknown. In Colorado, county health departments initiated extensive fogging and aerial spraying to control mosquitoes, regionally decimating many non-target insects.

Although application of DDT was banned since 1972, agricultural interests have urged permitting its use. African countries petitioned to use DDT for malaria control citing loss of millions of people to malaria annually. Locally, health officials may also promote DDT to counter West Nile Virus outbreaks. We urge biologists to remain vigilant so that downward changes in peregrine populations will be detected in time to respond with regulatory or management actions.

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GLOSSARY

Augmentation	- increasing productivity rate through fostering.
Breeding pair	- a pair that lays eggs.
Clutch	- eggs laid in one set.
Cliff orientation	- the direction a cliff faces.
Cross-fostering	- placing captive hatched young in the nest of another species.
Eyrie	- generally refers to a cliff used by nesting falcons; also refers to the ledge where the eggs are laid.
Falcon nest	- the ledge or stick nest where the eggs are laid
Fledgling	- when a young falcon first flies from the nest ledge.
Fledgling rate	- mean number of young fledged by successful pairs.
Fostered pair	- a pair receiving captive hatched young.
Fostering	- placing captive hatched young in a nest attended by a breeding pair.
Hacking	- Releasing and caring for young at a site where adults are absent.
Monitoring	- systematic counts of pairs and young over several years.
Nest success	- percent of nests that fledge one or more young.
Nesting population	- number of pairs known on territory.
Occupied site	- a cliff with one or two peregrines in residency.
Productivity rate	- mean number of young produced by all pairs on territory.
Range	- the area in which members of the pair hunt.
Recycle	- removal of the first clutch of eggs causing the pair to renest and lay a second clutch.
Scrape	- the indentation on the nest ledge where the eggs are laid.
Survey	- a search for newly occupied cliffs.
Territory	- an area defended by nesting falcons. Since territory is defined by the defending falcons, it ceases to exist when they are not present.

APPENDIX 1.

Peregrine Observers

Colorado Division of Wildlife Observers (team leaders marked in bold)

Alderman, Keith 94
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APPENDIX 2.

Early Accounts of Peregrines in the Colorado Region

Not until the latter half of the 19th Century were peregrines reported in the central Rocky Mountain region. Prior to the 1870s few naturalists were involved in ornithological surveys. In Colorado, the exception was an expedition led by Major Stephen Long in the summer of 1820. The party included a botanist, Edwin James, and an ornithologist, Thomas Say. They entered Colorado from the east along the South Platte River, searched the Front Range south to the Arkansas River, and recorded common species, such as the blue grouse (*Dendragapus obscurus*), for the first time. Without doubt, the expedition passed within a few miles of several cliffs now used by peregrines. Failure to notice the species cannot be attributed to lack of effort in general; Edwin James led a small group in the first ascent to the summit of Pike's Peak.

Apparently the first report of peregrines in Colorado was by Joel A. Allen who in 1872 saw the species in the Garden of the Gods near Colorado Springs, at Castle Rock, and on Bear Creek near Denver (Sclater 1912). The Castle Rock record is interesting because the site has been used for decades by prairie falcons, and is a setting typical of that species in the area. Allen wrote the Garden of the Gods site was also used in 1871, an account perhaps given to him by another observer. Allen went on to Montana where he reported peregrines on the Musselshell River, and in Utah he recorded peregrines near Ogden in September 1872. Strangely, he did not mention prairie falcons in Utah; this raises the possibility of confusion between the two falcons. Did Allen misidentify prairie falcons as peregrines? However easy that error, the Garden of the Gods record is supported by later records of peregrines.

Charles Aiken collected a peregrine in the Garden of the Gods in 1879 (Henderson 1903) and again in 1884 (Sclater 1912) and the species nested there at least until 1901. Apparently prairie falcons were contemporary with peregrines at the Garden of the Gods, and the former persist to the present. Incidentally, William L. Sclater held the peregrine in disdain. In his book, A History of the Birds of Colorado, he wrote "one of the few birds of prey in whose favor little can be said."

In his treatise on North American birds, Charles Bendire (1892) reported that Dennis Gale collected peregrine eggs at Gold Hill in Boulder County and at Cache la Poudre Creek near Fort Collins. Bendire provides an excellent lithograph of one of the eggs from the latter locations. The egg is evenly colored and medium in size, not clearly distinguishable from eggs of prairie falcons; the possibility of misidentification exists. W.W. Cooke (1897) refers to the two locations visited by Gale, and additionally reports that W.P. Lowe found young in St. Charles River canyon southwest of Pueblo, Colorado, in 1895. The latter gorge is shallow and today has at least two pairs of prairie falcons. Cooke considered peregrines "locally common" in Colorado. Another 19th Century record is at Caulkins Lake, just north of the Boulder County line, where Gale saw a pair nesting in 1889 (Henderson 1909). The validity of this report is doubtful; there are no cliffs in the vicinity of the present day Caulkins Lake.

In 1924 peregrines were reported nesting near Grand Junction, Colorado, by A. Benson in the bird migration file of the Bureau of Biological Surveys. Two pairs were reported in 1937 near Estes Park, Colorado, by R.K. Grater in a check-list of birds of Rocky Mountain National Park. He made his observations with H.C. Bryant and H.R. Gregg. Actually, a pair had been reported at Stanley Meadows near the town several decades earlier (Kellogg 1890). R.K. Grater, in a mimeograph report on bighorn sheep, mentioned peregrines nesting in the Black Canyon of the Gunnison National Monument in 1937, the same year he also saw a bird he believed nesting in the North St. Vrain canyon near Rocky Mountain National Park. To our knowledge, this latter area has not been checked since then. Pairs are now persistent in the Grand Junction area, near Estes Park, and in the Black Canyon.

In 1934, Game and Fish Laws in Colorado encompassed one page that established open seasons for harvest of fish and game animals. Also listed were protected species as follows:

> NO OPEN SEASON on Mountain Sheep, Antelope, Bear, Beaver, Turkey, Upland Plover, Ptarmigan, Partridges, Pigeon, Quail, Dove, Wood Duck, Swan, Eider Duck, Crane, Curlew, or any other wild non-game bird. (EXCEPT ENGLISH OR EUROPEAN HOUSE SPARROW, SHARP-SHINNED HAWK, COOPER'S HAWK, GOSHAWK, DUCK HAWK, GREAT HORNED OWL, PINON JAY, MAGPIE, BLUEJAY AND EAGLE.

Accipiters and duck hawks (peregrines) presumably killed poultry and game birds and eagles attacked livestock and were to be killed at every opportunity, a belief that prevailed among game managers until the early 1960's.

Despite its probable wide distribution where tall cliffs occurred in Colorado, the bird remained little known up to the 1960s. In 1940, Robert J. Neidrach of the Denver Museum of Natural History said he had yet to encounter nesting peregrines in the state. Finally, in 1943 he saw the species near Pagosa Springs, Colorado (Bailey and Neidrach 1946). French reported an eyrie near Boulder that was occupied until 1958 when a falconer removed all the nestlings (Bailey and Niedrach 1965). The site was abandoned from 1974-94. It was reoccupied by a pair in 1995. Other reports of peregrines nesting in Colorado came from O.A. Knorr (1959). He mentions two localities in El Paso County near Colorado Springs, which were occupied in the late 1940s and early 1950s (Fig. 50). These were in addition to the then vacant eyrie in the Garden of the Gods. Recently, we were able to discuss these sites with Knorr; one has been used steadily in the last decade, and the other, clearly typical of peregrines, was reoccupied in 2003.

In 1963, J. Stoddart (pers. comm.) learned of a fledgling peregrine found wounded beneath a cliff in Jefferson County, Colorado, not far from the town of Golden. A pair was present in 1963 and in 1964, but this site was vacant until 2003. Up to 1964, no dedicated surveys had been done in the Rocky Mountains or the Colorado Plateau. Westward, R.M. Bond (1946) collated data on locations mainly in Oregon, Washington, and California; he considered the bird exceedingly uncommon in the Rocky Mountains.

FIGURE 50. Eyrie in abandoned golden eagle nest with 3 spoiled eggs near Husted, El Paso County. Male was still incubating on July 10, 1949.

Photo courtesy Vern Seifert

APPENDIX 3.

Chronology of Peregrine Recovery Events

Aug. 29-Sept. 1, 1965. - Conference convened at Madison, Wisconsin to review and discuss the national decline in peregrine falcons. Results published in the book Peregrine Falcon Populations: Their Biology and Decline edited by J.J. hickey (1969).

Jan. 1972 - Colorado Division of Wildlife hires a nongame biologist and a raptor biologist.

June 1972 - Environmental Protection Agency bans application of DDT for agricultural purposes.

May 1973 - First peregrine of the *anatum* subspecies was produced in captivity by J.H. Enderson

May 11, 1974 - First foster attempt occurs at Royal Gorge containing 2 eggs which were replaced with 2 wild prairie falcon eggs that hatched and were subsequently replaced with 2 peregrine falcon chicks hatched at the Peregrine Fund's facilities in Ithaca, New York.

Nov 1974 - Peregrine Fund begins construction of breeding barns at their western facility on the CDOW Research Station at Fort Collins.

1975 - Enderson transfers 17 breeders and their young from his facilities to form the nucleus of the Peregrine Fund's Fort Collins breeding stock.

May 19, 1975 - First manipulation wild nesting peregrines was attempted. Only 7 sites were occupied and 5 pairs produced eggs. Two eggs from a clutch of 4 were removed from a Front Range nest and taken to Enderson's facilities for artificial incubation. After both eggs hatched, the young were returned at 5 days of age. The adults had abandoned the 2 unhatched eggs (one with a hole, the other missing) and did not accept the chicks. One young was added to a brood of 4 and the other was placed with to a brood of two.

Apr. 15, 1976 - First recycle of wild peregrines was successfully attempted. Two eggs of an incomplete clutch were encountered at the same Front Range site that manipulated in 1975. One egg was very thin and cracked and was replaced with a replica. Six days later later 2 more eggs were replaced with replicas. All 3 replicas were removed on April 22. The pair recycled and laid 4 eggs that were replaced with replicas on May 18. On May 28, the replicas were replaced with two 7-day-old prairie falcon chicks that were then exchanged for two 3-week-old peregrine chicks on June 2.

Aug. 3, 1977 - Recovery Plan for the American Peregrine Falcon (Rocky Mountain and Southwest population) was approved by the U.S. Fish and Wildlife Service.

1978 - Peregrine Fund initiates the first western hack site at Rocky Mountain National Park.

1982 - All sites east of the Continental Divide were abandoned. Only 7 breeding (egg producing) pairs existed west of the Continental Divide.

Dec. 4, 1984 - Revision of the Recovery Plan for the American Peregrine Falcon (Rocky Mountain and Southwest population) was approved by the U.S. Fish and Wildlife Service.

November 3-6, 1985 - Conference at Sacramento, California reviewed world wide peregrine population status and recovery. The results were published in *Peregrine Falcon Populations: Their Management and Recovery* T.J. Cade, J.E. Enderson, C.G. Thelander and C.M. White Eds. (1988).

June 1988 – Five peregrines were hacked in downtown Denver. All achieved independence.

June 1989 – Five peregrines were hacked in downtown Denver, 3 achieved independence.

June 1990 – Downtown Denver hacking was discontinued due to presence of a defensive female that returned from the 1988 release.

1990 - Population goals were achieved and augmentation efforts (fostering and recycling) were curtailed.

1991 - Hacking efforts were curtailed.

1993 - Peregrine downlisted from endangered to threatened on Colorado's list of threatened and endangered species. Two out of the three recovery criteria were met and eggshell thickness trends continued to improve.

May 1998 - Peregrine was removed from Colorado's list of threatened species with the provision that population monitoring would proceed for 5 years and that no falconry take would occur.

August 25, 1999 - Peregrine was removed from federal list of threatened and endangered species.

APPENDIX 4.

Field Procedures

Surveys for Breeding Peregrines

Searches for breeding peregrines required hours of tedious scanning with binoculars and spotting scopes at distant cliffs. The monotony was sometimes interspersed with moments of charged tension caused by the brief sighting of a flying falcon. Sometimes the bird vanished at a critical point. The purpose of field observations was to document behaviors associated with a particular stage of the reproductive cycle. Once the stage of reproduction was determined, dates of hatch and fledge were estimated so that the observers could return at appropriate dates to count young and document fledge.

The monitoring protocol we used was refined over several decades of surveying cliffs and observing breeding peregrines. We used the following procedures when surveying for peregrines or monitoring occupancy and reproductive success.

Field Teams

Although a single, experienced observer can accomplish the job, we usually sent teams of two people to observe peregrines. A team should comprise at least one member skilled in raptor identification and knowledgeable of peregrine breeding behaviors. The subordinate member, if inexperienced, must be patient, a good observer and willing to learn. Excellent eyesight and hearing are mandatory because of the long distances and faint vocalizations of falcon behaviors. Observers must be able to identify all raptor species where they are working. Valuable insight can be gained by tracking the activities of various raptors that come into view. For example, accipiters rarely draw the attention of peregrines while eagles almost always elicit a vigorous defense. Observers must be able to distinguish prairie falcons and peregrines. Failure in that regard can waste valuable field time. When inexperienced teams were able to observe the nest ledge, they were encouraged to continue to watch the behaviors to gain experience seeing the activity that was ordinarily out of their view.

Team members usually remained together and observed simultaneously. When falcons were in view both members remained vigilant to track flights and followed each bird. When a pair was present each team member kept track of one adult. On occasion, one member relieved the other as notes were taken or lunch prepared. If the team was experienced, the members split up for short intervals to view the cliffs from advantageous observation points. In these situations, radio communication was essential.

Sometimes observation points were more than one-half mile from nest cliffs. Eyrie ledges were often hidden from view in canyons and mountain sides. In these cases, the observers relied on inferences drawn from activities and behaviors of the falcons. When behaviors associated with a particular reproductive activity were not evident to the field observers, it is helpful for them to compare notes and speculate on what they observed. Several visits were sometimes necessary before a pattern of activities emerged. If the reproductive stage was not defined, field notes were read to an experienced biologist. Therefore, it was critical that each observer independently recorded detailed field notes.

As teams gained experience, the length of visits was often reduced. However, the team did not terminate their observations until both members were satisfied further watching was unwarranted. As a guide, field teams watched for a minimum of four hours at each visit to a territory.

Field Notes and Photographs

We found that field observations written in narrative fashion were most effective.

Each observation was preceded by the time it occurred. Notes included sketches of each cliff that identified key features such as important perches, prey caches and nest ledges. Notes included a brief summary including total duration of observations, presence or absence of each adult, reproductive stage, presence of bands or markers, and other biologically important occurrences. Daily notes were duplicated and filed, avoiding loss or destruction.

Photographs of each site a distant view of the cliff, a normal view from the observation point and when possible, telephoto images of each nest ledge. Photographs were usually taken on the first visit so that important features were transcribed on them in subsequent visits. We experimented with instant Polaroid® cameras but photographs often lacked detail and were difficult to reproduce. The best photos were colored 35mm glossy prints. Digital cameras in the 5-6 megapixel range provide sufficient resolution to permit enlargement of distant cliffs for adequate detail of most nest ledges. As soon as possible, the photos should be developed and pertinent information recorded directly on them. Subsequently, the photos can be digitally scanned for panoramas and enlargement of important features.

Use of Optical Equipment

A high quality spotting scope is indispensable. The larger objective lenses (60 mm and more) provide better lighting. Zoom oculars are an advantage, although magnifications over 40 power are rarely used due to loss of light and resolution. We generally scanned cliffs at 15 – 20X and zoomed to higher powers to identify birds or monitor their behaviors. Binoculars with 10X magnification were essential for scanning to locate falcons. A sturdy tripod was necessary to stabilize spotting scopes or binoculars. The tripod should accept interchangeable heads. A "fluid" with a friction adjustment aids in tracking a flying peregrine. Light weight aluminum folding chairs and portable sling chairs make viewing more comfortable.

Visits to Nest Sites

Observations were made at any time of day. Early morning and late afternoon observations tended to be productive since peregrines were active (incubation exchanges and hunting forays) at those times. However, we found that activity also increases at midday when prey and incubation exchanges occurred.

East facing cliffs were best viewed in the morning to avoid backlighting and glare in the optics. For the same reasons, we sought to observe west facing cliffs in the afternoon. Obviously, rain and snow storms reduced visibility. High winds did not seem to affect peregrine activity. However, buffeting can make it impossible to view through spotting scopes.

Teams documented presence of both adults, checked for presence of bands or markers and noted ages and plumage patterns for future reference. Facial color pattern was very important because individuals were often distinct. Observers tried to reaffirm that the same individual falcons were present on each visit. Helmet patterns (placement of narrow or wide cheek stripes) were often individualized and do not change from year to year (Enderson and Craig 1988). A change in the plumage of an individual on a subsequent visit meant replacement and probable interruption of the nesting sequence. Pairs with a subadult member rarely produced young. In Colorado, only two subadult females produced young, and no pairings of subadult males were successful. Subadult plumages were more evident early in the spring but tended to be more difficult to distinguish from adult plumage as the molt progressed.

Once the reproductive stage was known, a visit was scheduled to confirm the next reproductive event. The team then moved on to the next site. However, if the exact onset of the event could not be determined from observations, the team returned within a reasonable period (usually 10 – 14 days) to reaffirm their prediction. We estimated the timing of reproductive events using the following factors. Eggs were laid about every other day. Full time incubation occurred upon clutch completion (up to 4 eggs per clutch) and required about 33 days. Hatching occurred over one to two days and fledgling occurred at 40 days of age (males) and 42 days of age (females).

The number of visits made to a site depended upon the information to be obtained. Documentation of occupancy (presence of adults) could often be accomplished with a single visit. However a return visit was required to confirm no falcons were present on the first visit. Occupancy was ascertained early in the breeding season during courtship or incubation. Later visits tended to under count occupancy because unsuccessful pairs may abandon territories after failure. Complete documentation of nesting through fledgling required up to four visits. The first was made in courtship to locate pairs when they were displaying and most active. A second visit was made to locate potential nest ledges or confirm incubating adults. Depending upon the stage of reproduction observed on the second visit, a third visit was scheduled to confirm that young hatched. The final visit occurred at fledgling, based upon estimated ages of the young present on the third visit. When chick ages were not known, an interim visit was required when the young were likely to be seen moving about the ledge (three to four weeks) so that a fledgling date could be estimated.

In 2000-2001 collectively 511 visits were made to 278 nesting pairs and the teams devoted 1,470 hours of observation of breeding peregrines. Hence, the field teams averaged 1.8 visits per site and spent and about 3 hours in observation per visit to document presence of breeding falcons. In most cases, territory occupancy was confirmed in the first visit. During the same period, 40 additional sites were monitored more closely to confirm fledgling success. These sites averaged 4.5 visits and 3.26 hours of observation per visit. The number of visits ranged from one to eight, and hours of observation expended per visit ranged from 15 min. to 8 hours. We believe that teams should plan a minimum of four visits to confirm fledgling success. Although serendipitous circumstances may reduce the length of visits, about four hours of observation was normal although up to eight hours of observation may be required on occasion.

When the number of young in the eyrie could be determined, the maximum possible number of flying young was of course known. Unfortunately, counts of nestlings were not usually made. Observers often devoted six to eight hours to be certain all the fledged young scattered about the cliff were tallied. Over the course of our investigations, we encountered only one clutch of five eggs and no broods exceeded four young.

Nestlings were most easily counted immediately prior to fledgling since they were conspicuous as they exercised or converged when prey was delivered. After the first flight they became scattered about the cliff and on the talus and were difficult to locate. Once well on the wing, they were noticeable as they pursued the adults and each other.

Counts made solely several days or weeks after fledgling might seem the most economical use of limited observers. However, these counts may underestimate the number of young actually fledged due to early attrition resulting from accidents and predation.

Nesting Behavior Useful in Field Observations

Behaviors of adults were used to understand the status of the nesting attempt. When either or both adults went on a ledge for only several minutes early in the season, nest ledge selection or scrape preparation was suspected. If one adult remained on the ledge for long periods, incubation or brooding was indicated. Both adults assumed roles in these activities and switched places at the nest with a minimum of overlap. The casual observer might have thought only one bird was present, making a quick visit, then leaving; in reality, a nest duty exchange had occurred.

Prior to hatching of eggs, prey was rarely carried to the nest ledge. When prey was transferred to the female in the air, the male usually sought to incubate the eggs.

When young were present, prey usually was transferred from the male to the female and then was taken directly to the ledge. Females usually fed small young, but simply dropped off prey when the young were three weeks old. Both adults cached excess food in nooks about the cliff and were fully capable of recovering food stored in this way. Sometimes females stopped brooding, flew to a cache, and returned to the ledge to feed young. Large young required lots of food and it was rare for a male to arrive with food without a delivery to the female or the young.

When young were present, the adult female was usually present on the cliff. Females did most of the brooding and incubation. Females will hunt near the cliff locally when young no longer require brooding. Regardless of age of the young, females usually remain on the ledge in inclement weather.

Females repeatedly gave the "wail" call when hungry. A successful male also "wailed" when returning with prey. This call stimulated the females to streak from the ledge to intercept the incoming mate, sometimes a few hundred meters from the cliff. Peregrines gave the "echup, echup" call as a recognition of another adult. We never heard the call by a bird known to be alone and always assumed a pair was present. The defense "cack, cack" vocalization was given by both sexes when eggs or young were present. The presence of other raptors (especially golden eagles) and occasionally the observers would elicit the call. It would be brief or absent if young or eggs were not present.

FIGURE 21. Helicopters were often used to access remote cliff tops to reduce transport time for manipulated eggs and return of fostered young.

Transportation of Eggs and Young

Fostering required expeditious transportation of eggs removed from wild pairs to incubation facilities, and both fostering and hacking used young brought from The Peregrine Fund. Aircraft (Fig 51) were often employed to reduce transport time and avoid injury to eggs and young in rough terrain. Eggs were transported in a padded portable incubator operating on 12 volts (Fig. 52). Humidity was maximized by wet sponges. On occasion, eggs were held overnight when more than one day was required for visits to several eyries. From the moment eggs were collected, great care was taken to avoid damage to embryos by con-

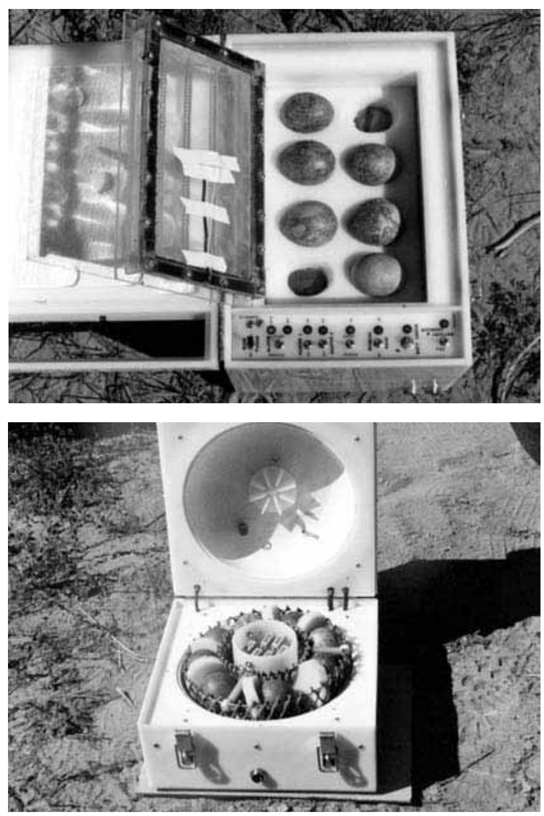

FIGURE 52. Portable incubators for transporting peregrine eggs. Heat provided by water bath in lid (*top*). Heat provided by resistors in center compartment and circulated by fan in the lid (*bottom*).

cussion. Foam rubber pads were used to cushion the portable incubator in vehicles and aircraft.

We experimented with several models of portable incubators in the course of this work. Initially we built an incubator that used an ether wafer to regulate temperature. The ether wafer type control yielded inconsistent temperatures when passing over mountain passes. At higher elevations, the wafer expanded prematurely reducing temperature within the incubator; then, when reset it would overheat the incubator at lower elevations. At one point, the wafer began to leak but the problem was discovered before the eggs were compromised. The ether wafer was then replaced with a mercury thermostat which performed reasonably well. In later incubators, the temperature was controlled electronically with thermisters. The first heat source was a heated hot water bottle within an insulated box. The temperature constantly changed and required frequent stops to reheat the water, often from a Coleman stove at the side of the road. A second heat source was a brake light bulb but the incubator did not maintain uniform temperature. Succeeding generations used a electrically heated hot water pillow, then eventually forced hot air. The incubators were powered from vehicle batteries in transit and transformers could convert to 120 volts as appropriate. The last adaptation was a small circular Rollex® incubator that had been altered to firmly cradle eggs. The incubator was normally 120v but was operated by a portable generator in transit.

The primary aircraft used for long distance transport of eggs and young was a Beechcraft C-35 Bonanza flown by J. Enderson. The plane was fast and the cabin could accommodate up to seven cartons holding a total of 21 three-week old peregrines. Four flights were made 1982 - 83, but became more numerous when The Peregrine Fund moved to Boise in 1984. Often multiple stops were made to drop off young from Boise at airports near widely separated release sites in Colorado. Up to 17 eggs were transported on a single flight. Flights ceased in 1990 when releases ended. In 1984, the number of flights peaked at 10, and in all, 38 flights were made covering a distance of more than 54,000 miles. Total time flown was about 360 hours. After 1983, nearly all of the eggs taken in fostering activities, most of the young hacked in Colorado, and many young also released in northwest Wyoming were transported in this airplane. Surprisingly, only two flights could not be completed because of weather; the aircraft was not equipped for instrument flying. In both cases transportation was quickly accommodated by vehicles. Upon arrival at the cliff, nestlings were transferred to wicker pack baskets for their final journey to the nest ledge (Fig. 53).

FIGURE 53. Bi-level pack basket used to transport fostered young to the eyrie.

APPENDIX 5.

Methods of DDE Analysis and Eggshell Thickness Measurement

Whole unhatched eggs and eggshell fragments were collected opportunistically during fostering activities and routine visits to eyries to band nestlings. Fostering involved removing entire sets of eggs before hatching, replacing them with replica eggs, artificial incubation of the wild eggs, and early rearing of hatched young. Later an entire brood of typically three-week old young were placed in the eyrie and the dummy eggs removed. Unhatchable eggs were wrapped with acetone-washed foil, and stored frozen. Later the contents were allowed to thaw slightly, the eggshell cut around the equator, and the contents stored frozen in an acetone washed jar with a foil liner in the lid. The half shells were then rinsed clear of egg contents and dried thoroughly.

Organochlorine Analysis

Oganochlorine analyses were accomplished using accepted extraction, cleanup, and GLC techniques by the USFWS laboratory at Patuxent, Maryland, Raltech Scientific Services at Madison, Wisconsin, the Mississippi State Chemical Laboratory under contract to the USFWS, and Long Marine Laboratory at the University of California, Santa Cruz. Only DDE is considered here because it alone causes significant shell thinning in peregrines (Peakall and Kiff 1988).

Egg contents were shipped frozen on dry ice, but sometimes thawed enroute. DDE amounts are reported here on a fresh wet weight basis. Included in the lab results was percent moisture of the sample tested. That value was used to adjust (usually downward) the reported DDE value to reflect a result had the contents been fresh. We assumed fresh egg contents contain 85% moisture.

Eggshell Measurement

All eggshells were measured optically. The freshly broken shell viewed edge-on with a microscope using and ocular scale calibrated with a stage micrometer, accurate to 0.004 mm. When shells were sufficiently intact so that the equator could be identified, three thickness measurements were spaced evenly around the waist. These measurements were averaged and considered representative of the whole shell. When more than one such whole shell determination was make in one clutch, the mean values for each were averaged. All eggshells in this report have been archived at The Peregrine Fund, Boise, Idaho.

Usually several fragments were found on each ledge when banding was done. All fragments large enough to handle were measured. The thickness values for all fragments from the same eyrie were averaged. Seldom was it possible to determine the number of eggs represented by fragments from an eyrie. Further, eggshells are several thousandths of a millimeter thinner at the poles compared to the equator. Because our samples of fragments surely contained pieces from the poles, the mean thickness of fragments was probably biased downward.

Sometimes the microscopic examination of whole shells or fragments revealed loss of the shell membrane. We found the mean membrane thickness, measured optically in a large sample of eggshells with membrane intact, was 0.079 mm. Therefore we added that value to shells without a membrane to correct for the loss. Other studies report the use of a membrane correction value as low as 0.063 mm (Monk et al 1988). Our measurement of the relatively soft membrane was made optically, while other studies usually used mechanical techniques that exert a force on the membrane. The optical technique does not compress the membrane.