POSTFLEDGING BEHAVIOR OF GOLDEN EAGLES

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ABSTRACT.--We predicted that extended parental care, asynchronous hatching, and incidences of siblicide in Golden Eagles (Aquila chrysaetos) could increase the chances for conflict between siblings, and between parents and offspring as juveniles aged. This conflict could motivate independence and dispersal in this species. To test our predictions, during the 1993 and 1994 breeding seasons we examined post-fledging behavior in Golden Eagles from the Little Missouri National Grassland and contiguous areas of western North Dakota. We collected observations of 28 radio-tagged juveniles to determine whether predispersal movements were correlated with age and with the presence of a sibling or parent during the first 6-10 weeks after fledging. We also recorded juvenile vocalization rates to determine if they changed with age or the presence of a parent. We found that distance from the natal nest increased with time since fledging. This was attributed to an increased proficiency in flight and gradual development of independence from parental care. We found that calling rate and distance between individuals of sibling pairs did not change with time after fledging but was highly variable. Calling rates of fledglings in the presence of parents were higher than when parents were absent. Increased calling may facilitate juvenile location or inform the parents of offspring nutritional status. Parents were not visible for most observation periods and we did not observe any aggression by parents directed toward offspring. Siblings engaged in "play" activity and we did not detect any signs of aggression between siblings. Our data do not support the predictions that an increase in parental and/or sibling aggression is associated with independence in this population of Golden Eagles. Received 15 Oct. 1998, accepted 20 April 1999.

Factors influencing the timing and duration of dispersal may be extrinsic (environmental), endogenous, or some combination of the two (Howard 1960, Ritchison et al. 1992, Belthoff and Duffy 1995). Extrinsic factors include parental aggression toward young (Alonso et al. 1987, Hiraldo et al. 1989, Wiggett and Boag 1993), sibling aggression (Holleback 1974, De Laet 1985, Strickland 1991), ectoparasitism (Brown and Brown 1992), increased predation risk (Harfenist and Ydenberg 1995), and declining food availability within the natal area (Messier 1985, Kenward et al. 1993, Bustamante 1994b). In raptors, the role of sibling and parental aggression in family break-up is disputed. In some species, dispersal may occur after a period of parent-offspring conflict, the parents being the ones who promote the independence of juveniles by gradually reducing the food supply or increasing aggression towards the juveniles (Alonso et al. 1987, Delannoy and Cruz 1988, Hiraldo et al. 1989). Family break-up may also take place without apparent conflict (Bustamante and Hiraldo

1990, Bustamante 1994b). Although Watson (1997) thought that there was little evidence of aggression between adult Golden Eagles and their young, Walker (1987) observed some aggression by parents toward offspring during the fledgling dependency period. There is little information on the factors that affect timing of dispersal in Golden Eagles because few studies have been conducted on the behavior of juvenile eagles during this stage (Watson 1997). We predicted that the extended parental care, asynchronous hatching (Watson 1997), and high incidence of siblicide (Edwards and Collopy 1983, Edwards et al. 1988) in this species would increase the probability of predispersal conflict.

METHODS

Study area.—We conducted this study from May to November 1993–1994 in the Little Missouri National Grassland (46° 00'– 48° 07' N, 102° 50'–104° 00' W) and contiguous areas in western North Dakota. The dominant habitat was mixed prairie with patches of shrubs managed primarily for livestock grazing (Hopkins et al. 1986, Fowler et al. 1991). Woodlands (1.8% of total vegetative cover) were found in areas of higher soil moisture, such as valley bottoms, lower valley slopes, and along stream banks and floodplains of the Little Missouri River (Girard et al. 1989). Large buttes, easily eroded sandstone, and clay badlands characterized the topography. The climate is semi-arid continental with wide daily fluctuations in temperature and

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variable precipitation. Annual precipitation averages 33-41 cm, and the average temperature in July is 21° C (Jensen 1972). We found Golden Eagle nests on siltstone and clay buttes, and in trees along rivers and streams.

Data collection.---We located active Golden Eagle nests by aerial and ground surveys. We aged chicks based on behavior and plumage (Ellis 1979), and sexed them based on bill depth and head, hallux claw, and tail length (A. Harmata, pers. comm.). We entered each of the 20 eagle nests (n = 10 in 1993; n = 10 in 1994) when nestlings were 8-10 weeks of age (near fledging). We selected this age because harassment can cause prolonged absence of eagle adults which could result in nestlings being exposed to direct sunlight or missed feedings-both fatal to younger chicks. Because young eagles will fledge prematurely if disturbed, we waited until nestlings were fully feathered and could fly well enough to avoid injury if they fledged in response to our presence (Fvfe and Olendorff 1976). Twenty-eight (12 male, 16 female) chicks (n = 12 in 1993; n = 16 in 1994) were weighed, measured, fitted with a 25-g backpack-style radio transmitter (L. L. Electronics, Mahomet, Illinois), and banded with an aluminum U.S. Fish and Wildlife Service leg band. After we instrumented and measured each eagle, we placed it back in the nest where it remained until it fledged. We spent an average of 51.3 (\pm 3.9 SE) min from eagle capture to replacement in the nest.

We considered a juvenile as fledged after its first flight from the nest. After fledging, we located birds using ground searches every 2–4 days for behavioral observations. We recorded over 416 hr of direct behavioral observations from 14 July to 20 August 1993, and 15 July to 22 August 1994. We recorded movements of radio-telemetered birds until they dispersed from their natal territories, or we found them dead. During the first five weeks, we were usually able to locate eagles visually (94.1% of attempts). We primarily used triangulation (Kenward 1987) by four observers to find juveniles in the later stages of the postfledging period.

We observed eagles during daylight hours (06:00-21:00 MST) using $14-45 \times$ zoom spotting scopes from vehicles or at locations at least 300 m from the bird. We determined target observation times by randomly selecting a 4-hr block of daylight. We covered the other time periods during later observations using the same method. During each observation period, we continually recorded data until the predetermined time elapsed, or until we could no longer observe the bird. We collected a mean of 15.4 (\pm 1.2) hr of observation per bird over 4.3 (\pm 0.3) observation periods. We recorded eagle locations and activities on a data checksheet. We did not record sibling behaviors simultaneously. We recorded the following data on adults: location in relation to focal bird, incidences of food deliveries by an adult, stooping and physical aggression directed toward the focal bird. We observed few prey deliveries (n = 9), so we could not analyze temporal changes in food provisioning rates.

We attempted to sample behavior equally among birds for different ages and times of day. We calculated distance from focal bird to the nest and the distance between siblings using simple geometry and UTM coordinates.

Statistical analysis.-Using Repeated Measures Analysis of Variance (ANOVA; Proc GLM; SAS Inst. Inc. 1987; PC ver. 6.10) we tested our predictions on the pooled 1993-1994 data because there were too few data to examine a year effect using repeated measures analysis. To determine the proper sampling unit for analysis (individual bird vs nest) we used the ratio of Type III Sum of Squares (Proc GLM). A relatively large ratio (>2) would indicate that individual birds should be combined into one "nest" unit because separate consideration results in unexplained error (Sum of Squared Errors; P. Chapman, pers. comm.). There was no evidence of a strong sibling effect (average ratio = 1.3), and because all behavioral observations were made after fledging, we used individuals as the unit of analysis.

We compared hourly calling rate between three age groups: 0-14, 15-28, and 29-42 days post-fledging; and a fledgling's distance from the natal nest over six age periods (0-15, 16-28, 29-52, 53-74, 75-97, and 98-137 days post-fledging). We tested whether the distance between siblings increased over three post-fledging age periods (0-37, 38-74, and 75-121 days). For analysis, we grouped fledgling ages differently because the data collected for calling, distance from the nest, and distance between siblings varied in quantity. We were able to collect data on distance from nest longer than any other measure. Also, calling rates were recorded hourly, unlike both distance measurements. The selected age groups fulfilled minimum sample size requirements for the most suitable statistical tests and to achieve a stratified distribution of data points (P. Chapman, pers. comm.). All data sets used for these analyses were log-transformed to equalize the variance of errors (SAS Inst. Inc. 1987; PC ver. 6.10) but the raw data are reported in this paper. The α level for all statistical tests was 0.05.

To analyze data on parent-offspring interactions, we used ANOVA (Proc GLM; SAS Inst. Inc. 1987; PC ver. 6.10) on log-transformed data to test whether calling rates or fledgling distance from the nest changed when parents were present. We also examined whether fledgling distance from the nest depended upon an interaction between parents' presence and fledging age.

RESULTS

Hourly calling rate.—The number of calls per hour did not change with time after fledging (Wilks' Lambda $F_{2,412} = 0.06$, P > 0.05). The mean values for each of the three groups were similar, with an overall mean of 11.4 (\pm 0.01) calls hr⁻¹ (Fig. 1). Calling rate did not differ between the sexes ($F_{1,413} = 0.50$, P >0.05).



FIG. 1. Mean number of calls |SE| per hour for Golden Eagles in three post-fledging time periods (0– 14, 15–28, 29–42 d) in the Little Missouri National Grassland of western North Dakota, 1993 and 1994.

Distance from nest.—The distance of fledglings from their nests increased significantly with time (Wilks' Lambda $F_{4,10} = 11.53$, P = 0.001; Fig. 2) and eventually resulted in loss of radio contact within the study area (27,500 km²) as the birds dispersed. There was no difference between sexes in the distance individuals dispersed ($F_{1,13} = 0.06$, P > 0.05).

Sibling interactions and juvenile behavior.—We collected data from six sibling pairs to determine the mean distance between siblings with time since fledging. There was no significant (Wilks' Lambda $F_{2,3} = 0.34$, P > 0.05) change over the time period of our study (Fig. 3).

Fledgling pairs frequently exhibited nonaggressive social behavior. Siblings often followed one another or flew together. We observed mutual preening or "nibbling" (Ellis 1979) when the fledglings perched together (n = 288), as they frequently did. We observed three different sibling pairs display "play" catching and plucking of prey together. We recorded no overtly aggressive social behavior between sibling pairs, and this social activity did not appear to change over time.

The mean age at first flight was 10.1 (\pm 0.08) weeks. We observed 11 attempts of prey capture by juveniles. Two of the observed at-



FIG. 2. Mean distance from the nest (m) ISEI for Golden Eagles in six post-fiedging time periods (0–15, 16–28, 29–52, 53–74, 75–97, 98–137 d) in the Little Missouri National Grassland of western North Dakota, 1993 and 1994.



FIG. 3. Mean distance |SE| between Golden Eagle siblings (6 pairs) in three post-fledging time periods (0–37, 38–74, 75–121 d) in the Little Missouri National Grassland of western North Dakota, 1993 and 1994.

tempts were successful, with prey items including an unidentified snake and a rodent.

Parental interactions.-We observed parents near the focal bird relatively infrequently (29.6%) during observation periods. Calling rates of the young were higher in the presence of parents than when parents were not visible $(F_{1,413} = 14.39, P = 0.001)$. The rate of calling nearly doubled for juveniles with a parent present ($\bar{x} \pm SE = 21.8 \pm 3.5$ calls hr⁻¹) versus parents absent (11.5 \pm 1.7 calls hr⁻¹). Fledglings were closer to the nest when parents were present ($F_{1,13} = 10.81, P = 0.001$), but distance from the nest was not significantly correlated with the interaction of fledgling age and parental presence ($F_{4,10} = 0.96$, P > 0.05). We did not observe any aggressive behavior by the parent toward the offspring.

DISCUSSION

Calling rate did not change as the birds aged after fledging, although we observed a high degree of individual variation. A similar finding was reported in a Japanese population of Black Kites (Milvus migrans; Koga and Shiraishi 1994). Increased calling with age was reported in Spanish populations of Black Kites (Bustamante and Hiraldo 1990), the Egyptian Vulture (Neophron perchopterus; Ceballos and Donazar 1990), and the Spanish Imperial Eagle (Aquila adalberti; Alonso et al. 1987). The increased calling rates in these studies were attributed to a decrease in provisioning by parents as the young aged. Our results do not corroborate findings of increased calling with age. It is possible that food provisioning did not decrease over time in our study, resulting in no change in calling rates. It is also possible that food provisioning decreased, but calling did not increase because the young were becoming independent and beginning to hunt on their own. We cannot evaluate these hypotheses because we did not have enough data to analyze food provisioning rates.

Throughout our study, the appearance of a parent resulted in increased juvenile calling compared with when parents were absent. Increased calling in the presence of a parent is commonly observed in raptors (Alonso et al. 1987, Ikeda 1987, Hiraldo et al. 1989, Bustamante 1994a). Calling by juveniles may facilitate juvenile location by parents (Ikeda 1987). Calling also informs the parents of the nutritional status of their offspring (Trivers 1974).

Distance from the nest increased as the juveniles aged, probably in part due to increased flying proficiency. As independence nears, movements may not represent a linear dispersal, but may resemble "wanderings" outside the natal area. Similar observations have been reported for other species (Boeker and Ray 1971, Beecham and Kochert 1975, Steenhof et al. 1984, Walker 1987, Bahat 1992).

Siblings tended to move together after leaving the nest, and the distance between them remained relatively constant. This contradicts Newton's (1979) idea that fledgling raptors tend to perch apart. Other studies also revealed increased distance between siblings with age (Hiraldo et al. 1989, Bustamante and Hiraldo 1990, Ceballos and Donazar 1990). Increased sibling distance has been attributed to "tension" between juveniles or increased flight proficiency. Bustamante (1994a) reported that Kestrels (Falco tinnunculus) perched close together and engaged in social behavior similar to the young Golden Eagles we observed. Bustamante (1993) also found siblings of Black-shouldered Kites often perched together. Kenward and coworkers (1993) saw the same tendency with Northern Goshawk (Accipiter gentilis) siblings.

If parents and offspring were in conflict, resulting in the adults "driving-off" the juveniles, or if parents used aggression to evaluate the young's flight proficiency (Ferrer 1992), we should have observed agonistic interactions during the times when the parents were seen with the offspring, but we did not. Although parental aggression has been observed in raptor species (Robertson 1985, Alonso et al. 1987, Walker 1987, Hiraldo et al. 1989), it is often the case that the parents feed their offspring long after they have fledged (Ikeda 1987, Walker 1987, Bustamante and Hiraldo 1990, Ceballos and Donazar 1990, Bahat 1992).

We did not find an increase in aggression between siblings, as we predicted. Although juveniles moved away from their parental home range, they apparently remained together, indicative of sibling attraction rather than aversion. Our data do not support the predictions that an increase in parental and/or sibling agression is associated with independence in this population.

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LITERATURE CITED

- ALONSO, J. C., L. M. GONZALEZ, B. HEREDIA, AND J. L. GONZALEZ. 1987. Parental care and the transition to independence of Spanish Imperial Eagle Aquila heliaca in Donana National Park, Southwest Spain. Ibis 129:212–224.
- BAHAT, O. 1992. Post-fledging movements of Golden Eagles (Aquila chrysaetos homeryeri) in the Negev Desert, Isreal, as determined by radio-telemetry. Pp. 612–621 in Wildlife telemetry: remote monitoring and tracking of animals (I.G. Preide and S.M. Swift, Eds.). Ellis Horwood Ltd, West Sussex, U.K.
- BEECHAM, J. J. AND M. N. KOCHERT. 1975. Breeding biology of the Golden Eagle in southwestern Idaho. Wilson Bull. 87:506–513.
- BELTHOFF, J. R. AND A. M. DUFFY, JR. 1995. Locomotor activity levels and the dispersal of Western Screech-Owl, *Otus kennicottii*. Anim. Behav. 50: 558–561.
- BOEKER, E. L. AND T. D. RAY. 1971. Golden Eagle population studies in the Southwest. Condor 73: 463-467.
- BROWN, C. R. AND M. B. BROWN. 1992. Ectoparasitism as a cause of natal dispersal in Cliff Swallows. Ecology 73:1718–1723.
- BUSTAMANTE, J. 1993. The post-fledging dependence period of the Black-Shouldered Kite (*Elanus caeruleus*). J. Raptor Res. 27:185–190.
- BUSTAMANTE, J. 1994a. Behavior of colonial Common Kestrels (*Falco tinnunculus*) during the postfledging dependence period in southwestern Spain. J. Raptor Res. 28:79–83.
- BUSTAMANTE, J. 1994b. Family break-up in Black and Red kites *Milvus migrans* and *M. milvus*: is time

of independence an offspring decision? Ibis 136: 176-184.

- BUSTAMANTE, J. AND F. HIRALDO. 1990. Factors influencing family rupture and parent-offspring conflict in the Black Kite (*Milvus migrans*). Ibis 132: 58–67.
- CEBALLOS, O. AND J. A. DONAZAR. 1990. Parent-offspring conflict during the post-fledging period in the Egyptian Vulture *Neophron percnopterus* (Aves, Accipitridae). Ethology 85:225–235.
- DELAET, J.V. 1985. Dominance and aggression in juvenile Great Tits, *Parus major major*, in relation to dispersal. Pp. 375–380 *in* Behavioral ecology: ecological consequences of adaptive behavior (Sibley, R. M. and R. H. Smith, Eds.). Blackwell Scientific Publ., London, U.K.
- DELANNOY, C. A. AND A. CRUZ. 1988. Breeding biology of the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*). Auk 105:649–662.
- Edwards, T. C., JR. AND M. W. COLLOPY. 1983. Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide. Auk 100:630–635.
- Edwards, T. C., Jr., M. W. Collopy, K. Steenhof, AND M. N. Kochert. 1988. Sex ratios of fledgling Golden Eagles. Auk 105:793–796.
- ELLIS, D. H. 1979. Development of behavior in the Golden Eagle. Wildl. Monogr. 43:1–94.
- FERRER, M. 1992. Regulation of the period of postfledging dependence in the Spanish Imperial Eagle Aquila adalberti. Ibis 134:128–133.
- FOWLER, A. C., R. L. KNIGHT, T. L. GEORGE, AND L. C. MCEWEN. 1991. Effects of avian predation on grasshopper populations in North Dakota grasslands. Ecology 72:1775–1781.
- FYFE, R. W. AND R. R. OLENDORFF. 1976. Minimizing the dangers of nesting studies to raptors and other sensitive species. Can. Wildl. Serv. Occas. Pap. 23:1–17.
- GIRARD, M. M., H. GOETZ, AND A. J. BJUGSTAD. 1989. Native woodland habitat types of southwestern North Dakota. USDA For. Serv. Res. Pap. RM-281:1–36.
- HARFENIST, A. AND R. C. YDENBERG. 1995. Parental provisioning and predation risk in Rhinoceros Auklets (*Cerorhinca monocerata*): effects on nestling growth and fledging. Behav. Ecol. 6:82–86.
- HIRALDO, F., M. DELIBES, AND R. R. ESTRELLA. 1989. Observations of a Zone-tailed Hawk family during the post-fledging period. J. Raptor Res. 23:103– 106.
- HOLLEBACK, M. 1974. Behavioral interactions and the dispersal of the family in Black-capped Chickadees. Wilson Bull. 76:28–36.
- HOPKINS, R. B., J. F. CASSEL, AND A. J. BJUGSTAD. 1986. Relationships between breeding birds and vegetation in four woodland types of the Little Missouri National Grasslands. USDA For. Serv. Res. Pap. MR-270:1–12.
- HOWARD, W. E. 1960. Innate and environmental dis-

persal of individual vertebrates. Am. Midl. Nat. 63:152-161.

- IKEDA, Y. 1987. Ecological research on the Japanese Golden Eagle *Aquila chrysaetos japonica* during the post-fledging period in the Hakusan Range. J. Raptor Res. 21:79–80.
- JENSEN, R. R. 1972. Climate of North Dakota. North Dakota State Univ., Fargo.
- KENWARD, R. E. 1987. Wildlife radio tagging: equipment, field techniques and data analysis. Academic Press, London, U.K.
- KENWARD, R. E., V. MARCSTROM, AND M. KARLBLOM. 1993. Post-nestling behavior of Goshawks, Accipiter gentilis. I. The causes of dispersal. Anim. Behav. 46:65–70.
- KOGA, K. AND S. SHIRAISHI. 1994. Parent-offspring relations during the post-fledging dependency period in the Black Kite (*Milvus migrans*) in Japan. J. Raptor Res. 28:171–177.
- MEISSIER, F. 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Can. J. Zool. 63:239–245.
- NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota.

RITCHISON, A. J., J. R. BELTHOFF, AND E. J. SPARKS.

1992. Dispersal restlessness: evidence for innate dispersal by juvenile Eastern Screech Owls? Anim. Behav. 43:57–65.

- ROBERTSON, A. S. 1985. Observations on the postfledging dependence period of Cape Vultures. Ostrich 56:58–66.
- SAS INSTITUTE, INC. 1987. SAS statistical guide for personal computers, version 6.10. SAS Inst. Inc., Cary, North Carolina.
- STEENHOF, K., M. N. KOCHERT, AND M. Q. MORITSCH. 1984. Dispersal and migration of southwestern Idaho raptors. J. Field Ornithol. 55:357–368.
- STRICKLAND, D. 1991. Juvenile dispersal in Gray Jays: dominant brood member expels siblings from natal territory. Can. J. Zool. 69:2935–2945.
- TRIVERS, R. L. 1974. Parent-offspring conflict. Am. Zool. 14:249-264.
- WALKER, D. G. 1987. Observations on the post-fledging period of the Golden Eagle Aquila chrysaetos in England. Ibis 129:92–96.
- WATSON, J. 1997. The Golden Eagle. T & A D Poyser, London, U.K.
- WIGGETT, D. R. AND D. A. BOAG. 1993. The proximate cause of male-biased natal emigration in Columbian ground squirrels. Can. J. Zool. 71:201–218.