MORTALITY OF PRAIRIE FALCONS DURING THE FLEDGING-DEPENDENCE PERIOD[1]

MARY E. MCFADZEN[2] AND JOHN M. MARZLUFF[3]

Greenfalk Consultants, 8210 Gantz Avenue, Boise, ID 83702

Abstract. We monitored the survival of 152 radio-tagged Prairie Falcon (*Falco mexicanus*) nestlings from 37 broods through the fledging-dependence period in southwestern Idaho during 1992 and 1993. Mortality rates were high but consistent between years, 28% in 1992 and 34% in 1993, despite a significant decline in the primary prey of falcons in 1993. Predation by Great Horned Owls (*Bubo virginianus*) was the primary cause of mortality. To a lesser extent, mortality was influenced by the presence of hematophagous ectoparasites (*Haematosiphon inodorus*) in aeries. We were unable to find or show an effect of parental behavior (territory attendance and prey delivery rates) during the late brood-rearing period, hatching date, brood size or fledging mass on mortality. The frequency of predation in our study may have negated or diminished the influences of these factors. Survivorship was lower during the fledging-dependence period than during the incubation or nestling periods.

Key words: mortality; survivorship; postfledging; predation; ectoparasites; Prairie Falcon; Falco mexicanus.

INTRODUCTION

Knowledge of age-specific mortality and its causes is important to furthering our understanding of avian population dynamics. Quantification of age-specific mortality is fundamental in predicting changes in avian population size (Ricklefs 1973), identifying which life-history stages are most susceptible to mortality (Newton 1979, Sullivan 1989, Spear and Nur 1994), quantifying the opportunity for natural selection (Arnold and Wade 1984), developing strategies for management and conservation (Verner 1992), and providing insight into inter- and intraspecific relationships in a community (Paine 1966).

Little research has been conducted on mortality beyond the nestling stage because of the difficulties associated with monitoring young after they leave the nest. Commonly, analysis of band recovery data has been employed to estimate age-specific survival rates. However, this method may produce erroneous results (Lakhani and Newton 1983, Anderson et al. 1985) and provides little insight into the cause of mortality. Recent studies of marked individuals within Yellow-eyed Junco (*Junco phaenotus*) and Western

Gull (*Larus occidentalis*) populations have been successful in quantifying survivorship at life history stages and in identifying factors that influence survivorship (Sullivan 1989, Spear and Nur 1994). In raptors, knowledge of age-specific mortality and its causes is scarce because they typically inhabit remote areas and nest at low densities making field research problematic (Newton 1979). To our knowledge, only one study has specifically investigated mortality of radio-tagged raptors during the postfledging-dependence period (Petty and Thirgood 1989). However, incidental reports from other studies have shown that mortality rates of fledglings prior to independence from their parents are variable and primarily influenced by food availability (Beissinger 1986, Beissinger and Snyder 1987, Snyder et al. 1989) or predation (Konrad and Gilmer 1986, Belthoff and Ritchison 1989, Varland et al. 1993).

The purpose of our study was to radio-tag a large number of Prairie Falcon (*Falco mexicanus*) nestlings and monitor their survival through the fledging-dependence period to: (1) determine the magnitude and causes of mortality, (2) examine the influences of parental behavior (attendance and prey delivery rates), hatching date, fledging mass, and brood size on mortality, (3) compare the survival rate during the fledging-dependence period with estimated survival rates of earlier life-history stages, and (4) compare mortality during years of high and low prey abundance.

METHODS

FIELD PROCEDURES

The study was conducted in the Snake River Birds of Prey National Conservation Area (NCA) in southwestern Idaho. Here, the Snake River Canyon, consisting of 5–200 m high basalt cliffs, traverses 60 km through a mosaic of shrubsteppe and non-native vegetation, and a few agricultural parcels. Abundant nesting sites in the canyon in conjunction with a rich prey base on the adjacent Snake River Plain, support one of the highest densities of breeding raptors in North America (U.S. Department of Interior 1979).

We monitored the survival of 152 radio-tagged Prairie Falcon nestlings from 37 broods in 1992 and 1993. The 1992 nesting territories ($n = 19$) we studied were a subset of a group of territories, which was randomly selected from historical territories for a companion study (see Marzluff et al. 1992). This subset of territories was chosen because of logistical constraints. One adult of each breeding pair was radio-tagged (see Marzluff et al. 1992). In 1993, we initially selected territories using the same method as in 1992; however, high nesting failure forced us to use all territories with young. Of the 18 broods we radio-tagged in 1993, a parent was radio-tagged in only nine broods. Radio-tagging had no measurable effect on adult behavior nor on nest success (Vekasy et al. 1996).

Nestlings, estimated to be 30 days old (aged according to Moritsch 1983) or 80% of fledging age (Steenhof 1987), were weighed within 5 g, measured, banded, and equipped with tarsal-mounted radio-transmitters. We measured the seventh primary as an indicator of nestling age. We categorized nestlings into two groups, female and male, based on footpad lengths less than and greater than 86 mm, respectively (Marzluff et al. 1991). Transmitter attachment followed Sherrod et al. (1981), but was modified by sewing the fastening point with a zigzag stitch to increase attachment longevity. The 6-g radio-transmitter (Advanced Telemetry Systems, Isanti, MN) represented 1% of mean body mass for nestling males ($\bar{x}_{mass} = 551$ g, $n = 67$) and <1% for nestling females ($\bar{x}_{mass} = 791$ g, $n = 84$), well below the maximum value of 3% recommended for birds by the United States Fish and Wildlife Service (Hegdal and Colvin 1986). The absolute effects of radio-transmitters on fledgling behavior or flight, and therefore on subsequent survivorship,

are unknown. We did not observe any unusual behavior or find birds entangled as a result of wearing the transmitters.

We defined the *fledging-dependence period* as the time from radio-tagging nestlings (approximately 30 days old) until fledglings dispersed from their natal territory. Known fledging age for Prairie Falcons ranges from 36 to 41 days old (Enderson 1964). Therefore, the fledging-dependence period in this study included the time immediately before fledging until natal dispersal. We spent 12 hr per day, from late May through late July in 1992 and 1993, monitoring nesting territories for radio-tagged young. Every 2–3 days, from the base or rim of the canyon walls, we used hand-held telemetry equipment to check signals of radio-tagged young. Because radio-tagged birds were sometimes difficult to see on cliffs, a change in transmitter signal strength indicated that an individual was still alive. We examined evidence at sites where fledglings were found dead. Each Prairie Falcon death was assigned to one of the following mortality causes: raptorial predation, mammalian predation, starvation, wing injury, ectoparasite infestation, and unknown. A fledgling *successfully dispersed* if we did not detect its signal in or near the natal territory on a minimum of two subsequent checks that were 2–3 days apart. After fledglings dispersed from the Snake River Canyon we searched the study area by ground and air to locate dispersed or dead birds. The combination of flat topography in the NCA and aerial tracking eliminated any possibility of not detecting radio-tagged birds.

We sampled parental behavior at nesting territories during the late brood-rearing and the early fledging-dependence periods (Table 1). Eight to ten observers collected data using spotting scopes and binoculars. We set up observation blinds in the canyon to optimize the view of aeries and the surrounding area, and to minimize observer-induced disturbance (Holthuijzen 1989). We observed territories continuously from 15 min before sunrise to 15 min after sunset; each observer watched for half of the sampling day (Holthuijzen 1989).

Location of aeries high on cliffs prohibited us from viewing activities inside aeries. However, parents could be seen entering and exiting the aerie. We identified individual parents by determining if the bird was wearing a radio transmitter, the placement and color of leg bands, and

the presence or absence of a transmitter signal. Observers recorded the beginning and ending times of the following adult behaviors: perching, flying, presence in the aerie and on the territory. The percentage of time each parent was on the territory (territory attendance) was calculated by summing the duration of the above behaviors and dividing by total observation time per day. We classified adult prey-handling activities as follows: fresh prey delivered to the territory (prey was cached or taken to nestlings), prey delivered to the aerie (cache retrievals and fresh prey taken to nestlings), prey cached, or prey retrieved from a cache. We identified and grouped prey according to taxonomic class or species when possible. We calculated daily prey delivery rates by dividing the number of prey items delivered to the aerie (total male and female deliveries) by total observation time.

The presence of hematophagous ectoparasites, identified as Mexican chicken bugs, *Haematosiphon inodorus* (McFadzen et al. 1996), in aeries prompted us to investigate their effects on nestling condition by measuring hematocrit. At banding we withdrew blood with a syringe from the brachial vein. The blood was drawn into two heparinized capillary tubes and was later centrifuged for 15 min at 12,000 rpm to obtain a mean hematocrit value. We took blood only during the latter half of the 1993 breeding season and during the 1994 breeding season.

Climbers recorded the level of the ectoparasite infestation in aeries when they retrieved nestlings for tagging. We grouped the infestation levels as follows: (1) no infestation or light infestation— no bugs or few bugs observed on nestlings or on rock surfaces inside of aerie, and (2) heavy infestation—many bugs present on nestlings, inside of aerie, and outside of aerie on adjacent rock surfaces.

NESTING DATA

We obtained NCA Prairie Falcon nesting data (1973–1994) from the National Biological Service's Raptor Research and Technical Assistance Center (RRTAC), Boise, Idaho, to calculate survivorship prior to fledging. Because the survival of eggs to fledging (80% of actual fledging age) was not known for every nest, we calculated a mean survival rate for the incubation and nestling stages from four data sets totaling 910 nests. Survival for the nestling stage may be underestimated because nests were not immediately

TABLE 1. Number of Prairie Falcon territories where behavioral observations were conducted during two periods of the nesting cycle at the Snake River Birds of Prey National Conservation Area. Numbers in parentheses indicate the range of days each territory was observed.

| | Nesting cycle | |
Year	Late brood rearing (nestlings 21–40 days old)	Early fledging dependence (fledglings 41–54 days old)
1992	11 (1–3 days)	1 (1 day)
1993	6 (1–2 days)	5 (1–4 days)

checked for hatching; successfully hatching nests that failed when nestlings were ≤ 10 days old could have been missed. We used the mean survival rate for the egg period (incubation = 32 days) and the nestling period (until nestlings reached 80% of actual fledging age or 30 days old) and our measure of survivorship during the fledging-dependence period (mean dispersal age = 65 days old) to compare survivorship among life-history stages.

DATA ANALYSES

We were unable to test for the influences of parental behavior during the fledging-dependence period on brood mortality because sampling days were few (one territory in 1992 and five territories in 1993) and only covered the early part of this period (offspring age 41–54 days old). Instead, we first used correlation analysis to describe the relationship between parental territory attendance and prey delivery rates during the late brood-rearing (nestling age 21–40 days old) and the early fledging-dependence periods. We then tested for the influence of parental behavior during the late brood-rearing period on brood mortality. Multiple observations of behavior at the same territory within the late brood-rearing or the early fledging-dependence periods were averaged and all percentages were transformed (arcsine square root) prior to analysis.

The influence of hatching date (mean per brood estimated by back dating from the mean age per brood at tagging), brood size at tagging, territory attendance rates, and rates of prey delivered to aeries on brood mortality was investigated with stepwise multiple regression analysis. When the 1992 and 1993 data did not differ significantly, we pooled the two years and used partial correlation analyses holding brood size constant for each response variable.

Because Prairie Falcons exhibit reversed size dimorphism, we calculated a mean mass separately for males and females within a brood for most analyses of fledging mass. We used individual nestlings, grouped by sex, for an analysis of co-variance testing fledging mass by mortality cause. We used brood size, footpad length, and seventh primary length as covariates for analyses involving mass. Adjusted least square means for analyses performed with covariates and unadjusted means are reported $\bar{x} \pm$ SE.

RESULTS

MAGNITUDE AND CAUSES OF FLEDGLING MORTALITY

Of the 152 radio-tagged nestlings, 69% ($n = 105$) survived to disperse from their natal territories, and 31% ($n = 47$) died before dispersal. The rate of mortality did not differ significantly between years although there was a slight increase in 1993 (1992: 28% mortality, $n = 22$ of 78 young; 1993: 34% mortality, $n = 25$ of 74 young; $G^2_1 = 0.53$, $P = 0.46$). There was no significant difference in the sex ratio (males : females) of young that died (19:28) versus those that survived (49:56) to disperse from their natal territory ($G^2_1 = 0.51$, $P = 0.47$).

Predation by raptors was the major cause of mortality in both years, accounting for 41% and 56% of all mortality in 1992 and 1993, respectively. Great Horned Owls (*Bubo virginianus*) were responsible for more deaths ($n = 19$ young) than were Golden Eagles (*Aquila chrysaetos*; $n = 2$ young). We assigned fledgling deaths to this mortality cause based on the following circumstances: transmitter found in raptor aerie or in casted pellet; Great Horned Owl feathers found at mortality site; a fresh, partially consumed carcass found near a Great Horned Owl family; and transmitters with feathers found at a location 3 km from natal territory, a distance too great for a newly fledged bird to travel on its own. Evidence for two other deaths caused by raptors did not implicate the species involved.

Mexican chicken bugs contributed to the deaths of four nestlings from two broods in 1992. At tagging time all nestlings ($n = 8$) from two heavily ectoparasitized aeries looked weak and gaunt. Several days later, two young were found dead in an aerie and two were found dead below an aerie. Four young survived jumping from the two aeries, but one was subsequently preyed upon by a Great Horned Owl. The remaining three survived to disperse from their natal territory. Two weeks prior to the deaths of the above birds, we had observed unmarked nestlings jumping from an ectoparasitized aerie; one likely died from impact of jumping and the other survived. The parents continued to provide food to this survivor.

Three fledglings died from less common sources of mortality. An intact fledgling carcass was found buried at the base of a rock outcrop. Its burial, and the presence of puncture wounds and internal hemorrhaging suggested that a mammalian predator captured and killed the bird. A recently fledged Prairie Falcon was found on a river island 600 m below and away from its aerie. On four occasions the fledgling was observed alive in the same location and with no apparent injuries. On the fifth check we found the bird dead but not scavenged. Tall, dense vegetation may have prevented flight from the island, and as a result the bird likely starved to death. The third fledgling was brought into captivity with a compound wing fracture. Because the injury prevented the bird from flying, the bird would have eventually succumbed to predation or starvation, so we identified the wing injury as the cause of death.

The causes of 36% of all mortality could not be identified because of lack of evidence. With an abundance of scavengers, including mustelids, rodents, corvids, and canids, and extremely high temperatures in the study area, dead organisms are rapidly consumed or decomposed. Consequently, we frequently found only a pile of feathers and/or a leg with the radio-transmitter attached ($n = 9$ young) or intact or partially decomposing carcasses ($n = 8$ young).

TIMING OF PREDISPERSAL MORTALITY

Prairie Falcon survivorship was slightly lower during the fledging-dependence period than during the egg and nestling periods (Fig. 1). From 1973–1994, Prairie Falcon nests contained an average of 4.5 eggs. Eighty-two percent of these eggs survived to hatching. Each nest produced an average of 3.7 nestlings. Survivorship of eggs that survived to the nestling stage decreased by an additional 18% through the brood-rearing period; approximately 2.9 fledglings were produced per nest. Incorporating our 69% survivorship rate, we estimated that 44% of all eggs survived to hatching and dispersed (Fig. 1). On average, we estimated that each Prairie Falcon nest produced

two young that survived to disperse from the natal territory.

Survivorship rates and the occurrence of specific mortality causes varied during the fledging-dependence period. Timing of mortality during the weeks following radio-tagging differed significantly between 1992 and 1993 (lumping weeks three, four, and five: $G^2{}_2 = 6.78$, $P = 0.03$; Fig. 2A, B). In 1992, half of all mortality ($n = 11$) occurred during the first week after tagging. In contrast, only 16% of mortality ($n = 4$ young) occurred during this time in 1993. The largest decline in survivorship in 1993 happened during the second week post-tagging; 36% of the mortality occurred during this time. The abrupt decline during the first week after tagging in 1992 included four young that died from the influence of ectoparasite infestations (Fig. 2A). The cause of mortality for five of the 11 deaths could not be identified. Two of these young were found dead in separate aeries after their nest mates fledged. At a third territory three young were found dead below the aerie but not consumed, and the remains of their fourth nest mate were found in a neighboring Great Horned Owl aerie. Because this Prairie Falcon aerie contained no ectoparasites at tagging, the three young may have fallen from the aerie while trying to escape an owl attack. Predation, primarily by raptors, accounted for seven of the nine deaths that occurred during the second week post-tagging in 1993 (Fig. 2B). Fledgling survival remained stable during the third week post-tagging for the 1992 birds but decreased by 9.4% for the 1993 birds (Fig. 2A, B). For the next two weeks the number of individuals dying was relatively low and similar for both years (Fig. 2A, B).

FACTORS THAT MAY INFLUENCE FLEDGLING SURVIVORSHIP

Stepwise multiple regression revealed no significant relationships between brood size, hatching date, parental attendance rates, total prey delivery rates, or year and the percentage of young dying per brood (all P values > 0.40). Although the relationship between brood size and brood mortality was not significant ($P = 0.42$) we held brood size constant in the partial correlation analyses.

Parental behavior. Of the six territories where we observed parental behavior during the early fledging-dependence period, only four were observed during both the late brood-rearing and
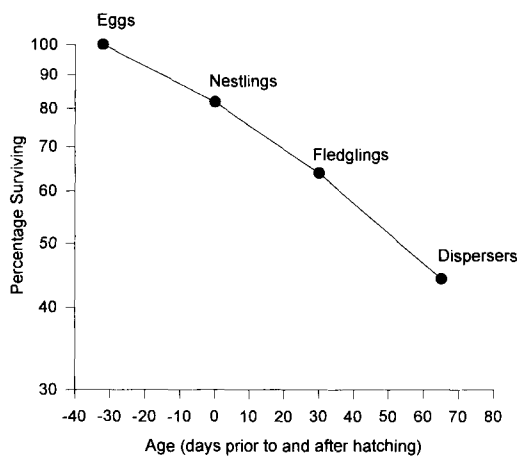

FIGURE 1.   Composite survivorship curve of Prairie Falcons prior to dispersal from natal territories. The survivorship rates for the egg and nestling stages are mean rates calculated from four data sets for 910 nests from 1973–1994 (unpubl. data, RRTAC). Fledgling survivorship data are from 1992 and 1993.

the early fledging-dependence periods. Mean attendance rates during late brood rearing for these four sites were similar to rates during the early fledging-dependence period for males ($r = 0.80$, $P = 0.20$), but not for females ($r = -0.75$, $P = 0.25$). The rates of prey delivered to the aerie during late brood rearing correlated positively with the early fledging-dependence period rates ($r = 0.98$, $P = 0.02$, $n = 4$ territories). Although sample sizes were small for these correlations, the positive relationship for some behaviors indicates that the relative amount of care parents provided to their young during the late brood-rearing period may reflect the relative care during the early fledging-dependence period. Therefore, we used data from the late brood-rearing period to determine if there was a relationship between parental behavior and brood mortality during the fledging-dependence period.

Parental attendance in the territory and delivery rates of prey to the aerie during the late brood-rearing period were not significantly correlated with the percentage of the brood dying (partial correlations holding brood size constant, $n = 17$ broods; all P values > 0.20).

Fledging mass. Mean mass per sex per brood at tagging (fledging mass) did not influence subsequent survival for males or females during the fledging-dependence period in 1992 and 1993 (males: $\bar{x}_{\text{mass for survivors}} = 558 \pm 9$ g, $n = 23$ broods;
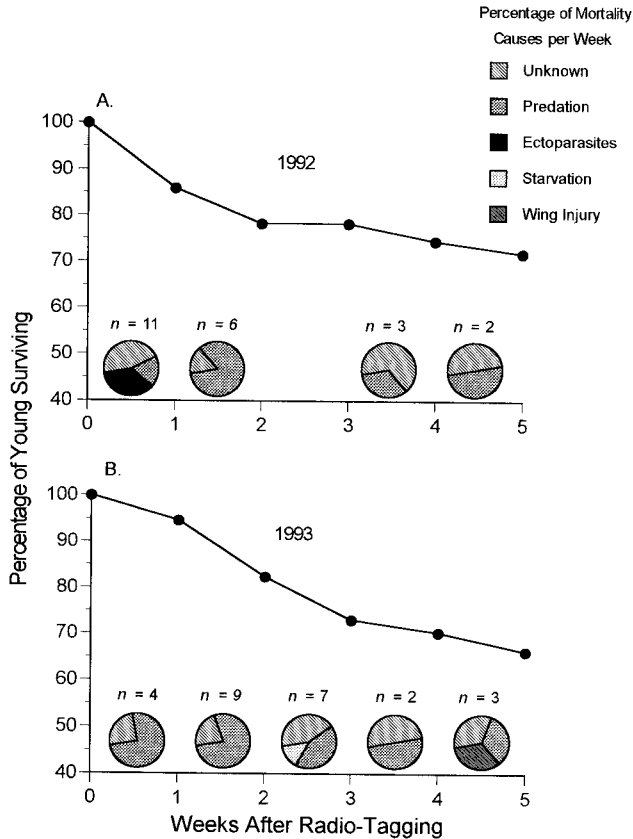
FIGURE 2.   Percentage of Prairie Falcon young surviving per week after radio-tagging during the fledging-dependence period in 1992 (A) and 1993 (B). Pie charts represent the percentage of mortality causes that occurred per week after radio-tagging. Sample size above pie charts indicate the number of young that died per week.

$\bar{x}_{\text{mass for non-survivors}} = 548 \pm 12$ g, $n = 12$ broods; $F_{1,28} = 0.43$, $P = 0.52$; females: $\bar{x}_{\text{mass for survivors}} = 787 \pm 11$ g, $n = 30$ broods; $\bar{x}_{\text{mass for non-survivors}} = 769 \pm 15$ g, $n = 16$ broods; $F_{1,39} = 0.83$, $P = 0.37$). We pooled years in these analyses because male and female masses did not differ between years (males: $F_{1,28} = 0.24$, $P = 0.63$; females: $F_{1,39} = 1.66$, $P = 0.21$).

Fledging mass differed among males grouped by mortality cause and males that survived to disperse ($F_{3,60} = 6.23$, $P = 0.001$). Males that died from the influence of ectoparasites had lower masses than those that died from predation, unknown causes, and those that survived (Tukey's pairwise comparison: all P values < 0.003; Fig. 3). Fledging mass did not differ significantly among males or females that died from predation, unknown causes, and those that survived (males: Tukey's pairwise comparison, all P values > 0.78; females: $F_{2,74} = 1.05$, $P = 0.36$; Fig.

3). We excluded the ectoparasite mortality cause from analysis of female mass because it included only one bird.

Mean fledging mass per sex per brood differed significantly between the two levels of ectoparasite infestation in 1992–1994 (males: $F_{1,40} = 11.17$, $P = 0.002$, $n = 46$ broods; females: $F_{1,43} = 10.48$, $n = 49$ broods, $P = 0.002$). Mean fledging masses of males ($\bar{x} = 490 \pm 18$ g, $n = 4$ broods) and females ($\bar{x} = 715 \pm 23$ g, $n = 5$ broods) occupying heavier infested aeries were lower than mean masses of males ($\bar{x} = 552 \pm 5$ g, $n = 42$ broods) and females ($\bar{x} = 791 \pm 7$ g, $n = 44$ broods) from noninfested or lightly infested aeries. Mean hematocrit values were significantly lower for broods occupying aeries with heavier ectoparasite loads in 1993 and 1994 (adjusted mean hematocrit using hatching date as a covariate: $\bar{x}_{\text{no/light infestation}} = 36.25 \pm 0.53$, $n = 23$ broods; $\bar{x}_{\text{heavy infestation}} = 30.83 \pm 1.16$; $F_{1,25} = 17.79$,
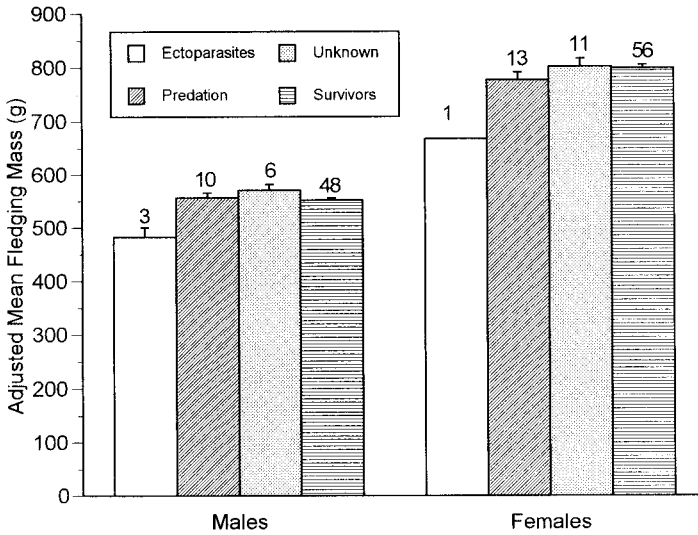
FIGURE 3.   Mean (± SE) fledging mass of males and females grouped by mortality cause for those that died and for those that survived to disperse from natal territories in 1992 and 1993. Means are adjusted for covariates (brood size, seventh primary, footpad length) suspected to influence fledging mass. Numbers above histograms refer to the number of young per group.

$n = 5$ broods, $P < 0.001$). Hematocrit values did not differ between male and female nestlings ($\bar{x}_{males} = 34.3 \pm 1.18$, $n = 26$ broods; $\bar{x}_{females} = 33.6 \pm 0.96$, $n = 24$ broods; $t = 0.46$, df = 48, $P = 0.68$), so we calculated a mean hematocrit value per brood for the previous analysis.

Hatching date. Mean hatching dates did not differ significantly between 1992 ($\bar{x} = 27$ April, $n = 19$ broods) and 1993 ($\bar{x} = 3$ May, $n = 18$ broods; $t = -1.31$, df = 35, $P = 0.20$), but the range of hatching dates was less in 1993 (24 days) than in 1992 (39 days). Hatching date did not correlate significantly with brood mortality in 1992 ($r_{partial\ (holding\ brood\ size\ constant)} = 0.33$, $n = 19$ broods, $P > 0.10$) or in 1993 ($r_{partial\ (holding\ brood\ size\ constant)} = 0.18$, $P > 0.20$, $n = 18$ broods). Prairie Falcon young that died from predation had similar hatching dates ($\bar{x} = 30$ April ± 2 days, $n = 24$) to those that survived (Tukey's: $P = 0.93$). Young that died from the influence of ectoparasites had the latest hatching dates ($\bar{x} = 18$ May ± 2 days), but we excluded this group from statistical analysis because of small sample size ($n = 4$).

DISCUSSION

Prairie Falcon survivorship declined through all developmental periods prior to natal dispersal. Survivorship was slightly lower during the fledging-dependence period than during the egg and nestling periods (Fig. 1). The mortality rate during the fledging-dependence period (31%) was higher than most rates reported for other raptor species during the postfledging-dependence period. Our mortality rate included young that died during the latter part of the nestling period. However, of the 15 birds that died during this period only four were found dead in the their aeries. Mortality rates vary from 11–18% for Ferruginous Hawks (*Buteo regalis*; $n = 18$ color-marked birds; Konrad and Gilmer 1986), Northern Goshawks (*Accipiter gentilis*; $n = 156$ radio-tagged birds; Kenward et al. 1993), Eastern Screech-Owls (*Otus asio*; $n = 22$ radio-tagged birds; Belthoff and Ritchison 1989), and Red Kites (*Milvus milvus*: $n = 37$ color-marked birds of which 11 were radio-tagged; Bustamante 1993). American Kestrels (*Falco sparverius*) experienced a 26% mortality rate ($n = 61$ radio-tagged birds; Varland et al. 1993). Eleven of 12 radio-tagged Tawny Owls (*Strix aluco*) died before dispersal from their natal territories (Petty and Thirgood 1989). Mortality of fledgling Red-tailed Hawks (*Buteo jamaicensis*) was very low during the early post-fledging-dependence period ($n = 26$ color-marked birds of which 9 were radio-tagged) and was believed to remain low until dispersal (Johnson 1973).

Mortality of Prairie Falcons beyond the fledg-

ing-dependence period has not been quantified, but first year mortality rates of 65% (Denton 1975) and 74% (Enderson 1969) have been estimated using band recovery data. Depending on the accuracy of these estimates, our 31% mortality rate prior to natal dispersal may account for almost half of first-year mortality. High mortality during the fledging-dependence period provides an opportunity for natural selection (Arnold and Wade 1984) to have profound effects on Prairie Falcon ecology.

Despite a dramatic decline in the 1993 population of Townsend's ground squirrels (*Spermophilus townsendii*) (Van Horne et al. 1993), the primary prey of Prairie Falcons in the NCA (Steenhof and Kochert 1988, Holthuijzen 1990), falcon mortality rates were relatively high and consistent during both years of the study. If the 1992 ectoparasite influenced deaths are attributed to the nestling period, mortality rates during the fledging-dependence period between years remains statistically non-significant. The effects of previous drought and weather resulted in low ground squirrel densities and low juvenile squirrel production in 1993 compared to 1992 (Van Horne et al. 1993). In contrast, mortality rates of young Florida Everglade Snail Kites (*Rostrhamus sociabilis plumbeus*) and Tawny Owls have tracked changes in prey conditions (Southern 1970, Beissinger 1986, Beissinger and Snyder 1987, Petty and Thirgood 1989, Snyder et al. 1989). Consistency in mortality rates of Prairie Falcons during low and high ground squirrel years may have been attributable to parental quality and increased use of birds and reptiles as prey (McFadzen and Marzluff, unpubl. data). In contrast to 1992, fewer breeding Prairie Falcon pairs successfully produced young in 1993. These pairs may have had higher quality territories, and therefore were more capable of successfully producing offspring. The absence of starvation related deaths in young during 1993 also suggests that parents were able to compensate for the drastic reduction in ground squirrels during the fledging-dependence period.

Predation, primarily by Great Horned Owls, was the major cause of mortality. Predatory events, which reached their highest frequency two weeks after tagging (fledgling ages 38–44 days old: Fig. 2A, B), coincided with actual Prairie Falcon fledging age of 36–41 days old (Enderson 1964). Predation also was a major source of mortality of recently fledged young in other studies

(Belthoff and Ritchison 1989, Petty and Thirgood 1989, Sullivan 1989, Varland et al. 1993). Poor flying skills and inexperience may make recently fledged Prairie Falcons vulnerable to Great Horned Owls and Golden Eagles.

Hematophagous ectoparasites also were an additional source of mortality, as noted for other raptors (Platt 1975, Grubb et al. 1986). Mexican chicken bugs exerted their greatest impact on nestlings prior to radio-tagging age in 1993. Seven of our target aeries that contained nestlings on previous checks were empty and infested with Mexican chicken bugs at tagging time. We also found dead nestlings below aeries at some of these territories. Deaths influenced by ectoparasites occurred only during the first week after tagging in 1992; four of the 11 deaths that week were due to the infestations (Fig. 2A). At the time of death these four tagged young were not yet capable of flight. The two young that died in the aerie were probably very weak and could not jump as the seven others did to escape the bugs. Death, due to jumping from ectoparasitized nests, has been observed in nestling Purple Martins (Loye and Regan 1991). The low hematocrit and fledging mass of young occupying aeries with high parasites loads indicated that hematophagous ectoparasites directly affected nestling condition, as also noted for Cliff Swallows (*Hirundo pyrrhonota*; Brown and Brown 1986, Chapman and George 1991). We did not know the survival fate of all young we sampled blood from, but some fledglings from heavily infested aeries survived to dispersal. The long-term impact of low hematocrit and mass on their survivorship is unknown.

We were unable to show any relationship between hatching date, fledging mass, brood size, or parental behavior on brood mortality during the fledging-dependence period. Some of these factors have been correlated with postfledging survivorship in other studies (Perrins 1966, Nisbet and Drury 1972, Nur 1984, Magrath 1991, Spear and Nur 1994), whereas other studies have shown no relationship (Newton and Moss 1984, Nur 1984, Magrath 1991). Small sample size and resulting low power for some of our analyses may provide some explanation for not finding any significant relationships. The high incidence of predation in this study also may have obscured or diminished the influence of these factors. Additionally, the lack of correlation between the factors we examined and subsequent survivor-

ship also may be attributed to the inability to detect such a relationship during the relatively short fledging-dependence period. Newton and Marquiss (1984) found that the influence of fledging date on survival of Sparrowhawks (*Accipiter nisus*) occurred after the postfledging period. Newton (1986) postulated that Sparrowhawks fledging earlier in the season survived longer than young fledged later because early fledged young had more time to exploit prey and to develop hunting skills.

ACKNOWLEDGMENTS

LITERATURE CITED

ANDERSON, D. R., K. P. BURNHAM, AND G. C. WHITE. 1985. Problems in estimating age-specific survival rates from recovery data of birds ringed as young. J. Anim. Ecol. 54:89–98.

ARNOLD, S. J., AND M. J. WADE. 1984. On the measurement of natural and sexual selection theory. Evolution 38:709–719.

BEISSINGER, S. R. 1986. Demography, environmental uncertainty, and the evolution of mate desertion in the Snail Kite. Ecology 67:1445–1459.

BEISSINGER, S. R., AND N. F. R. SNYDER. 1987. Mate desertion in the Snail Kite. Anim. Behav. 35:477–487.

BELTHOFF, J. R., AND G. RITCHISON. 1989. Natal dispersal of Eastern Screech-Owls. Condor 91:254–265.

BROWN, C. R., AND M. B. BROWN. 1986. Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). Ecology 67:1206–1218.

BUSTAMANTE, J. 1993. Post-fledging dependence period and development of flight and hunting behaviour in the Red Kite *Milvus milvus*. Bird Study 40:181–188.

CHAPMAN, B. R., AND J. E. GEORGE. 1991. The effects of ectoparasites on Cliff Swallow growth and survival, p. 69–92. *In* J. E. Loye and M. Zuk [eds.], Bird-parasite interactions: ecology, evolution and behaviour. Oxford Univ. Press, Oxford.

DENTON, S. J. 1975. Status of Prairie Falcons breeding in Oregon. M.Sc. thesis, Oregon State Univ., Corvallis.

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

ENDERSON, J. H. 1969. Peregrine and Prairie Falcon life tables based on band-recovery data, p. 505–509. *In* J. J. Hickey [ed.], Peregrine Falcon populations: their biology and decline. Univ. of Wisconsin Press, Madison.

GRUBB, T. G., W. L. EAKLE, AND B. N. TUGGLE. 1986. *Haematosiphon inodorus* (Hemiptera: Cimicidae) in a nest of a Bald Eagle (*Haliaeetus leucocephalus*) in Arizona. J. Wild. Diseases 22:125–127.

HEGDAL, P. L., AND B. A. COLVIN. 1986. Radiotelemetry, p. 679–698. *In* A. Y. Cooperrider, R. J. Boyd, and H. R. Stuart [eds.], Inventory and monitoring of wildlife habitat. Bur. Land Manage., U.S. Dept. of Interior, Denver, CO.

HOLTHUIJZEN, A. M. A. 1989. Behavior and productivity of nesting Prairie Falcons in relation to construction activities at Swan Falls Dam. Final report, Idaho Power Co., Boise, ID.

HOLTHUIJZEN, A. M. A. 1990. Prey delivery, caching, and retrieval rates in nesting Prairie Falcons. Condor 92:475–484.

JOHNSON, S. J. 1973. Post-fledging activity of the Red-tailed Hawk. Raptor Res. 7:43–48.

KENWARD, R. E., V. MARCSTROM, AND M. KARLBOM. 1993. Post-nestling behaviour in Goshawks, *Accipiter gentilis*: II. Sex differences in sociality and nest-switching. Anim. Behav. 46:371–378.

KONRAD, P. M., AND D. S. GILMER. 1986. Post fledging behavior of Ferruginous Hawks in North Dakota. Raptor Res. 20:35–39.

LAKHANI, K. H., AND I. NEWTON. 1983. Estimating age-specific birds survival rates from ring recoveries-can it be done? J. Anim. Ecol. 52:83–91.

LOYE, J., AND T. W. REGAN. 1991. The Cliff Swallow bug *Oeciacus vicarius* (Hemiptera: Cimicidae) in Florida: ectoparasite implications for hole-nesting birds. Med. Vet. Entomol. 5:511–513.

MAGRATH, R. D. 1991. Nestling weight and juvenile survival in the Blackbird, *Turdus merula*. J. Anim. Ecol. 60:335–351.

MARZLUFF, J. M., C. J. COODY, T. L. MAECHTLE, M. MCFADZEN, T. C. MILES, L. S. SCHUECK, AND M. VEKASY. 1991. Influence of military training on the behavior of raptors in the Snake River Birds of Prey Area, 1991, p. 37–95. *In* K. Steenhof [ed.], Snake River Birds of Prey Area 1991 annual report. U.S. Dept. of Interior, Boise, ID.

MARZLUFF, J. M., M. VEKASY, L. S. SCHUECK, M. MCFADZEN, R. R. TOWNSEND, B. A. KIMSEY, J. O. MCKINLEY, AND C. J. COODY. 1992. Influence

of military training on the behavior of raptors in the Snake River Birds of Prey Area, 1992, p. 49–143. *In* K. Steenhof [ed.], Snake River Birds of Prey Area research and monitoring annual report. U.S. Dept. of Interior, Boise, ID.

McFADZEN, M. E., M. S. VEKASY, T. Y. MORISHITA, AND J. H. GREVE. 1996. Northern range extension for *Haematosiphon inodorus* (Duges) (Hemiptera: Cimicidae). Pan-Pacific Entomol. 72:41–42.

MORITSCH, M. Q. 1983. Photographic guide for aging nestling Prairie Falcons. U.S. Dept. of Interior. Bur. Land Manage., Boise, ID.

NEWTON, I. 1979. Population ecology of raptors. T. & A. D. Poyser, Berkhamsted, U.K.

NEWTON, I. 1986. The Sparrowhawk. T. & A. D. Poyser, Calton, U.K.

NEWTON, I., AND M. MARQUISS. 1984. Seasonal trend in the breeding performance of Sparrowhawks. J. Anim. Ecol. 53:809–829.

NEWTON, I., AND D. MOSS. 1984. Post-fledging survival of Sparrowhawks *Accipiter nisus* in relation to mass, brood size and brood composition at fledging. Ibis 128:73–80.

NISBET, I. C. T., AND W. H. DRURY. 1972. Post-fledging survival in Herring Gulls in relation to brood-size and date of hatching. Bird-Banding 43: 161–172.

NUR, N. 1984. The consequences of brood size for breeding Blue Tits II. Nestling weight, offspring survival and optimal brood size. J. Anim. Ecol. 53:497–517.

PAINE, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100:65–75.

PERRINS, C. M. 1966. Survival of young Manx Shearwaters *Puffinus puffinus* in relation to their presumed date of hatching. Ibis 108:132–135.

PETTY, S. J., AND S. J. THIRGOOD. 1989. A radio tracking study of post-fledging mortality and movements of Tawny Owls in Argyll. Ring. Migr. 10:75–82.

PLATT, S. W. 1975. The Mexican chicken bug as a source of raptor mortality. Wilson Bull. 87:557.

RICKLEFS, R. E. 1973. Fecundity, mortality, and avian demography, p. 366–435. *In* D. S. Farner [ed.], Breeding biology of birds. Natl. Acad. Sci., Washington, DC.

SHERROD, S. K., W. R., W. A. BURNHAM, J. H. BARCLAY, AND T. J. CADE. 1981. Hacking: a method for releasing Peregrine Falcons and other birds of prey. Peregrine Fund, Boise, ID.

SITTER, G. 1983. Feeding activity and behavior of Prairie Falcons in the Snake River Birds of Prey Natural Area in southwestern Idaho. M.Sc. thesis, Univ. Idaho, Moscow, ID.

SNYDER, N. F. R., S. R. BEISSINGER, AND R. E. CHANDLER. 1989. Reproduction and demography of the Florida Everglade (Snail) Kite. Condor 91: 300–316.

SOUTHERN, H. N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). J. Zool. 162: 197–285.

SPEAR, L., AND N. NUR. 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in Western Gulls. J. Anim. Ecol. 63:283–298.

STEENHOF, K. 1987. Assessing raptor reproductive success and productivity, p. 157–170. *In* B. A. Giron Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird [eds.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC.

STEENHOF, K., AND M. N. KOCHERT. 1988. Dietary responses of three raptor species to changing prey densities in a natural environment. J. Anim. Ecol. 57:37–48.

SULLIVAN, K. A. 1989. Predation and starvation: age-specific mortality in juvenile Juncos (*Junco phaenotus*). J. Anim. Ecol. 58:275–286.

UNITED STATES DEPARTMENT OF THE INTERIOR. 1979. Snake River birds of prey special research report. Bur. Land Manage., Boise, ID.

VAN HORNE, B., G. S. OLSON, AND K. P. BURNHAM. 1993. Patterns of density, reproduction, and survival in Townsend's ground squirrels, p. 158–183. *In* K. Steenhof [ed.], Snake River Birds of Prey Area research and monitoring annual report. U.S. Dept. Interior, Boise, ID.

VARLAND, D. E., E. E. KLASS, AND T. M. LOUGHIN. 1993. Use of habitat and perches, causes of mortality and time until dispersal in post-fledging American Kestrels. J. Field Ornithol. 64:169–178.

VEKASY, M., J. M. MARZLUFF, M. N. KOCHERT, R. N. LEHMAN, AND K. STEENHOF. 1996. Influence of radio-transmitters on Prairie Falcons. J. Field Ornithol. 67:680–690.

VERNER, J. 1992. Data needs for avian conservation biology: have we avoided critical research? Condor 94:301–303.