

## SUPPLEMENTAL FEEDING EXPERIMENTS OF NESTING BALD EAGLES IN SOUTHEASTERN ALASKA

SCOTT M. GENDE AND MARY F. WILLSON

Forestry Sciences Laboratory  
2770 Sherwood Lane  
Juneau, Alaska 99801 USA

Abstract.—Nesting success of Bald Eagles (*Haliaeetus leucocephalus*) near Juneau, Alaska was compared for experimental nests (supplementally fed pink salmon [*Oncorhynchus gorbusha*] for seven weeks) and control nests (no supplemental food) to determine if food limits reproductive success during the nestling period. Although supplemental food accounted for at least 50% of the estimated nestling energy requirements, brood reduction and the number of nests failing post-hatch was small and differed little in experimental and control nests. Most active nests that failed were abandoned during incubation, which may be a critical phase determining nesting success of eagles nesting along the coast of southeastern Alaska.

### EXPERIMENTOS DE ALIMENTACIÓN SUPLEMENTARIA EN INDIVIDUOS DE *HALIAEETUS LEUCOCEPHALUS* DURANTE SU ANIDAMIENTO EN ALASKA

Sinopsis.—Se estudio el éxito de anidamiento de individuos nidificantes del aguilá *Haliaeetus leucocephalus*, cerca de Juneau, Alaska. A un grupo se le suplementó con comida por siete semanas (salmón rosado—*Oncorhynchus gorbusha*) mientras que a un segundo grupo no se le suplementó (control). Esto se hizo para determinar si el alimento imponía límites en el éxito reproductivo de la especie durante el periodo de cría de pichones. Aunque el alimento suplementario suplió al menos el 50% de los requerimientos energéticos de los pichones, la reducción en el tamaño de la camada y el número de nidos que fracasaron, luego del eclosionamiento, varió muy poco del grupo control. La mayoría de los nidos activos que fracasaron fueron abandonados durante la incubación, lo que podría ser la fase más crítica o que determina el éxito de anidamiento en las aguilas que se reproducen a lo largo de la costa sureste de Alaska.

The importance of food availability to avian reproductive success varies with many factors. Although food may be limiting throughout the nesting cycle, critical periods of food availability can occur during distinct stages (Martin 1987). Experimental manipulation of food supply has shown that food may be critical for successful reproduction before egg-laying (e.g., Newton and Marquiss 1981, von Brömssen and Jansson 1980) or when nestlings are present (e.g., Ens et al. 1992, Simons and Martin 1990), but the effects may differ annually due to differences in population density (e.g., Arcese and Smith 1988, Simmons 1993) or weather (Dhindsa and Boag 1990, Högstedt 1981). The effects of food availability during critical periods may alter the probability of offspring recruitment to the breeding population, long after the nesting season in which food limitation occurred (Richner 1992).

For raptors, Newton (1979:95) emphasized two critical periods of food availability: before egg-laying, when females need to acquire ample reserves for egg production and incubation, and post-hatching, when adults must obtain adequate prey for self-maintenance and nestling growth. Incubation may also be a critical period of food availability (Steidl and Anthony 1995). However, many studies that examine the relationship be-

tween food and reproduction in raptors are not experimental and do not identify a critical period of food availability in the reproduction cycle. Most studies use raptors with specialized diets and examine correlations between overall reproductive success and densities of one or more principal prey species (see review by Högstedt 1991). Likewise, studies that manipulate food availability often do not identify critical stages of nesting by altering food supply during several different stages of reproduction (but see Ward and Kennedy 1996).

For Bald Eagles (*Haliaeetus leucocephalus*), the availability of food is considered to be the primary factor regulating reproduction for populations nesting in relatively pristine environments (Dzus and Gerrard 1993, Hansen 1987, Steidl and Anthony 1995, Swenson et al. 1986). However, the opportunistic foraging strategies exhibited by many populations of eagles (Ofelt 1975, Sherrod et al. 1976, Swenson et al. 1986, Todd et al. 1982, Watson et al. 1991) have made it difficult to monitor the effects of differential prey availability on nesting success and to identify if specific periods are critical in terms of food availability. In addition, assessing the effects of food limitation on reproduction for any species is confounded by difficulties in accurately measuring food availability (Hutto 1990), as food density is not necessarily equivalent to food availability (e.g., Janes 1984).

To test if food is limiting for eagles during the nestling stage of reproduction, we conducted a supplemental feeding experiment for pairs nesting along coastal shores in southeastern Alaska. Nests were intensively monitored during both incubation and nestling periods, to determine when most nest failures occurred.

#### STUDY AREA

Supplemental feeding experiments were carried out along the coast, near Juneau, Alaska (ca. 58°22'N, 134°35'W). The terrestrial habitat is characterized by mature stands of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) on the mainland and nearshore islands. This study location was chosen because of ease of access and the high density of breeding eagles in this area, as reproductive success may be influenced more by supplemental food in high-density populations (e.g., Smith et al. 1980). Long-term (1986, 1988–1995) nesting success has been relatively high in one small part of the Juneau shoreline (Auke Bay mainland; Gende et al., unpubl. data) compared to other parts of southeastern Alaska. Therefore, nests associated with this area were excluded from feeding experiments, because food supplementation would be less likely to have a detectable effect on these nests.

#### METHODS

In 1994, helicopter surveys were used to identify active nests (those with an adult seen in incubating posture) in mid-May. Incubation behavior was then monitored in as many nests as logistically possible to determine when hatching occurred (Bortolotti et al. 1985). If a nest failed,

nest trees were climbed shortly thereafter to collect eggs for assessment of embryonic development. Adverse weather delayed some climbs in 1994, and the eggs were depredated by corvids during the delay. In 1995, nests were monitored beginning in early April, to record laying dates. If a nest became active (eggs laid or an adult eagle observed consistently sitting in incubation posture), clutch size was determined by a climb to the nest. Disturbance to incubating adults was minimized by climbing during warm or sunny weather and minimizing time spent near the nest tree (Bortolotti et al. 1985). In addition, nest climbs were conducted late in the incubation period to ensure that adequate time was provided for the female to complete egg-laying, which can exceed 7 d for three-egg clutches (Stalmaster 1987:57). Following climbs, nests were monitored from a distance to determine that adults returned to incubate. Two nests were excluded from analysis when the adults were observed to remain off the nest for an extended period, following a climb to the nest.

Once the eggs hatched in a nest, that nest was randomly designated as an experimental (supplementally fed) or control nest (unfed) by a coin flip and matched with a nest that had similar location and hatching date. In 1995, experimental and control nests were also matched according to clutch size, except in two cases for which no matching clutch sizes were available in the study population. Average straight-line distances between experimental and control nests was 3.2 km in 1994 and 7.9 km in 1995. All nests used in the study were located in dominant Sitka spruce or western hemlock, within 50 m of shore. To determine if the nesting history of experimental and control nests differed, nesting success from the preceding 7 yr for experimental and control nests was compared.

Feeding experiments were conducted by boat during two breeding seasons. Deposition of supplemental food began the day after hatching (mean hatching date was 30 May in 1994 and 6 June in 1995) and continued until nestlings were approximately 7-wk old. One adult pink salmon (*Oncorhynchus gorbuscha*) was placed in the intertidal area near the nest every other day. Frozen carcasses were thawed and cut open, and the exposed flesh was dyed with red food coloring. Red dye was applied to enhance the appearance of freshness and possibly increase the likelihood that pairs would feed the supplemental food to nestlings (see Gerrard and Bortolotti 1988:88). Experimental pairs often accepted dyed carcasses before gulls or corvids pecked at the flesh. During feeding experiments, the same boat and clothing were used, to acclimate nesting pairs and facilitate recognition of supplemental food. Once carcasses were offered, pairs were monitored from a distance to determine if they accepted the food and delivered it to the nest. Control nests were subjected to similar disturbance by briefly walking along the intertidal area in front of the nest, as if food were to be deposited.

The quality of supplemental food is important in feeding experiments (Ewald and Rohwer 1982) but was not assessed in this study. However, pink salmon was an appropriate supplemental food for feeding experiments, because they are natural prey for breeding eagles in southeastern

Alaska (Cain 1985, Ofelt 1975). One adult pink salmon ( $\bar{x} \approx 1$  kg) is equivalent to approximately twice the daily amount of energy needed for an adult Bald Eagle in winter (Stalmaster and Gessaman 1984). Our observations suggest that a large pink salmon (ca. 1.5 kg) is about the upper size limit that an eagle can carry, thereby maximizing the amount of energy returned to the nest per feeding trip.

The total mass of supplemental fish carried to each nest was recorded to estimate the proportion of nestling energy budgets provided by supplemental food. Nestlings were estimated to need 1250 Kj/d until 3-wk old (modified from Dykstra 1995, because original estimates of nestling energy requirements were made for nestlings 36–70-d old), and 2500 Kj/d for the remaining 4 wk of feeding (Dykstra 1995). Carcasses were estimated to be 90% edible. This is slightly higher than previously estimated for chum salmon (Stalmaster and Gessaman 1982), because most carcasses were deheaded before being provided to eagles, which rid the carcass of much of the inedible portion. Furthermore, pink salmon flesh was estimated to have 7.1 Kj/g wet mass, similar to energy content of lake trout (Dykstra 1995). This is probably conservative, because many carcasses contained some roe, which probably enhanced energy content. Once adults took the pink salmon to the nest, it was difficult to determine if adults were eating any of the flesh or if all of the fish was fed to nestlings. However, in calculating energy to nestlings, we assumed nestlings had sole access.

All nest trees were climbed late in the nesting season to measure, weigh, and band nestlings. Nestlings were lowered to the ground and measured using calipers and a 10-kg Pesola scale. Crop fullness was estimated to account for variation in nestling weight. In 1994, nest climbs occurred when eaglets were 8–9-wk old. However, one nestling jumped from the nest and several others became unreachable by walking out of the nest to the end of a tree limb. Therefore, in 1995, climbs occurred 1–2 wk earlier.

Nest failure during incubation and nestling phases was recorded, and average clutch size was calculated in 1995. Nestling mass was compared for matched nests only for broods of equal size. Because of sexual size dimorphism and differences in skeletal mass, it was impossible to control for all factors that may affect nestling mass, when matching experimental and control nests. On average, sex ratios were likely to be equal in experimental and control nests, but gender determinations were not made, because distinctions based on linear measurements, which have been successful in other studies (Bortolotti 1984a), were not sufficiently clear.

Controlling for hatching dates, clutch size (1995 only), geographic location, and history of nesting success, experimental and control nests were tested for differences in success (% of nests succeeding), number of young fledged, and nestling mass, using Wilcoxon matched pairs signed-ranks tests.

## RESULTS

Most nest failures occurred during incubation. Of 29 active nests monitored in 1994, 9 were abandoned before hatching and 2 failed post-hatch, after nests were blown down during a windstorm. Thus, pre-hatch failures constituted 82% (9 of 11) of observed nest failures after eggs were laid (100% if "chance" failures such as windthrow are excluded). Of 31 active nests monitored in 1995, 10 of 11 failures (91%) occurred during incubation (three additional nests that failed during incubation were excluded; two failures may have been due to monitoring activities and the other to disturbance from a boat dock built near a nest after the nesting pair laid eggs). Similar percentages of failure during incubation in both years suggest that nest climbs during incubation, which occurred in 1995 only, did not affect nesting success (see also Anthony et al. 1994). Although climbs to the nest during incubation averaged 21 min, incubating adults usually did not flush until climbers were just under the nest and returned to incubate soon after eggs were counted. Thus, adults were off the nests for periods much shorter than the duration of climbs.

All nests in which adults were observed in incubation posture contained eggs, as evidenced by the presence of eggs or eggshell fragments. Average clutch size (measured only in 1995) was 1.94 ( $n = 31$ ), with 13% (4) containing one egg, 6% (2) containing three eggs, and 81% (25) containing a clutch size of two. In nests that failed during incubation, all eggs that were not depredated contained developing embryos.

All nests that succeeded in hatching young were incorporated into supplemental feeding experiments (18 experimental and control nests in 1994 and 1995). There was no difference in clutch size (in 1995) or historical nesting success (average number of young fledged/active nest for 7 yr prior to the experiment) between experimental and control nests (Table 1), showing that the probability of nesting successfully and fledging similar numbers of young was equivalent for experimental and control nests. Hatching dates of experimental and control nests were similar in 1994, but experimental nests were significantly later than controls in 1995 (Table 1), because of the limited availability of neighboring nests with matching clutch sizes.

A total of 240.8 kg of supplemental pink salmon was carried to experimental nests (107.7 kg in 1994, 133.1 kg in 1995), averaging 13.4 kg per nest per year. This accounted for approximately 51% of the total energy needed by broods (until 7 wk of age) in 1994 and 55% in 1995. Despite the supplemental food provided to experimental nests, the percent of nests that were successful was nearly identical to controls. In 1994, 100% (9 of 9) of both experimental and control nests succeeded in fledging at least one young. In 1995, 100% (9 of 9) of experimental nests and 89% (8 of 9) of control nests succeeded in fledging at least one young. In addition, the number of young fledged per nest and nestling mass was similar in experimental and control nests (Table 1).

We could not detect a difference in the percent of eggs that eventually

TABLE 1. Nesting parameters of experimental and control nests for two years of supplemental feeding experiments. Wilcoxon matched pairs signed-ranks tests were used for all comparisons. ND = not determined.

	1994						1995					
	Median			Median			Median			Median		
	Experi- mental	Control	n	Z	P	n	Experi- mental	Control	n	Z	P	n
Nesting success <sup>a</sup>	1.0	1.25	9	0.25	0.799	9	1.0	1.3	9	0.32	0.752	9
Hatching date (Julian)	144	141	9	0.35	0.726	9	164	153	9	-2.03	0.043	9
Clutch size	ND	ND					2.0	2.0		0.00	1.000	9
Fledged young	2.0	2.0	9	1.41	0.157	9	2.0	2.0	9	-1.13	0.257	9
Nestling mass (kg)	4.4	4.2	3	-0.48	0.655	3	4.0	4.1	9	0.67	0.500	9

<sup>a</sup> For seven years prior to experiment; total number of young fledged/total number of years nest was active.

fledged in experimental vs. control nests (median for experimental and control nests = 100%; Wilcoxon matched pairs signed-ranks test,  $Z = -1.29$ ,  $P = -0.20$ ). However, the number of fledged young was less than the number of eggs laid in 1995. Three control nests with a clutch size of two eggs fledged only one young each and one experimental nest with a clutch size of three fledged two young, but the stage at which failure occurred was not known; one experimental nest with a clutch of two fledged one chick because the other egg was inviable.

#### DISCUSSION

Similar percentages of nests that were successful, number of fledged young, and nestling mass in experimental and control nests suggest that eagles nesting along the coast of southeastern Alaska are generally not food-limited during the nestling phase. Several studies have found a diversity of prey species for breeding eagles in southeastern Alaska (Imler and Kalmbach 1955, Ofelt 1975), and nest climbs early in the nestling period (first few weeks in June) in this study revealed that fish cached in the nest and partially eaten were both diverse and abundant. With a wide variety of prey available, eagles should be buffered from a local depletion of any one prey item (Högstedt 1991). In addition, beginning in early July, pink salmon returned in large near-shore schools and were accessible to coastal breeding eagles for three weeks, before the salmon gradually entered natal streams to spawn. During nest climbs in July, remains of pink salmon were often the only species in the nest, as reported by Cain (1985). Thus, food may not be limiting during the nestling phase.

The percentage of nests succeeding was nearly identical for experimental and control nests in the 2-yr study, although small sample sizes limited the ability to detect statistical differences. Only one known case of post-hatch nest failure was recorded. A control nest failed in 1995 approximately 6 d after hatching, when both adults were observed perched several meters from the nest for over an hour. The nest was climbed 2 d later but no nestlings were present. Several lines of evidence suggest that young had hatched but were abandoned shortly thereafter. First, adults were seen in a brooding posture typical for nests containing newly hatched young (Bortolotti et al. 1985) for 6 d, after which they perched nearby. Second, whereas all other nests that failed during incubation in this study contained partial or whole eggs, buried eggs and eggshell fragments were absent in this nest. Finally, Northwestern Crows (*Corvus caurinus*) were seen on the nest rim on several occasions after adults had apparently abandoned it, suggesting that newly hatched young were depredated or scavenged before nest contents could be checked.

Nestling mass was also unaffected by supplemental food. There are several possible explanations for this result. (1) Small sample sizes probably increased the chance that factors independent of supplemental feeding, such as unequal sex ratios in matched nests, produced unreliable results. (2) There is much day-to-day variation in nestling mass (P. Schempf, Office of Raptor Management, U.S. Fish and Wildlife Service,

pers. comm.), and control nestlings may simply have been weighed on days when no food was available. However, almost all nests (both experimental and controls) contained partially eaten fish remains when inspected, suggesting that food was available if nestlings were hungry. (3) It is possible that supplemental feeding in this experiment actually led to a temporary mass advantage for experimental nestlings that was later eliminated when natural, abundant runs of pink salmon began. For American Kestrels (*Falco sparverius*), short periods of food reduction produced no long-term effects on nestling mass, if food availability was returned to adequate levels (Negro et al. 1994). (4) The observed results may indeed indicate the absence of an effect of supplemental food on nestling mass. Supplemental feeding during the nestling stage also did not significantly affect nestling size in Northern Goshawks (*Accipiter gentilis*) (Ward and Kennedy 1996).

There are several other lines of evidence that support the idea that food was not generally limiting during the nestling phase. Only one known instance of possible brood reduction occurred in either study year. Brood reduction should be present in raptor populations that are food limited (Bortolotti 1984b, Steidl and Griffin 1991). In 1994, a control nest, in which two eggs had hatched, contained one live nestling and one emaciated dead nestling. Sibling competition may have contributed to the death of this nestling, because most such mortality occurs early in nestling life, when the size disparity between siblings is the greatest (Bortolotti 1986a, b). However, the dead nestling appeared (from feather development) to be 3-wk old, which is slightly older than the period of maximum brood reduction (age 1–2 wk; Bortolotti 1986a, b), so cause of death can not be ascribed with certainty.

In addition, most nest failures occurred during incubation (95% over two years; failures attributed to windthrow excluded). Similar results (92% of failures during incubation) were found in the Gulkana River basin, Alaska (Steidl and Anthony 1995). Because of the high failure rate during incubation and a low level of brood reduction during the nestling phase, Steidl and Anthony (1995) suggested that food availability during incubation, rather than post-hatch, may be the most important variable determining nesting success.

However, we cannot exclude the possibility that food deprivation might have accounted for the loss of single chicks from successful nests. Clutch size was greater than the number of young fledged in five successful nests in 1995 (three control nests, two experimental). Aside from one inviable egg found in a successful experimental nest, no eggs or eggshell fragments were found in the nest bowl of any of the other nests, suggesting that nestlings had died and were removed or eaten. In the three control nests only one young fledged from a clutch of two eggs, although all experimental nests with two viable eggs fledged both young. If the deaths occurred after hatching, this might constitute evidence of food limitation in these particular nests, even though there was no statistical difference in the average number of young fledged between experimental and con-



trol nests. In an experimental nest, two young fledged from a clutch of three eggs. Rarely will all three young survive to fledge from three-egg clutches, as the disparity between oldest and youngest nestling is often too great to overcome by the youngest nestling when vying for limited food resources (Gerrard and Bortolotti 1988:85–86, Wiebe and Bortolotti 1995). Despite food supplementation, conditions may not have been good enough for the third nestling to survive. For nesting pairs in the Chilkat Valley, Alaska, supplemental food in May and June significantly increased the number of offspring surviving to fledge (Hansen 1987). Nesting success (fledged young/active nest) is much poorer in the Chilkat Valley than along coastal shores in southeastern Alaska (Hodges 1981), suggesting that food may be more limiting for river-nesting pairs and thus increasing the probability of significantly altering nesting success with supplemental food.

Likewise, certain fitness-related variables that were not measured in this study may have been altered by supplemental food. Linear measurements may be a better predictor of nestling quality than nestling mass (Richner 1992), because longer flight feathers may aid soaring for juveniles that migrate long distances in their first year (Gerrard et al. 1974, 1978; Hodges et al. 1987; but see Bortolotti 1994). In addition, food supplementation may reduce the cost of reproduction of the parents (Wiebe and Bortolotti 1994), rather than affecting the nestlings, if supplemental food increased survival or enhanced lifetime reproductive success for the breeding pair (e.g., Garcia et al. 1993, Johnston 1993, Verhulst 1994). Parental protection was better for goshawk nestlings with supplemental food (Ward and Kennedy 1996) but predation has never been observed for Bald Eagle nestlings in southeastern Alaska. More detailed studies are needed to test if these variables are affected by increased food.

There was little evidence of food limitation during the nestling period for coastal nesting eagles. Food limitation is also unlikely during egg production. Egg formation is not thought to be energetically costly for ospreys (*Pandion haliaetus*) (Poole 1985), and the same may be true for eagles. Bald Eagle eggs are approximately 3% of the female's body mass (Stalmaster 1987:56), one of the smallest egg/adult mass ratios of any bird (Lack 1968:186, Newton 1977). In addition, eagles are not constrained to the nesting territory before eggs are laid, although duration spent away from the territory is minimized to insure retention of the nesting territory (Kralovec 1993). Thus, the distribution of food near the nest is less critical before laying, due to decreased restraints on movements.

The importance of food near the nest may increase significantly, however, during incubation. Both adults share incubation responsibilities (Cain 1985), thereby constraining at least one adult to the nest at all times. Most food must be acquired near the nest, because adults switch incubating duties frequently (Cain 1985). If food is not easily acquired, eagles may abandon the nesting attempt with little invested. Early aban-

donment would be advantageous for long-lived birds, such as eagles, in order to reduce the costs to future reproduction (Stearns 1992).

#### ACKNOWLEDGMENTS

Tom Shirley, Lew Haldorson, Alan Springer, Gary Bortolotti, and Stan Boutin provided helpful comments on the manuscript. Brian Marston provided field assistance throughout the project. Armstrong-Keta and Douglas Island Pink and Chum hatcheries provided pink salmon carcasses for supplemental feeding experiments. Special thanks to Phil Schempf, Karl Halupka, and Josh Weinstein for support in the lab and aid in the field.

#### LITERATURE CITED

- ANTHONY, R. G., R. W. FRENZEL, F. B. ISAACS, AND M. G. GARRETT. 1994. Probable causes of nesting failures in Oregon's bald eagle population. *Wild. Soc. Bull.* 22:576-582.
- ARCESE, P., AND J. N. M. SMITH. 1988. Effects of population density and supplemental food on reproduction in song sparrows. *J. Anim. Ecol.* 57:119-136.
- BORTOLOTTI, G. R. 1984a. Criteria for determining age and sex of nestling bald eagles. *J. Field Orn.* 55:467-481.
- . 1984b. Evolution of growth rate and nestling sex ratio in bald eagles (*Haliaeetus leucocephalus*). Ph.D. dissertation. Univ. Toronto, Toronto, Ontario.
- . 1986a. Evolution of growth rates in eagles: sibling competition vs. energy considerations. *Ecology* 67:182-194.
- . 1986b. Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *Am. Nat.* 127:495-507.
- . 1994. Physical development of nestling Bald Eagles with emphasis on the timing of growth events. *Wilson Bull.* 96:524-542.
- , J. M. GERRARD, P. N. GERRARD, AND D. W. A. WHITFIELD. 1985. Minimizing investigator-induced disturbance to nesting bald eagles. Pp. 85-103, in J. M. Gerrard and T. N. Ingram, eds. *The bald eagle in Canada*. White Horse Plains Publishers, Headingley, Manitoba.
- CAIN, S. L. 1985. Nesting activity time budgets of bald eagles in Southeast Alaska. M.Sc. thesis. Univ. Montana, Missoula, Montana.
- DHINDSA, M. S., AND D. A. BOAG. 1990. The effect of food supplementation on the reproductive success of Black-billed Magpies *Pica pica*. *Ibis* 132:595-602.
- DYKSTRA, S. J. R. 1995. Effects of contaminants, food availability, and weather on the reproductive rate of Lake Superior bald eagles (*Haliaeetus leucocephalus*). Ph.D. dissertation. Univ. Wisconsin, Madison, Wisconsin.
- DZUS, E. H., AND J. M. GERRARD. 1993. Factors influencing bald eagle densities in north-central Saskatchewan. *J. Wildl. Manage.* 57:771-778.
- ENS, B. J., M. KERSTEN, A. BRENNINKMEIJER, AND J. B. HULSHER. 1992. Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *J. Anim. Ecol.* 61:703-715.
- EWALD, P. W., AND S. ROHWER. 1982. Effects of supplemental feeding on timing of breeding, clutch-size, and polygyny in red-winged blackbirds *Agelaius phoeniceus*. *J. Anim. Ecol.* 51: 429-450.
- GARCIA, P. F. J., M. S. MERKLE, AND R. M. R. BARCLAY. 1993. Energy allocation to reproduction and maintenance in mountain bluebirds (*Sialia currucoides*): a food supplementation experiment. *Can. J. Zool.* 71:2352-2357.
- GERRARD, J. M., AND G. R. BORTOLOTTI. 1988. *The Bald Eagle*. Smithsonian Institution Press, Washington, D.C. 177 pp.
- , D. W. A. WHITFIELD, P. GERRARD, P. N. GERRARD, AND W. MAHER. 1978. Migratory movements and plumage of subadult Saskatchewan bald eagles. *Can. Field-Nat.* 92:375-382.
- GERRARD, P., J. M. GERRARD, D. W. A. WHITFIELD, AND W. J. MAHER. 1974. Post-fledging movements of juvenile Bald Eagles. *Blue Jay* 32:218-226.

- HANSEN, A. J. 1987. Regulation of bald eagle reproductive rates in Southeast Alaska. *Ecology* 68:1387-1392.
- HODGES, J. I. 1981. Chilkat River Valley bald eagle nest surveys-1966, 1979, and 1980. Unpublished report. Office of Raptor Management. U.S. Fish and Wildlife Service, Juneau, Alaska.
- , E. L. BOEKER, AND A. J. HANSEN. 1987. Movements of radio-tagged bald eagles, *Haliaeetus leucocephalus*, in and from Southeastern Alaska. *Can. Field-Nat.* 101:136-140.
- HÖGSTEDT, G. 1981. Effect of additional food on reproductive success in the magpie (*Pica pica*). *J. Anim. Ecol.* 50:219-229.
- . 1991. Natural fluctuations in food supplies-effects on breeding results in European birds. *Acta XX Congressus Internationalis Ornithologici*: 1584-1594.
- HUTTO, R. L. 1990. Measuring the availability of food resources. *Stud. Avian Biol.* 13:20-28.
- IMLER, R. H., AND E. R. KALMBACH. 1955. The bald eagle and its economic status. U.S. Fish and Wildlife Service, Circular 30. Washington, D.C. 51 pp.
- JANES, S. W. 1984. Influences of territory composition and interspecific competition on red-tailed hawk reproductive success. *Ecology* 65:862-870.
- JOHNSTON, R. D. 1993. The effect of direct supplementary feeding of nestlings on weight loss in female Great Tits *Parus major*. *Ibis* 135:311-314.
- KRALOVEC, M. L. 1993. Bald eagle movements in and from Glacier Bay National Park and Preserve, Alaska. Final report. Glacier Bay National Park and Preserve, National Park Service, Gustavus, Alaska.
- LACK, D. L. 1968. Ecological adaptations for breeding in birds. Western Printing Services Ltd., Bristol, Great Britain. 409 pp.
- MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Ann. Rev. Ecol. Syst.* 18:453-487.
- NEGRO, J. J., A. CHASTIN, AND D. M. BIRD. 1994. Effects of short-term food deprivation on growth of hand-reared American Kestrels. *Condor* 96:749-760.
- NEWTON, I. 1977. Breeding strategies in birds of prey. *Living Bird* 16:51-82.
- . 1979. Population Ecology of Raptors. Buteo Books, Vermillion, South Dakota. 399 pp.
- , AND M. MARQUISS. 1981. Effect of additional food on laying dates and clutch sizes of Sparrowhawks. *Orn. Scand.* 12:224-229.
- OFELT, C. H. 1975. Food habits of Bald Eagles in Southeast Alaska. *Condor* 77:337-338.
- POOLE, A. 1985. Courtship feeding and Osprey reproduction. *Auk* 102:479-492.
- RICHNER, H. 1992. The effect of extra food on fitness in breeding carrion crows. *Ecology* 73:330-335.
- SHERROD, S. K., C. M. WHITE, AND F. S. L. WILLIAMSON. 1976. Biology of the Bald Eagle on Amchitka Island, Alaska. *Living Bird* 15:143-182.
- SIMMONS, R. 1993. Effects of supplementary food on density-reduced breeding in an African Eagle: adaptive restraint or ecological constraint? *Ibis* 135:394-402.
- SIMONS, L. S., AND T. E. MARTIN. 1990. Food limitation of avian reproduction: an experiment with the Cactus Wren. *Ecology* 71:869-876.
- SMITH, J. N. M., R. D. MONTGOMERIE, M. J. TAITT, AND Y. YOM-TOV. 1980. A winter feeding experiment on an island song sparrow population. *Oecologia* 47:164-170.
- STALMASTER, M. V. 1987. The Bald Eagle. Universe Books, New York. 227 pp.
- , AND J. A. GESSAMAN. 1982. Food consumption and energy requirements of captive bald eagles. *J. Wildl. Manage.* 46:646-654.
- , AND ———. 1984. Ecological energetics and foraging behavior of overwintering bald eagles. *Ecol. Monogr.* 54:407-428.
- STEARNS, S. K. 1992. The evolution of life histories. Oxford University Press, New York. 249 pp.
- STEIDL, R. J., AND R. G. ANTHONY. 1995. Recreation and bald eagle ecology on the Gulkana National Wild River, Alaska. Unpublished Final Report to the Bureau of Land Management, Cordova, Alaska. 71 pp.
- , AND C. R. GRIFFIN. 1991. Growth and brood reduction of mid-Atlantic coast Ospreys. *Auk* 108:363-370.
- SWENSON, J. E., K. L. ALT, AND R. L. ENG. 1986. Ecology of bald eagles in the Greater Yellowstone Ecosystem. *Wildl. Monogr.* 95:1-46.

- TODD, C. S., L. S. YOUNG, R. B. OWEN, AND F. J. GRAMLICH. 1982. Food habits of bald eagles in Maine. *J. Wildl. Manage.* 46:636–645.
- VERHULST, S. 1994. Supplementary food in the nestling phase affects reproductive success in Pied Flycatchers (*Ficedula hypoleuca*). *Auk* 11:714–716.
- VON BRÖMSEN, A., AND C. JANSSON. 1980. Effects of food addition to Willow Tit (*Parus montanus*) and Crested Tit (*P. cristatus*) at the time of breeding. *Ornis. Scand.* 11:173–178.
- WARD, J. P., AND P. L. KENNEDY. 1996. Effects of supplemental food on size and survival of juvenile Northern Goshawks. *Auk* 113:200–208.
- WATSON, J. W., M. G. GARRETT, AND R. G. ANTHONY. 1991. Foraging ecology of Bald Eagles in the Columbia River estuary. *J. Wildl. Manage.* 55:492–499.
- WIEBE, K. L., AND G. R. BORTOLOTTI. 1994. Energetic efficiency of reproduction: the benefits of asynchronous hatching for American kestrels. *J. Anim. Ecol.* 63:551–560.
- , AND ———. 1995. Food-dependent benefits of hatching asynchrony in American kestrels (*Falco sparverius*). *Behav. Ecol. Sociobiol.* 36:49–57.

Received 31 Jul. 1996; accepted 11 Dec. 1996.