

POST-FLEDGING SURVIVAL OF BURROWING OWLS IN SASKATCHEWAN

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Abstract: Extensive research into the decline of the endangered burrowing owl (*Athene cunicularia*) has focused on breeding biology, but has largely ignored the post-fledging period. To determine whether post-fledging survival was an important factor in the decline, we used radiotelemetry to monitor post-fledging juveniles in a migratory population of burrowing owls in southern Saskatchewan, Canada, during 1997–2000. As part of a concurrent study, 92% of the owl pairs nested in artificial nest boxes, and 64% received supplemental food from hatch until fledging. Survival of juvenile owls during the 3-month, post-fledging period was significantly higher in 1997 (1.00, $n = 12$) than 1998–2000 (0.55 [95% CI: 0.44 to 0.70], $n = 64$; $P = 0.02$). Unusually high survival during 1997 may have been related to the unusually high abundance of voles (*Microtus* spp.) that year. From 1998 to 2000, 27 of 64 radiomarked owls died. Predators caused the majority of post-fledging mortality (15 of 27), with juveniles at greatest risk the first 14 days after fledging. Other sources of mortality were related to anthropogenic factors (5 of 27) and starvation (5 of 27). Following each of 3 years with moderate juvenile post-fledging survival, the breeding population of burrowing owls declined 11–48% and contained correspondingly few yearling recruits ($\bar{x} = 2.1\%$). However, following the year of high post-fledging survival (1997), the breeding population increased by 32%, and yearling recruitment was substantially higher (8.3%). These results suggest that post-fledging survival has a considerable influence on population size in the subsequent breeding season, and that management strategies for this species of concern should include this life stage.

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Burrowing owls are endangered (Wellicome and Haug 1995) due to substantial and consistent population declines throughout their Canadian range. A number of factors—such as decreased productivity (Wellicome 1997, Wellicome et al. 1997), reduction of potential nest and roost burrows (James et al. 1990, Miller et al. 1994, Desmond et al. 2000), increased pesticide and insecticide use (James and Fox 1987, Fox et al. 1989), and habitat loss or fragmentation (Wellicome and Haug 1995, Warnock 1996, Clayton and Schmutz 1999)—have contributed to the decline. Adding information from other life-history stages to existing data on nesting biology should improve our understanding of why burrowing owl populations have declined.

Identifying factors that affect age-specific survival is fundamental to understanding population dynamics, and may provide insight into life-history stages that impact viability of threatened populations (Lack 1954, 1966; Ricklefs 1973; Verner 1992). To date, research focused on burrowing owl post-fledging, premigratory life stage has shown that it is a potentially limiting stage in this species'

life history (Clayton and Schmutz 1999, King and Belthoff 2001). However, empirical data linking post-fledging survival to changes in the subsequent population size have not been previously reported in the literature. Examining this linkage will improve our understanding of burrowing owl population dynamics and could potentially identify management options to reverse the decline.

We measured post-fledging survival and cause-specific mortality of juvenile burrowing owls by locating radiomarked individuals from fledging to migration. Our study objectives were to determine (1) survival of juvenile burrowing owls prior to migration, and the relationship to population change the following year; (2) major causes of mortality for post-fledged juvenile owls; and (3) whether risk of mortality varied through the post-fledging period.

STUDY AREA

We conducted our study on the Regina Plain in southern Saskatchewan, Canada, currently the northern limit of the burrowing owl's range. Our study area encompassed approximately 12,200 km² of moist mixed-grass prairie in the Grassland Ecoregion (Harris et al. 1983), between the cities of Moose Jaw (50°34'N, 105°17'W), Regina

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(50°25'N, 104°39'W), and Weyburn (49°40'N, 103°52'W). The Regina Plain is intensively cultivated for cereal crop production (Riemer et al. 1997) due to its productive agricultural soils (lacustrine clays). In our study area, remnant native grassland patches are fragmented into small pastures (≤ 64 ha) that are separated from other grassland patches by 1–30 km. Vegetation in native grassland patches is dominated by northern wheatgrass (*Agropyron dasystachym*) and June grass (*Koeleria cristata*). Few burrows exist in cultivated areas; therefore, the cropland separating grassland patches is essentially unavailable as burrowing owl nesting habitat (Clayton and Schmutz 1999; King and Belthoff 2001; L. D. Todd, personal observation).

METHODS

Burrowing owls that breed in Saskatchewan are migratory, arriving on the Regina Plain in mid- to late April each year. They nest underground in burrows originally excavated by Richardson's ground squirrels (*Spermophilus richardsonii*) or badgers (*Taxidea taxus*). We searched for owls returning to our study area each year (1997–2000) beginning mid-April. We located nests by visiting historically occupied sites and systematically searching grassland pastures on foot, looking for suitable burrows and signs of owls. We determined the population size and were able to compare population trends over time by counting the total number of adults found in areas searched consistently each year.

Once we located active nests, we installed artificial nest boxes (as described by Wellicome et al. 1997) where any pair was found using a natural burrow. Ninety-two percent (72 of 78) of nests included in our study were in artificial nest boxes; 6 nests were in natural burrows. Artificial nest boxes protected owl nests from fossorial predators during the nesting period (Wellicome et al. 1997). They also allowed us access to nest chambers to determine laying and hatching dates, determine size and diversity of prey caches, monitor productivity and nestling survival, and capture juveniles for banding and radiotransmitter attachment.

As part of a supplemental feeding experiment (Wellicome 2000), we provided selected owl pairs (64%; 50 pairs) with 255 g of supplemental food (dead lab mice) every 3 days from just prior to hatching until fledging (41 days post-hatch). We selected pairs alternately to either receive supplemental food or not based on clutch initiation date (Wellicome 2000).

At approximately 20–30 days post-hatch, we banded each juvenile with a U.S. Fish and Wildlife Service leg band and a color band specific to hatching year. We determined age of each owlet in nest boxes using observed hatch day. When nearing expected hatch date, we checked nests in artificial nest boxes once every 2–3 days to get an accurate assessment of hatch date. We determined age of owlets from nests in natural burrows by comparing their morphological measures (tarsus and feather lengths) to those of known-age nestlings from artificial burrows. In 1999 and 2000, we used genetic analysis of blood to determine sex of juvenile owls (tests conducted by Vita-tech, Markham, Ontario, Canada). Results were available within 7 days of first capture, at which time we fitted radio-transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) weighing 4–6 g (representing a maximum of 4% adult body mass) onto recaptured juvenile owls of known sex. Transmitters were attached just prior to fledging when juveniles were between 35 and 40 days old. We did not affix transmitters to any owl weighing < 120 g, to minimize the possibility that transmitters would affect survival.

From 1997 to 2000, we fitted 106 transmitters onto juveniles from 78 different nests. A random subset of nests was chosen in 1997 ($n = 12$ of 38 known nests) and 1998 ($n = 31$ of 56 nests) due to a limited number of transmitters. All nests with fledglings were included in 1999 ($n = 20$) and 2000 ($n = 15$). We followed radiomarked owls from July through early October each year for a total of 5,310 transmitter-days. We used necklace-style transmitters ($n = 95$) in all 4 years and backpack-style transmitters ($n = 11$) in 1999 and 2000. In 1997 and 1998, we fitted transmitters onto 1 juvenile per nest. In 1999 and 2000, we fitted transmitters onto 2 chicks per nest; 1 on a male ($n = 32$) and 1 on a female ($n = 29$) sibling. To assess effects of transmitters on the bird's physical condition, we recaptured and weighed 8 juveniles (4 with transmitters, 4 without) approximately 2 weeks prior to migration in 2000.

With a portable receiver (Wildlife Materials Inc., Carbondale, Illinois, USA) and a 2-element Yagi antenna, we determined the location of each radiomarked owl every 2–3 days from fledging until radio failure, death, or migration. We examined owl carcasses to determine cause of death. We concluded that an avian predator had killed an owl when we found the transmitter with a pile of plucked feathers, and that a mammalian predator was responsible when we found a carcass, feathers, legs, or the transmitter with evidence of having been chewed or ripped apart.

When we could not detect transmitter signals from the ground, we conducted aerial searches within 1–2 days from a single-engine Cessna 172 equipped with strut-mounted radiotracking equipment. We assumed radio failure when we could not detect transmitter signals during ground or aerial searches at a time of year before juveniles were capable of migrating or dispersing long distances. We assumed that owls had begun migration when radio signals were lost in the fall (post-hoc examination of our data indicated the first radiomarked juveniles began migration 21 Aug).

Data Analysis

In years when 2 juveniles per nest received transmitters (1999 and 2000), we used the data from 1 randomly chosen juvenile per nest in the analyses to ensure statistical independence, since the fate of siblings from the same nest cannot be considered independent (Massot et al. 1994). In our study, in 26 nests where we radiomarked 2 siblings, their fate was the same 70% of the time ($n = 20$ nests). Therefore, to compare overall post-fledging survival among the 4 years of our study, we used data from 76 radiomarked juveniles, for a total of 3,662 transmitter-days. In 23 nests, both a male and female sibling received a transmitter. To determine differences in survival between sexes, we randomly selected half of the 23 nests to estimate male survival and used the other half to estimate female survival.

To assess effects of habitat continuity, we defined patches of grassland as either isolated or continuous, based on the size of the patch and the extent to which it was surrounded by cropland. The landscape in our study area is almost entirely divided into quarter sections (800 × 800 m) of pasture or cropland. Small cattle pastures typically are a quarter section in size (64 ha). Therefore, we defined a patch as isolated if it was 64 ha or smaller and surrounded on all sides by cropland. We defined a patch as continuous if the total area of continuous pasture was >64 ha.

Post-fledging Survival

We used the Kaplan-Meier product-limit method (Kaplan and Meier 1958, Cox and Oakes 1984) and SYSTAT (SPSS 1998) to estimate post-fledging survival. For our survival analysis, we assumed that survival times of individuals were independent; that juveniles tracked were representative of the population; that trapping, handling, and carrying a radiotransmitter did not influence survival probability; and that censoring (radio-loss or migra-

tion) did not indicate death. If the final assumption was not valid, and some owls actually died when we classified them as having migrated, our analysis would result in an overestimation of survival. However, we believe that the assumption is valid since we were easily able to find and recover dead birds, very few radiosignals were lost where fate of the owl was unknown, and owls that we classified as having migrated did so at a time when initiation of migration was expected (late Aug–Oct).

We used Tarone-Ware log-rank test and SYSTAT to assess the effect of year, sex, transmitter style, habitat continuity, and feeding treatment on survival distributions. To test for possible effects of fledging mass, number of siblings, and hatch date on individual survival, we used Cox regression (Cox and Oakes 1984). For all statistical analyses, significance was assessed against $\alpha = 0.05$.

Changes in Survival through Time

To determine whether risk of mortality was constant throughout the post-fledging period, we converted the Kaplan-Meier survival function to a cumulative hazard function, which represents relative risk of mortality over time. We defined intervals of constant slope based on obvious changes in the hazard function. These intervals represented periods during the post-fledging period when risk of mortality was constant. We tested for differences between interval survival rates using the chi-square statistic in CONTRAST (Sauer and Williams 1989).

Cause-specific Mortality

We calculated cause-specific mortality rates by determining probability of death due to specific sources using MICROMORT (Heisey and Fuller 1985). Daily mortality rates were calculated as probability of death due to a specific cause during 1 day, given that the animal had survived up to that day. We calculated interval mortality rates as the sum of probabilities that the individual survived to a particular day, and then was killed by a specific mortality agent on that day. Overall mortality rate due to specific sources was calculated as the sum of the probabilities of death due to a particular mortality agent over all intervals.

RESULTS

Post-fledging Survival

We found a significant difference in juvenile survival between 1997 and 1998–2000 ($n = 76$ owls; $\chi^2 = 5.79$, $df = 1$, $P = 0.02$). None of 12 radiomarked juveniles died prior to migration in 1997, whereas

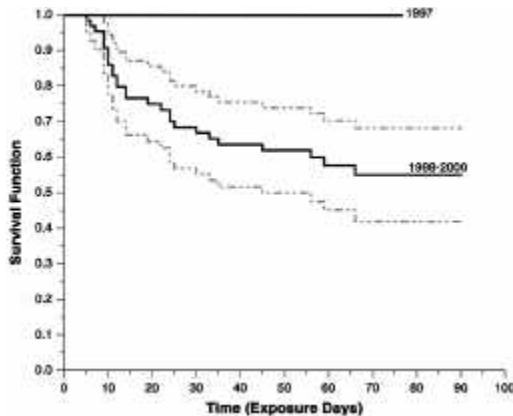


Fig. 1. Kaplan-Meier survival curve for juvenile owls in Saskatchewan, Canada, illustrating post-fledging survival in 1997 and 1998–2000 combined. The dashed lines surrounding the 1998–2000 survival curve indicate upper and lower 95% confidence intervals.

in 1998–2000, approximately half (45%) of the 64 radiomarked juveniles died before migrating. Survival did not differ among 1998, 1999, and 2000 ($\chi^2 = 0.61$, $df = 2$, $P = 0.74$). Therefore, we pooled data from those 3 years for subsequent analysis ($n = 64$ owls). Overall post-fledging survival for 1998–2000 was 0.55 (95% CI: 0.44 to 0.70; Fig. 1).

Probability of survival did not differ between males and females ($\chi^2 = 0.013$, $df = 1$, $P = 0.93$; $n = 12$ males, 11 females). Therefore, random selection of 1 juvenile per nest for subsequent survival analysis was not affected by differences between males and females.

The style of transmitter, either backpack ($n = 11$) or necklace ($n = 95$), did not appear to affect survival probability ($\chi^2 = 0.60$, $df = 1$, $P = 0.44$). We found no obvious physical effects (i.e., no skin abrasions or lost feathers), or difference in mass between radiomarked ($\bar{x} = 179.3$ g; $n = 4$) and nonradiomarked owls ($\bar{x} = 177.3$ g; $n = 4$) when we recaptured them approximately 2 weeks prior to migration ($t_6 = 2.45$, $P = 0.79$). Juvenile survival did not differ significantly between individuals raised in isolated and continuous habitat patches ($\chi^2 = 0.09$, $df = 1$, $P = 0.77$). The overall probability of survival in large, continuous patches ($n = 19$) was 0.63 (95% CI: 0.41 to 0.85), compared to 0.52 (95% CI: 0.36 to 0.67) in small, isolated patches ($n = 45$).

We found no effect of brood size ($\chi^2 = 0.30$, $df = 1$, $P = 0.58$) on post-fledging survival. However, survival was significantly affected by mass at fledging ($\chi^2 = 3.99$, $df = 1$, $P = 0.04$). Juveniles that died

during the post-fledging period averaged 6% lighter at fledging than those that survived ($\bar{x}_{\text{died}} = 143.4 \pm 3.79$ g, $n = 14$; $\bar{x}_{\text{survived}} = 152.1 \pm 3.11$ g, $n = 18$; $t_{30} = 1.70$, $P = 0.04$). Supplemental feeding during the nestling stage did not affect overall post-fledging survival ($\chi^2 = 1.53$, $df = 1$, $P = 0.22$), nor did we find a significant difference ($t_{30} = 2.04$, $P = 0.18$) in mass at fledging between juveniles who received supplemental food during the nestling period ($\bar{x} = 145.1 \pm 3.64$ g, $n = 17$) and those that did not ($\bar{x} = 151.9 \pm 3.22$ g, $n = 15$). We found no correlation between age and body mass when transmitters were attached ($F_{57} = 0.22$, $P = 0.64$), suggesting that the juveniles had reached adult mass by the time transmitters were attached.

Mean date of migration was 24 September ± 1.7 days (median = 26 Sep; $n = 45$). Initiation of migration ranged from 21 August to 16 October. We were unable to determine the fate of 4 radiomarked juveniles between 1997 and 2000. We assumed radio failure occurred, since signals were lost before owls likely would have begun migration (Jul and early-Aug).

Changes in Survival through Time

Probability of survival for juvenile owls was not affected by hatch date ($\chi^2 = 0.16$, $df = 1$, $P = 0.69$), suggesting that early-fledged owls were at no higher or lower risk of mortality than those that fledged later in the year. However, risk of mortality was not constant throughout the post-fledging period. Based on the cumulative hazard function, we defined 3 intervals (Fig. 2), each of which corresponded to a different daily risk of mortality. The first interval (fledging) encompassed the first 14 days after fledging, and was associated with the highest daily risk. The second interval

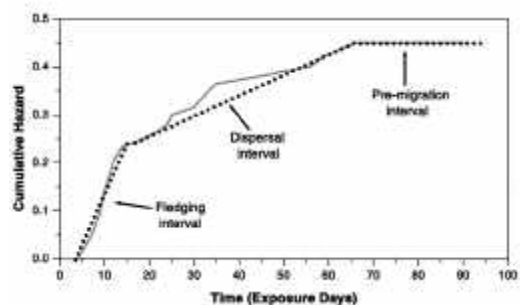


Fig. 2. Cumulative hazard rate depicting relative risk of mortality for juvenile owls in Saskatchewan, Canada, throughout the post-fledging period. Dashed lines indicate areas of constant slope and therefore intervals of constant mortality risk. Intervals approximately correspond to behaviors associated with fledging, dispersal, and pre-migration activities.

Table 1. Survival probability and cause-specific mortality for juvenile burrowing owls in Saskatchewan, Canada, 1998–2000. Intervals of fledging, dispersal, and pre-migration correspond to intervals of constant slope on the cumulative hazard function.

Interval	Days after fledging	Exposure days	No. of owls	Deaths	Interval survival rate ^a	Interval mortality rate ^b			
						Predation	Starvation	Human disturbance	Unknown
Fledging	0–14	835	64	15	0.78 (0.68–0.88)	0.16 (11)	0.05 (3)	0.02 (1)	0
Dispersal	15–70	1,960	49	12	0.71 (0.58–0.86)	0.10 (4)	0.05 (2)	0.10 (4)	0.05 (2)
Pre-migration	71–90	660	18	0	1.00	0	0	0	0
<i>Overall rate:</i>					0.55	0.24	0.08	0.09	0.04
<i>(95% CI):</i>					(0.44–0.70)	(0.13–0.35)	(0.01–0.15)	(0.02–0.17)	(0.00–0.09)

^a Numbers in parentheses indicate 95% confidence intervals.

^b Numbers in parentheses indicate number of juveniles killed by each source.

(dispersal) included days 15–70 after fledging, a time when most dispersal movements occurred (Todd 2001). During the pre-migration interval (days 71–90 after fledging), none of the remaining radiomarked owls died.

Cause-specific Mortality

Of 64 radiomarked juveniles we monitored during 1998–2000, 27 died prior to migration. We attributed 15 of these 27 deaths to predation, 5 to starvation, 5 to anthropogenic sources (4 collisions with vehicles, 1 collision with a barbed-wire fence), and 2 to unknown causes. Predation was the predominant cause of death for juvenile owls during the fledging interval, while probability of mortality due to anthropogenic factors increased during the dispersal interval (Table 1).

Post-fledging Survival and Population Change

In sites searched consistently each year between 1997 and 2001, we found 38, 56, 29, 26, and 22 pairs of owls, respectively. The number of artificial nest boxes in the area remained relatively constant during this time. When juvenile survival was moderate (1998–2000), the breeding population declined by 11–48% in the subsequent year. However, the population increased by 32% following the only year of high post-fledging survival (1997). Based on our banding data from our study population, local recruitment for yearling birds in 1998 (8.3%; 18 banded birds returned of 219 banded in the previous year) was substantially higher than the other 3 years (1999 = 2.4%, 6 of 247; 2000 = 0.9%, 1 of 114; 2001 = 3.1%; 4 of 128). This indicates that not only were juvenile owls in 1997 more likely to survive the post-fledging period, they also were more likely to survive migration and overwintering and return to the breeding area in 1998.

DISCUSSION

Post-fledging Survival and the Population Decline

Although low post-fledging survival alone is not likely responsible for the burrowing owl population decline in Canada, we suggest that it may play an important role in the dynamics of the southern Saskatchewan population. Even though we increased pre-fledging productivity in our study by using nest boxes and providing supplemental food during the nesting period, we believe that our results accurately reflect survival during the post-fledging period and apply and compare to other systems. Juvenile owls usually flew away from the burrow when approached during the post-fledging period (therefore, a nest box would provide little protection), and because we stopped all supplemental feeding by fledging age, we feel these 2 management practices had little or no impact on survival of juvenile owls during the post-fledging period. To our knowledge, only 2 other studies of post-fledging survival exist that compare to ours, both of which used supplemental feeding either alone or in combination with artificial nest boxes. Clayton and Schmutz (1999) had similar results, reporting 45% survival of post-fledging juvenile owls in Alberta in 1995–1996, and 48% survival in Saskatchewan in 1996. King (1996) reported a much higher post-fledging survival rate (85.4%) in southwestern Idaho during 1994–1995.

Post-fledging survivorship in 1 year appeared to be correlated with recruitment of yearling owls into the subsequent breeding population. Local yearling recruitment in our study (determined by birds we banded as fledglings returning the following year to breed) in 1999–2001 averaged only 2.1%, and corresponded to a decline in the

breeding population from the previous year. In 1998, however, we observed relatively high local yearling recruitment (8.3%), as well as the only increase in this breeding population in 13 years (James et al. 1997, Wellicome et al. 1997, Poulin et al. 2001). This coincidence raises the possibility that post-fledging juvenile survival in a given year has an important influence on size of the breeding population in the following year.

The most likely cause for the extraordinarily high survival rate in 1997, and subsequent recruitment in 1998, was a superabundance of voles during spring and summer 1997. Prior to 1997, it had been 28 years (1969) since vole populations reached similar magnitudes in southern Saskatchewan (Houston 1997). In most years, voles account for only a small percentage (ranging 0–32% over 9 yr, based on prey cache analysis) of the small mammals in the diet of burrowing owls in our study area. However, in 1997, voles accounted for 87% of the small mammals in owl diets (Wellicome 2000, Poulin et al. 2001). As a result of this abundant food source, more nestlings survived from hatching to fledging in 1997 (i.e., high productivity; see Wellicome 2000), and those fledglings survived the post-fledging period better than they did in other years. The vole outbreak likely benefited juvenile owls in 2 ways: directly, by serving as abundant prey for the owls; and indirectly, as an alternative prey source for owl predators. Although avian predators were more abundant in southern Saskatchewan in 1997 than in other years (Poulin et al. 2001), no radiomarked owls were killed prior to migration in 1997. Search intensity of potential predators was possibly reduced because they were satiated by abundant voles (alternative prey hypothesis; e.g., Korpimäki et al. 1990). These data suggest that availability of natural prey after fledging plays an important role in the probability of juvenile survival.

Sources and Timing of Post-fledging Mortality

Although we found no significant difference in survival between owls wearing 1 style of transmitter versus another, these results should be interpreted with caution as we had far more juveniles wearing necklace ($n = 95$) than backpack ($n = 11$)-style transmitters. Our finding that daily risk of predation for juvenile owls was highest in the first 2 weeks after fledging was similar to that of King (1996) for burrowing owls in Idaho, and Clayton and Schmutz (1999) for burrowing owls

in Alberta and Saskatchewan. This pattern is common in birds (e.g., Belthoff and Ritchison 1989, Petty and Thirgood 1989, McFadzen and Marzluff 1996) and generally is thought to be a result of inexperience with predators, poor flying skills, and loud begging. Relative risk of predation for juvenile owls declined during dispersal, likely due to juveniles' increased familiarity with predators, improved flying ability, and more scattered distribution throughout the landscape. In contrast, deaths attributable to anthropogenic sources increased during dispersal as juveniles began to move away from their nest and increased their contact with human-created dangers. In contrast to Clayton and Schmutz (1999), we did not find deaths due to human influences to be as frequent as those due to predation.

Although we found no significant difference in survival between continuous and isolated habitat patches in our study, we did detect a tendency, though not significant, toward higher survival in larger patches. Most native grassland on the Regina Plain has been converted to cropland. Consequently, our entire study area consisted of isolated patches of varying sizes. Therefore, comparisons with estimates of juvenile survival from areas of vast grasslands may better indicate whether habitat loss plays a significant role in post-fledging survival.

MANAGEMENT IMPLICATIONS

Relatively high recruitment, coincident with an increase in the breeding population following a year of high post-fledging survival, suggests that low post-fledging juvenile survival may be an important factor in the population decline of burrowing owls. High juvenile owl survival during a population peak of voles suggests that abundant natural food may be an important correlate of survival for post-fledging juveniles. Conservation and management plans to benefit burrowing owls should include steps to improve juvenile survival, such as minimizing anthropogenic dangers and managing habitat to increase natural food availability during the post-fledging period.

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