

- STILES, F. G. AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Cornell Univ. Press, Ithaca, New York.
- WHEELER, B. K. AND W. S. CLARK. 1995. A photographic guide to North American raptors. Academic Press, San Diego, California.
- WHITE, C. M., D. A. BOYCE, AND R. STRANECK. 1989. Observations on *Buteo swainsoni* in Argentina, 1984, with comments on food, habitat alteration and agricultural chemicals. Pp. 79–87 in *Raptors in the modern world* (B. U. Meyburg, and R. D. Chancellor, Eds.). World Wildlife Group on Birds of Prey, London, U.K.
- WOODBIDGE, B., K. K. FINLEY, AND S. T. SEAGER. 1995. An investigation of the Swainson's Hawk in Argentina. *J. Raptor Res.* 29:202–204.

Wilson Bull., 111(3), 1999, pp. 432–436

Siblicide at Northern Goshawk Nests: Does Food Play a Role?

Wendy A. Estes,^{1,2} Sarah R. Dewey,^{1,3} and Patricia L. Kennedy^{1,4}

ABSTRACT.—Siblicide as a mechanism for brood reduction has been reported in a number of asynchronously hatching bird species. Although researchers have documented the occurrence of facultative siblicide in several raptor species, its cause is still debated. Most hypotheses relate incidences of siblicide to food availability. The food-amount hypothesis predicts a negative relationship between the amount of food available and nestling aggression. While the food-amount hypothesis has received much attention, few studies show more than correlational support for this activity in raptors. Our observation of a siblicide event at a Northern Goshawk (*Accipiter gentilis*) nest used as a control in a supplemental feeding experiment, and a similar incident where a nestling goshawk's death can be attributed to siblicide provide support for the negative correlation between food amount and sibling aggression. These observations and the lack of any reported sibling aggression at seven supplementally fed nests showing extreme hatching asynchrony also indicate a relationship between food resources and brood reduction. Our observations are consistent with the idea that goshawks exhibit facultative siblicide, and that resource levels as predicted by the food-amount hypothesis directly influence it. *Received 7 Oct. 1998, accepted 16 Feb. 1999.*

ling is at a competitive disadvantage if resources provided by the parents prove inadequate. In asynchronously hatched broods, the youngest nestling occasionally dies from aggressive sibling behavior including pecking, exclusion during feeding bouts, or eviction from the nest (Lack 1954, Mock et al. 1990, Creighton and Schnell 1996). Asynchronous hatching results in adapting a brood size to an unpredictable food supply by allowing all young to survive when food is plentiful, but ensuring brood reduction to match parental provisioning capabilities when prey levels are meager (Lack 1954, Newton 1979, Bryant and Tatner 1990, Heeb 1994). Species in which the frequency of siblicide events are variable are termed facultative, while those in which siblicide occurs in nearly all nest attempts are called obligate (Edwards and Collopy 1983). Although the occurrence of obligate siblicide appears to be largely innate (Mock et al. 1990, Gerhardt et al. 1997), the causes of facultative siblicide are still debated (Forbes and Mock 1994).

Hatching asynchrony in birds facilitates brood reduction because the last hatched nest-

Fatal sibling aggression has been documented in a range of avian species (Stinson 1979, Braun and Hunt 1983, Anderson 1989, Drummond and Garcia Chavelas 1989, Bryant and Tatner 1990, Mock et al. 1990, Mock and Lamey 1991, Heinsohn 1995, Reynolds 1996). However, an understanding of the proximate factors that influence the occurrence of facultative siblicide remains elusive because such events are rare and unpredictable. Most similar hypotheses attempt to explain facultative siblicide in relation to food.

¹ Dept. of Fishery and Wildlife Biology, Colorado State Univ., Fort Collins, CO 80523.

² Present address: 104 Biological Sciences East, Univ. of Arizona, Tucson, AZ 85721.

³ Present address: USDA Forest Service, Ashley National Forest, Vernal Ranger District, 355 N. Vernal Ave., Vernal, UT 84078.

⁴ Corresponding author;
E-mail: patk@cnr.colostate.edu

The food-amount hypothesis predicts a negative relationship between the amount of food available and nestling aggression (Mock et al. 1987, Creighton and Schnell 1996). By killing its sibling when food is scarce, a nestling may increase its chance of survival by increasing its share of food delivered to the nest. Mock and coworkers (1990) found that smaller food morsels can be monopolized through combat and, therefore, reward sibling aggression. Higher rates of aggression were observed in larger broods of Cattle Egrets (*Bubulcus ibis*) where individual food portions are expected to be smaller (Mock et al. 1987).

Because siblicide events are uncommon, and tend to go unwitnessed unless nests are under constant watch, few studies have established a causal link between food resources and fatal sibling aggression (but see Mock et al. 1987). Facultative siblicide has been documented in several raptor species, but its cause has not been fully investigated (Schnell 1958, Pilz and Seibert 1978, Newton 1979, Bechard 1983, Zachel 1985, Bortolotti et al. 1991, Boal and Bacorn 1994). Although the hypothesis that food supplies influence sibling aggression is intuitively appealing, few studies, with the exception of Wiebe and Bortolotti (1995) and Wellicome (1997), have provided more than correlational support for this activity in raptors.

Northern Goshawks (*Accipiter gentilis*) hatch asynchronously and exhibit siblicide (Newton 1979, Stinson 1979). Observational accounts of siblicide in goshawks are rare (Schnell 1958, Zachel 1985, Boal and Bacorn 1994), and its occurrence is thought to be limited to times when food is in very low supply (Newton 1979). Experimental data linking food resources and incidence of siblicide in this species are nonexistent. In this paper, we report the occurrence of a siblicide event at a goshawk nest in northeastern Utah. We also describe another incident in which a nestling's death was likely the result of siblicide and we provide experimental evidence that the incidence of sibling aggression may be related to food supplies. Our observations are consistent with the hypothesis that goshawks exhibit facultative siblicide directly influenced by food resources.

Our siblicide observations occurred at nests that were part of a study on the influence of

food provisioning on female nest attendance and nestling begging vocalizations. This investigation was part of a larger experiment examining the influence of supplemental food on parental care strategies and juvenile survival (Dewey 1999). In 1997, 14 nests were included in the food supplementation experiment (experimental design similar to that of Ward and Kennedy 1996). Seven of these nests were randomly assigned as treatments and were provided Japanese Quail (*Coturnix coturnix*) from hatching through the fledgling dependency period. We visited treatment nests every two to three days and provided sufficient food to meet the energy requirements of the female and young until the next scheduled visit (see Dewey 1999 for details). Control nests were visited at the same interval and for the same amount of time, but were not given food. The nest attendance/vocalization study was conducted from mid-June to mid-July 1997 and consisted of a subset of the nests used in the food supplementation experiment. Each nest was observed for a 3 h period on three different occasions from a portable blind located approximately 30 m from the nest. Observation times were rotated to include both mornings and afternoons.

The first event was witnessed during a 3 h observation period on the afternoon of 10 July at control nest LGD. The adult female had not been observed in the nest stand since 8 July, and likely had deserted the nest or died. Although we were unable to trap the female to verify her age prior to her disappearance, her unusually dark maroon colored eyes, behavior, and degree of scarring above and around her right eye indicated old age. The role of the male in caring for the nestlings after the female's disappearance is unknown because he was never observed visiting the nest.

Shortly after observations had begun, two nestlings (21 and 22 days old) were begging periodically. The older nestling (N1) then began flapping its wings and pecking at the head of nestling 2 (N2). Nestling 2 initially retaliated by flapping its wings and pecking at the head of N1, but soon turned its back to N1 and assumed the defense stance described by Schnell (1958), with its head lowered and its rump elevated. Nestling 1 responded by increasing its intensity of pecking and then began pulling down out of N2's thighs and

rump. Nestling 2 uttered a high-pitched call and moved toward the edge of the nest. This behavior continued as N2 was forced out of the west side of the nest and onto the nest branch. Nestling 1 perched on the edge of the nest and continued pulling down from N2's rump until N2 moved out of reach, at which point N1 walked to the center of the nest and rested.

After approximately 15 min, during which several strong gusts of wind nearly blew N2 off the branch, N2 moved back into the nest; N1 resumed aggressive attacks within 5 min. Nestling 2 again assumed a defense stance, and N1 began tearing down from N2's backside, forcing N2 onto the south edge of the nest. Nestling 1 then began rushing at N2 and colliding with N2's hind end. This behavior continued while N2 called and flapped its wings in an attempt to maintain balance as it clung to the rim of the nest. Nestling 2 then turned quickly and climbed over N1 and into the center of the nest. Nestling 1 pursued N2 to the east edge of the nest next to the tree trunk, where N2 again took a defense stance. Nestling 1 resumed ramming and tearing down from N2. Nestling 2 was knocked out of the nest but caught its wing on a branch. Nestling 1 leaned out of the nest and continued to rip down from N2 while N2 screamed. Nestling 1 then backed off, uttered an adult-like alarm call, and returned to the center of the nest. Nestling 2 climbed back into the nest and remained in the nest for approximately 10 min until N1 again chased N2 out of the nest and onto the nest branch. Nestling 2 was not allowed back onto the nest for the rest of the observation period.

Two days later we found N2 dead on the ground under the nest. Nestling 1 directed loud alarm and begging calls at us throughout the visit to the nest stand. Nestling 1 was found dead in the nest on 14 July 1997. Bodies of both nestlings were sent to the Colorado Veterinary Diagnostic Laboratory at the College of Veterinary Medicine, Colorado State University, where necropsies were performed. Nestling 2 was mildly emaciated, had two fractured ribs, and pulmonary hemorrhaging, presumably incurred during its fall from the nest tree. The exact cause of death for N1 was unknown; however, the necropsy showed this bird suffered from advanced emaciation re-

sulting in pectoral muscle atrophy, which strongly suggests starvation.

The other probable case of siblicide occurred at the control nest SNK on 2 July 1997. When we entered the nest stand the female was not in the immediate vicinity. Two nestlings (20 and 22 days old) were in the nest; one was obviously dead with blood around its head. The adult female returned shortly thereafter, poked at the dead nestling briefly, and then carried the body away from the nest. She returned within several minutes without the dead nestling. Although we did not witness aggression between the siblings, the fact that the dead nestling was still in the nest suggests that a predator did not kill it. Because of the obvious head injury, we believe the nestling's death resulted from siblicide and not merely starvation. Although, it is possible that the remaining nestling attempted cannibalism after its sibling had died, we did not observe the nestling trying to feed on its dead sibling. The SNK nestling's death could also have been the result of filial infanticide if parental behavior (e.g., nest desertion, favoritism, or aggression) contributed to its death (Mock and Parker 1997). However, O'Connor's (1978) brood reduction model predicts that conditions favorable to siblicide will occur more often than those favorable to filial infanticide. To our knowledge, filial infanticide resulting from fatal parental aggression has not been documented in goshawks; nevertheless, we cannot rule it out as a possibility.

Several details of these observations differed from those of similar events observed in goshawks and other raptors. Cannibalism was documented to have followed siblicide in a Swainson's Hawk (*Buteo swainsoni*) nest (Pilz and Seibert 1978), three Burrowing Owl (*Athene cunicularia*) nests (Wellicome 1997), four American Kestrel (*Falco sparverius*) nests (Bortolotti et al. 1991), and three goshawk nests (Schnell 1958, Zachel 1985, Boal and Bacorn 1994). However, cannibalism was not observed at either nest in this study. At the LGD nest cannibalism might have occurred if N2 had not fallen to its death; but N1's behavior gave no indication that it was attacking N2 for the purpose of consumption. Nestling 1 seemed intent on expelling N2 from the nest and N1's aggression stopped once N2 was out of the nest. If N1 was at-

tempting to kill N2 for consumption we would have expected the aggression to continue until N2 was dead. Cannibalism was also not observed at the SNK nest but this may have been due to the presence of the adults that were providing food to the remaining nestling, or to the removal of the dead nestling before it could be cannibalized.

A second disparity between our observations and those in the literature is the potential function of the submissive posture of the defense stance. According to Schnell's (1958) observations of nestling aggression, the aggressor terminated attacks when its sibling assumed the defense stance. In our observations, N1 continued aggressive attacks after N2 assumed the defense stance. Nestling 1's behavior also differed from aggressor behavior in other documented siblicide events in that N1's attacks were aimed primarily at N2's rump and thighs instead of at its sibling's head (Schnell 1958, Pilz and Seibert 1978, Boal and Bacorn 1994).

Although our LGD siblicide observation differs in the aforementioned ways from those previously reported by Schnell (1958), Zachel (1985), and Boal and Bacorn (1994), our event is similar in that it occurred during a period of apparent low food supply. We did not measure food availability in our study area, but provided half of our experimental goshawks with supplemental food. Including the LGD nest failure and the SNK mortality, we documented brood reductions at four of the seven control nests in 1997 and no nestling deaths at any of the treatment nests. Three of the seven (43%) control nests failed (i.e., fledged no young). In addition, the youngest nestling at one supplemented nest hatched 10 days after its closest sibling (mean age difference between oldest sibling and each of the younger siblings = 2.12 days) and was noticeably smaller than its two nest mates, yet survived to fledging age with little aggression between siblings. Ward and Kennedy (1996, unpubl. data) documented similar results in their experiment, where a nest with supplemental food successfully fledged four young including a nestling 7–10 days younger than its closest sibling. Because nestlings that hatch significantly later than their siblings in asynchronous broods often die unless enough food is provided (Bryant and Tatner 1990, Wiebe

and Bortolotti 1995), we attribute the higher survival of these treatment nestlings to the high food abundance.

Although our study was not designed to investigate the role of food in sibling aggression in goshawks, our finding of higher survival for supplementally fed nestlings, coupled with the siblicide observations provided us with the opportunity to consider this relationship. Lack (1954) hypothesized that asynchronous hatching in avian species occurs to facilitate brood size reduction to match available levels of resources provided by parents. If Lack's hypothesis is correct, occurrences of siblicide should be influenced by levels of prey abundance. Forbes and Mock (1994) differentiate two types of facultative siblicide: one in which aggression is triggered by food shortage and the other where it is not. Mock and coworkers (1987) observed that the occurrence of fatal sibling aggression in some species was only indirectly influenced by food. They observed aggressive behavior between siblings regardless of food levels, but mortality from aggression was lower if food was abundant because the younger siblings were sufficiently strong to withstand the attacks. Our observations are consistent with the form of facultative siblicide directly influenced by resource levels and provides evidence for the hypothesis that low food supplies trigger sibling aggression in goshawks. Additional empirical research, coupled with measurement of background resource levels is needed to further substantiate this assertion and clarify the nature of the relationship.

ACKNOWLEDGMENTS

These observations were made while conducting research funded by the USDA Forest Service, Ashley National Forest. We thank C. W. Boal, R. P. Gerhardt, J. S. Marks, D. W. Mock and two anonymous referees for their helpful reviews of the manuscript. We would also like to thank J. Cropley, S. Lewis, C. Neilson, M. Painter, and S. Rayroux for assistance in the field, K. Paulin for her support of this research, and C. Sigurdson for generously volunteering her time and expertise to conduct necropsies.

LITERATURE CITED

- ANDERSON, D. J. 1989. The role of hatching asynchrony in siblicidal brood reduction of two booby species. *Behav. Ecol. Sociobiol.* 25:363–368.
- BECHARD, M. J. 1983. Food supply and the occurrence

- of brood reduction in Swainson's Hawk. *Wilson Bull.* 95:233-242.
- BOAL, C. W. AND J. E. BACORN. 1994. Siblicide and cannibalism at Northern Goshawk nests. *Auk* 111: 748-750.
- BORTOLOTTI, G. R., K. L. WIEBE, AND W. M. IKO. 1991. Cannibalism of nestling American Kestrels by their parents and siblings. *Can. J. Zool.* 69:1447-1453.
- BRAUN, B. M. AND G. L. HUNT, JR. 1983. Brood reduction in Black-legged Kittiwakes. *Auk* 100: 469-476.
- BRYANT, D. M. AND P. TATNER. 1990. Hatching asynchrony, sibling competition and siblicide in nestling birds: studies of swiftlets and bee-eaters. *Anim. Behav.* 39:657-671.
- CREIGHTON, J. C. AND G. D. SCHNELL. 1996. Proximate control of siblicide in Cattle Egrets: a test of the food-amount hypothesis. *Behav. Ecol. Sociobiol.* 38:371-377.
- DEWEY, S. R. 1999. Effects of supplemental food on parental care strategies and juvenile survival in Northern Goshawks. M.Sc. thesis, Colorado State University, Fort Collins.
- DRUMMOND, H. AND C. GARCIA CHAVELAS. 1989. Food shortage influences sibling aggression in the Blue-footed Booby. *Anim. Behav.* 37:806-819.
- 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.
- FORBES, L. S. AND D. W. MOCK. 1994. Proximate and ultimate determinants of avian brood reduction. Pp. 237-256 in *Infanticide and parental care* (S. Parmigiani and F. S. vom Saal, Eds.). Hardwood Academic Publ., Chur, Switzerland.
- GERHARDT, R. P., D. M. GERHARDT, AND M. A. VASQUEZ. 1997. Siblicide in Swallow-tailed Kites. *Wilson Bull.* 109:112-120.
- HEEB, P. 1994. Intraclutch egg-mass variation and hatching asynchrony in the Jackdaw *Corvus monedula*. *Ardea* 82:287-297.
- HEINSOHN, R. G. 1995. Hatching asynchrony and brood reduction in cooperatively breeding White-winged Choughs *Corcorax melanorhamphos*. *Emu* 95: 252-258.
- LACK, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, Oxford, U.K.
- MOCK, D. W. AND T. C. LAMEY. 1991. The role of brood size in regulating egret sibling aggression. *Am. Nat.* 138:1015-1026.
- MOCK, D. W. AND G. A. PARKER. 1997. The evolution of sibling rivalry. Oxford Univ. Press, Oxford, U.K.
- MOCK, D. W., T. C. LAMEY, AND B. J. PLOGER. 1987. Proximate and ultimate roles of food amount in regulating egret sibling aggression. *Ecology* 68: 1760-1772.
- MOCK, D. W., H. DRUMMOND, AND C. H. STINSON. 1990. Avian siblicide. *Am. Sci.* 78:438-449.
- NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota.
- O'CONNOR, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide. *Anim. Behav.* 26:79-96.
- PILZ, W. R. AND L. K. SEIBERT. 1978. Fratricide and cannibalism in Swainson's Hawk. *Auk* 95:584-585.
- REYNOLDS, P. S. 1996. Brood reduction and siblicide in Black-billed Magpies (*Pica pica*). *Auk* 113: 189-199.
- SCHNELL, J. H. 1958. Nesting behavior and food habits of goshawks in the Sierra Nevada of California. *Condor* 60:377-403.
- STINSON, C. H. 1979. On the selective advantage of fratricide in raptors. *Evolution* 33:1219-1225.
- WARD, J. M. AND P. L. KENNEDY. 1996. Effects of supplemental food on growth and survival of juvenile Northern Goshawks. *Auk* 113:200-208.
- WELLCOME, T. I. 1997. Reproductive performance of Burrowing Owls (*Speotyto cunicularia*): effects of supplemental food. *J. Raptor Res.* 9:68-73.
- WIEBE, K. L. AND G. R. BORTOLOTTI. 1995. Food-dependent benefits of hatching asynchrony in American Kestrels *Falco sparverius*. *Behav. Ecol. Sociobiol.* 36:49-57.
- ZACHEL, C. R. 1985. Food habits, hunting activity, and post-fledging behavior of Northern Goshawks (*Accipiter gentilis*) in interior Alaska. M.Sc. thesis, Univ. of Alaska, Fairbanks.