

EFFECTS OF SUPPLEMENTAL FOOD ON PARENTAL-CARE STRATEGIES AND JUVENILE SURVIVAL OF NORTHERN GOSHAWKS

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ABSTRACT.—Using food supplementation, we tested whether food limits juvenile survival in a population of Northern Goshawks (*Accipiter gentilis*) in northeastern Utah. The influence of additional food on female nest attendance also was investigated because those strategies may influence predation mortality rates of juveniles. We provided supplemental food near 13 nests from close to hatching until close to independence during the 1996 and 1997 breeding seasons. Thirteen additional nests served as controls and received no supplemental food. We compared the following variables at treatment and control nests: (1) adult female mass, (2) nestling mass and size, (3) female nest attendance, and (4) juvenile survival. Following supplemental feeding, adult females from treatment nests were heavier than their control counterparts, and remained closer to the nest during the latter part of the nestling period and throughout the postfledging period. Nestlings from supplemented nests were significantly heavier than those from unsupplemented nests, but results for size measurements were equivocal. Survival rates for treatment nestlings were significantly higher than controls in 1997, but not in 1996. Those results support the hypothesis that food does not limit avian reproductive success on an annual basis. Most deaths in 1997 were the result of starvation or sibling competition. That observation, and the fact that fed nestlings were heavier, is consistent with the idea that treatment nestlings were in improved nutritional condition. Overall patterns of mass and nest-attendance for adult female goshawks supports the hypothesis that female condition and behavior are adjusted in response to food supplies. However, it is less clear what role the females' presence in the nest stand plays in mediating juvenile deaths, because we did not document predation as a primary mortality factor during the two years of this study. The apparent flexibility in female nest attendance behavior suggests that such plasticity may be an adaptation to lower the risk of predation. Received 22 September 1999, accepted 3 December 2000.

MANY STUDIES have investigated influence of food on survival and subsequent recruitment of young birds into the breeding population, but much of the work is correlative and few studies have experimentally examined the proximate mechanisms behind food limitation. For avian populations, it is commonly assumed that starvation or predation operating as singular, direct regulating mechanisms influence reproductive success (Lack 1954, Craighead and Craighead 1956, Ricklefs 1969, Newton 1979, 1998). Consequently, few studies have examined alternate regulation pathways or individual linkages along those paths. Food availability may directly influence brood reductions through starvation, or other mortality factors such as predation or sibling aggression alone

may limit reproductive success (Fig. 1). Alternatively, availability of food resources may interact with parental-care behavior (e.g. Martin 1992) or sibling competition to regulate populations.

Previous studies have correlated (Hamer et al. 1991, Doyle and Smith 1994, Bukacinska et al. 1996) and experimentally linked (Yom-Tov 1974, Högstedt 1981, Arcese and Smith 1988, Ward and Kennedy 1996, Soler and Soler 1996) low food supplies with poor reproductive success. Poor breeding success in those studies was attributed to a reduction in adult nest attendance that resulted in higher predation rates. Experimental manipulations of food resources also have demonstrated that parent birds adjust their behaviors in response to food supplies by becoming more sedentary (Marquiss and Newton 1982), contracting their home ranges (King 1996, Rohner and Smith 1996), or reducing hunting efforts and prey de-

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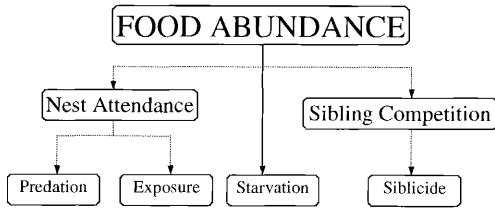


FIG. 1. Schematic diagram depicting possible food limitation mechanisms for avian reproduction (broken line indicates indirect pathway, solid line indicates direct pathway).

livery rates (Cook and Hamer 1997, Wiehn and Korpimäki 1997). Prior studies have not experimentally examined causal linkages between food resources, parental-care behavior, and juvenile survival with accurate documentation of causes of juvenile mortality to understand how food may limit avian reproductive success.

We chose to investigate those interactions using a population of Northern Goshawks (*Accipiter gentilis*) because it was recently evaluated for listing as threatened under the Endangered Species Act (Martin 1998). An understanding of how reproduction is regulated in that species could aid its conservation efforts, and food-supplementation methods have been used successfully with that species (Kenward et al. 1993, Ward and Kennedy 1994, 1996). Moreover, Ward and Kennedy's (1996) food-supplementation experiment provided limited evidence for interaction between predation, food, and parental-care in that species. In this paper, we summarize results of a supplemental feeding experiment to determine if goshawk parental-care strategies are adjusted in response to food availability and if they play a role in mediating juvenile mortalities. In addition, we examine influence of supplemental food on adult condition, nestling mass and size, and juvenile survival. Our predictions are that (1) supplemental food improves adult condition and allows parents to spend more time near their nests because they do not have to hunt to meet their energy requirements or those of the brood, (2) supplemental food improves nestling condition, and (3) supplementally fed juveniles survive at a higher rate, because mortality due to starvation, predation, or both are reduced.

STUDY AREA AND METHODS

Study area.—We studied a population of goshawks in the Uinta Mountains of northeastern Utah. All

nests in the study were located on land administered by the U.S. Department of Agriculture, Forest Service, Ashley National Forest. Elevations range from 1,830 to 4,125 m. The average annual precipitation is 70 cm (range 40 to 90 cm), with roughly equal precipitation resulting from winter snowfall (November to April) and summer rains (May to October, Ashcroft et al. 1992). Lodgepole pine (*Pinus contorta*), Engelmann spruce–sub-alpine fir (*Picea engelmanni* and *Abies lasiocarpa*), mixed conifer (includes lodgepole pine, Engelmann spruce, and sub-alpine fir), and ponderosa pine (*Pinus ponderosa*) are the most prevalent forest communities in the study area. Douglas fir (*Pseudotsuga menziesii*), quaking aspen (*Populus tremuloides*), pinyon-juniper (*Pinus edulis-Juniperus osteosperma*), subalpine meadows, sagebrush (*Artemisia* spp.) grasslands, and riparian woodlands are also present.

Methods.—We conducted the experiment from late May to August in 1996 and 1997. Each year we randomly selected a sample of nests from a pool of known territories where female goshawks were observed incubating (1996, $n = 12$; 1997, $n = 14$). Half of each sample was randomly assigned to the treatment group (1996, $n = 6$; 1997, $n = 7$) and half to the control group (1996, $n = 6$; 1997, $n = 7$). We began food-supplementation close to hatching. We placed Japanese Quail (*Coturnix coturnix*) on a podium located along clear sight and flight paths roughly 20 m from the nest. We visited nests every two to three days and provided sufficient food to meet the energy requirements of the female and the brood until the next scheduled visit. The amount of quail provided was based on a modification of the age-specific energetic calculations for juvenile goshawks summarized in Ward and Kennedy (1994). Because Ward and Kennedy (1994, 1996) observed adult females eating the experimental quail, we estimated the energetic requirements of a typical adult female (see Dewey 1999 for details of calculations) and added this value to their estimates of the brood's energy requirements.

All feeding boxes were equipped with a motorized cover triggered by a solar sensor to hide the food at dark and expose it again at daylight (box design modified after Ward et al. 1997). This allowed us to leave enough food for several days without attracting nocturnal predators that might take the food or prey upon the goshawks. Non-motorized podiums also were placed at control nests and visited at the same interval and for the same amount of time to standardize the level of disturbance.

Adult female goshawks were trapped near their nests using dho-gaza nets and a mechanical Great Horned Owl (*Bubo virginianus*) when nestlings were approximately 10 to 20 days old (roughly two weeks after feeding began). Each bird was weighed, measured, and banded with a U.S. Fish and Wildlife Service aluminum leg band and a color leg band with a

unique alpha-alpha or alpha-numeric code. Following measurement and banding, females were fitted with a 28 g backpack radio transmitter (Biotrack Ltd., Dorset, United Kingdom) using a Teflon ribbon harness (S. Walls pers. comm.). Three females tagged in 1996 were included in the 1997 experiment. To avoid undue disturbance, those birds were not re-trapped the second year, because their radios were still working.

We climbed the nest tree and retrieved the nestlings when the oldest chick was estimated to be 25 to 30 days of age. Nestlings were weighed, measured, and banded in a manner similar to the females. The size measurements included culmen and hallux length, and tarsus width and length. To reduce variation in measurements, one researcher (S.R.D.) collected all size measurements. We collected measurements only once during the nestling period. Nestling age was determined on the basis of known dates of hatching (when available) and a photographic guide developed by Boal (1994). When possible, nestling sex was determined using size measurements because the sexes are size dimorphic. Each nestling was fitted with a 9 g tarsal mount radio transmitter (Advanced Technology Services [ATS], Isanti, Minnesota), equipped with a mortality switch, which were activated if a bird (or transmitter) was motionless for 8 h. This feature allowed us to identify if a bird was dead and recover its remains quickly to determine cause of death.

We measured 56 nestling goshawks; 28 each in 1996 (13 treatments, 15 controls) and 1997 (18 treatments, 10 controls). Because of hatching asynchrony, some nestlings were older ($n = 6$) or younger ($n = 7$) than the target age (25–30 days) at the time of measurement. Two nestlings of undetermined sex and three for which measurements were collected post-mortem were not included in the analysis. The latter three were not included in analyses because measurements may not accurately reflect their condition prior to death, due to tissue water loss (J. Gessaman pers. comm.). In addition, one nest in 1996 and two in 1997 were located in snags that were unsafe to climb. As a result, seven additional nestling goshawks (three in 1996 and four in 1997) were not measured or banded; however, we still followed the fates of those birds throughout the study. Mass and size measurements also were not collected for two nestlings in 1996 and five in 1997 because they died before age 25 days.

Every two to three days, prior to visiting nests for feeding, teams of two observers obtained simultaneous bearings on adult female and juvenile goshawks from established telemetry points using hand-held, three-element Yagi antennae and receivers. Telemetry points were located with a global positioning system (GPS) unit accurate to within 5 m following differential correction. Goshawk bearings were obtained by sighting hand-held compasses to-

ward the peak transmitter signal. Visual locations were obtained for females that were not radio-tagged when nests were visited for feeding (1996; $n = 2$; 1997, $n = 4$).

We rotated order of visiting nests to obtain locations through a morning-midday-afternoon cycle so all time periods were represented. During the late nestling and postfledging periods, adult females began ranging farther from their nests and occasionally were out of range of the telemetry equipment. If attempts to locate a female from several stations failed, no position was recorded for that bird because observers had to visit other nests. In those situations, observers were usually able to determine whether the female was present in her nest area. Within each territory, the nest area was defined *a priori* as a 200 m radius circle centered on the nest (Reynolds 1983, Reynolds et al. 1992). A female was considered within her nest area if her estimated location was within 200 m of the nest.

The estimated position of the female was obtained from telemetry station coordinates and bearings to goshawks from those stations using program Locate II version 1.5 (Pacer, Truro, Nova Scotia, Canada). We calculated the Euclidean distance between the UTM coordinates of the estimated location and those of the nest to obtain an estimate of the female's position relative to her nest.

Because location data were collected on individual females over successive occasions, those data points cannot be considered completely independent. Therefore, we reduced data for each female to a mean value for five biologically relevant phases of the brood-rearing period on the basis of the behavior of adult female and fledgling goshawks. Newton (1979) described three phases of female behavior typical of breeding raptors during the nestling period: (1) almost continuous brooding and shading of the young prior to development of their own thermoregulatory capacities, (2) attendance near the nest to feed and defend the young (may hunt opportunistically near the nest, but remains close enough to respond to alarm calls) and, (3) nestlings left unattended while female hunts elsewhere. In the goshawk, the approximate duration of each phase is as follows: phase 1, days 0 to 10; phase 2, days 11 to 28; and phase 3, days 29 to fledging (Zachel 1985, Squires and Reynolds 1997). We used a fledging age of 42 days, the age by which most females have left the nest, as the cutoff for phase 3 (Squires and Reynolds 1997). There is little information regarding behavior of the female after the young fledge. Kenward et al. (1993) reported that fledglings are typically found within 300 m of the nest until approximately 65 days of age when their flight feathers harden and they are capable of extended flight. If attendance near the nest continues to reduce the risk of predation after fledging, then a difference in attendance patterns would be expected until fledglings begin ranging long distances from

the nest where parents are unable to protect them effectively. Using 65 days of age as a cutoff, we divided the postfledging period into two phases: phase 4, day 43 to day 65; and phase 5, day 66 to study termination.

We estimated our telemetry error following a method outlined in White and Garrott (1990) (see Dewey 1999 for details). Estimated bearings to goshawk locations were unbiased (mean difference between true bearings and estimated bearings, 1.063° ; $n = 92$ bearings; not significantly different from 0, paired t -test: $t = 1.98$, $P = 0.5071$), but imprecise (SD of bearing errors = 15.31°). The mean linear error associated with test transmitters was 165 ± 33.5 (SE) m ($n = 46$). However, the actual linear error is probably lower than that reported here, because GPS coordinates of visual locations were used when the female was known not to have changed her position following tracking. Although location estimates were relatively imprecise, we assumed that errors were similar for all females.

Following collection of goshawk locations, observers visited the nest area for feeding. During nest visits, each juvenile was located visually. Prior to radio tagging, if fewer birds were observed in the nest on a subsequent visit, the area was searched to locate the missing bird. After transmitter attachment, if a radio was transmitting a mortality signal, we located the bird or dropped transmitter. Bodies of dead juveniles were recovered to determine cause of death. If cause of death was not readily apparent from recovered remains, birds were sent to the Colorado Veterinary Diagnostic Laboratory at Colorado State University, College of Veterinary Medicine, where necropsies were performed (1996, $n = 1$; 1997, $n = 3$).

Size and mass of goshawks.—To test for differences in size and mass between groups of adult females and nestlings, we used analysis of variance (ANOVA) with full models. Significance level for all tests was set *a priori* at $\alpha = 0.1$ to better balance the probabilities of committing Type I and Type II errors. We report the results of one-tailed tests throughout.

To examine differences in mass between treatment and control females we used a two-factor ANOVA in PROC GLM (SAS Institute, 1997). In that analysis, treatment, year, and treatment \times year were considered fixed effects in the modeling process. The experimental unit for that test was the individual bird.

We used a mixed-effects, nested ANOVA in PROC MIXED (SAS Institute 1997) to compare the size and mass of treatment and control nestlings. Treatment, year, sex, age, and brood size were fixed effects, and nest within treatment \times year was a random effect. Brood size and age were continuous variables, and all other variables were categorical. We also considered several two-way interactions and one three-way interaction. Because siblings from the same brood cannot be considered strictly independent, we con-

sidered brood the experimental unit by including the nested term, brood within treatment \times year, in the model. Defining that term as a random effect sets up a common correlation among all observations drawn from the same brood (SAS Institute 1997). In other words, mass and size of young goshawks are more correlated with their siblings than with those from other broods. The nested term itself accounts for variation between broods within groups (treatment or control) and years. Biologically, that term accounts for variation between broods that may be due to differences in parental or habitat quality. Means were calculated for each morphometric measure for both treatment groups using the least square means option in PROC MIXED (SAS Institute 1997).

Nest attendance.—Differences in patterns of female nest attendance were examined in two ways. First, proportion of locations within the nest area were compared for treatment and control groups for the middle three phases of the brood-rearing period using logistic regression in PROC GENMOD (SAS Institute 1993). Effects due to year, treatment, and year \times treatment were considered in the modeling process. Because all females were located on their nests for the first 10 days posthatching, no statistical comparison was made for the first phase of the nestling period. Logistic regression could not be used for analysis of phase 5 data because the model would not converge due to zero cell counts. Therefore, we used Fisher's exact test (SAS Institute 1987) to test for difference during that last phase.

In 1997, we also examined influence of the treatment on the distance treatment, and control females were located from their nests for phases 2 through 5 using one-way ANOVA in PROC GLM (SAS Institute 1997). Data for each female were reduced to a mean value for each phase of brood rearing, and those means were compared between groups. Location data collected in 1996 were sufficient to determine whether the female was present in the nest area. However, due to logistical problems, too few actual locations were collected to make the latter analysis meaningful.

Juvenile survival.—We estimated survival rates for juveniles each year using the Kaplan–Meier procedure (Kaplan and Meier 1958) in SAS using code in White and Garrott (1990). The Kaplan–Meier estimator accounts for animals lost due to radio failure, or emigration from the study area through censoring, and also allows for staggered entry of individuals as they are born or added to the study (Pollock et al. 1989). Survivorship for treatments and controls was estimated separately for each year, and survival curves and rates were compared between groups using the log rank test (Pollock et al. 1989) and a chi-square test (White and Garrott 1990), respectively. The Kaplan–Meier survival estimator assumes that the fate of an individual bird is independent of others in the study. That assumption is probably not val-

TABLE 1. Mass and size measurements of treatment and control nestling goshawks^a from the Uinta Mountains of Utah in 1996 and 1997.

| | Treatment (<i>n</i> = 29) | Control (<i>n</i> = 22) | Effect Size |
|-------------------------|-------------------------------|-----------------------------|---------------------|
| | $\bar{x} \pm SE$ | $\bar{x} \pm SE$ | Difference $\pm SE$ |
| Mass (g) | 777.61 \pm 19.58 | 723.27 \pm 24.25 | +54.35 \pm 31.22 |
| Culmen length (mm) | 19.48 \pm 0.28 | 19.66 \pm 0.33 | -0.19 \pm 0.44 |
| Hallux length (mm) | 24.05 \pm 0.32 | 24.07 \pm 0.38 | -0.02 \pm 0.51 |
| Tarsus width (mm) | 9.2 \pm 0.08 | 9.1 \pm 0.08 | -0.12 \pm 0.12 |
| Tarsus length (mm) | 80.16 \pm 0.74 | 79.24 \pm 0.89 | +0.93 \pm 1.17 |
| Age ^b (days) | 27.03 \pm 0.34 | 28.64 \pm 0.72 | — |

^a Males and females are combined and data are pooled over two years.

^b Represents the average age at time of measurement.

id for broodmates, but may hold once the young have left the nest. Therefore, we also calculated survival during the nestling period on a nest basis and compared those rates between treatment groups using Fisher's exact test (SAS Institute 1987). For that test, we assumed a nest was successful if all young survived and unsuccessful if any young were lost.

RESULTS

Food-supplementation experiment.—Treatment families consumed the supplemental quail. Females were observed removing quail from the feeding platform to feed nestlings, delivering quail to fledglings, and consuming quail themselves. Juveniles also were observed taking quail from the feeding box once they had fledged. In addition, males were occasionally observed removing and caching quail. Males may have fed infrequently on the supplemental quail, but generally they continued to hunt and deliver natural prey throughout brood rearing.

Condition of adult female and nestling goshawks.—Treatment females were on average 11% heavier than controls ($\bar{x} \pm SE$; treatment 1,103.75 \pm 45.14 g, *n* = 8; control 993.22 \pm 25.01 g, *n* = 9). Supplemental feeding had a significant effect on adult female mass ($F = 4.25$, *df* = 1 and 13, $P = 0.03$). Effects due to year ($F = 0.06$, *df* = 1 and 13, $P = 0.4$) and treatment \times year ($F = 0.08$, *df* = 1 and 13, $P = 0.39$) were nonsignificant.

Mean mass and size measurements of treatment and control nestling goshawks and the effects size (magnitude of treatment effect measured as difference between means) are summarized in Table 1. The effects size provides a way to estimate "retrospective" power of the statistical test and is useful to quantify the uncertainty of the results when the null hy-

pothesis is not rejected (Steidl et al. 1997, Thomas 1997). Supplementally fed male and female nestlings were significantly heavier, but except for tarsal length, not larger than those that were not fed (Table 2). A sex effect was significant for mass, hallux length, and tarsal length, but not culmen length or tarsal width. The effect due to age was significant for all morphometric measurements except tarsal width (Table 2). Several interaction terms were significant in analyses of mass, hallux length, and tarsal length and width (Table 2).

Nest attendance of adult female goshawks.—In 1996 and 1997, control and treatment females were always found in the nest area and on or very close to their nests for the first 10 days posthatching (phase 1) (Table 3). Treatment females were in the nest area more often than controls during all of the latter phases of brood rearing (Table 3), although differences were only significant for phases 2 and 4 (Table 4). The treatment \times year interaction term was also significant for phases 2–4. Treatment females were also located significantly more often in the nest area than controls during phase 5 (Fisher's exact test, $P = 0.02$).

In 1997, there was no difference between treatment groups in distances females were found from the nest for the first 10 days posthatching (phase 1) (Table 5). However, throughout the remainder of brood rearing, treatment females were significantly closer to their nests than controls (phase 2, $F = 10.37$, *df* = 1 and 1, $P = 0.008$; phase 3, $F = 14.25$, *df* = 1 and 1, $P = 0.004$; phase 4, $F = 11.43$, *df* = 1 and 1, $P = 0.01$; phase 5, $F = 10.78$, *df* = 1 and 1, $P = 0.02$; Table 5 and Fig. 2).

Survival of juvenile goshawks.—We followed the fates of 33 and 37 young goshawks in 1996

TABLE 2. ANOVA table of fixed effects for model comparing mass and size of treatment and control nestling goshawks from the Uinta Mountains of Utah in 1996 and 1997.

| Source | Mass | | | Culmen length | | | Hallux length | | | Tarsal width | | | Tarsal length | | |
|------------------------|------|-----------------|--------|---------------|-----------------|-------|---------------|-----------------|-------|--------------|-----------------|------|---------------|-----------------|-------|
| | F | df ^a | P | F | df ^a | P | F | df ^a | P | F | df ^a | P | F | df ^a | P |
| Treatment | 3.63 | 47.6 | 0.03 | 0.44 | 51 | 0.26 | 1.86 | 51 | 0.09 | 1.91 | 50.5 | 0.09 | 8.89 | 50.6 | 0.002 |
| Year | 0.29 | 19 | 0.29 | 0.04 | 19.9 | 0.42 | 1.17 | 17.9 | 0.15 | 0.58 | 11.9 | 0.23 | 0.04 | 16.8 | 0.42 |
| Sex | 3.64 | 30.9 | 0.03 | 0.16 | 40.2 | 0.34 | 4.08 | 37.9 | 0.03 | 0.01 | 44.1 | 0.46 | 9.03 | 32.2 | 0.003 |
| Age | 16.5 | 44.3 | <0.001 | 7.15 | 48.6 | 0.005 | 13.30 | 47.9 | 0.001 | 1.29 | 50.8 | 0.13 | 3.39 | 46.2 | 0.04 |
| Brood size | 0.02 | 25.3 | 0.44 | 1.45 | 40.5 | 0.12 | 2.01 | 38 | 0.08 | 0.49 | 48.9 | 0.25 | 0.04 | 30.2 | 0.42 |
| Treatment × year | 1.77 | 19 | 0.09 | 1.65 | 19.9 | 0.11 | 0.36 | 17.9 | 0.28 | 0.12 | 11.9 | 0.37 | 6.21 | 16.8 | 0.01 |
| Treatment × sex | 0.28 | 31.2 | 0.29 | 1.54 | 42.1 | 0.11 | 2.35 | 39.7 | 0.07 | 1.69 | 49.4 | 0.99 | 0.02 | 33.1 | 0.44 |
| Treatment × age | 1.71 | 44.3 | 0.09 | 0.13 | 48.6 | 0.36 | 3.01 | 47.9 | 0.09 | 5.6 | 50.8 | 0.01 | 2.81 | 46.2 | 0.05 |
| Sex × age | 0.13 | 31.2 | 0.36 | 0.89 | 42.3 | 0.18 | 3.83 | 39.9 | 0.03 | 1.05 | 49.4 | 0.16 | 2.45 | 33.2 | 0.06 |
| Sex × age × treatment | 0.23 | 31.2 | 0.32 | 1.21 | 42.3 | 0.14 | 2.10 | 39.9 | 0.08 | 1.5 | 49.4 | 0.11 | 0.00 | 33.2 | 0.50 |
| Treatment × brood size | 1.11 | 22.7 | 0.15 | 0.62 | 33.4 | 0.22 | 0.02 | 30.6 | 0.45 | 1.42 | 33.2 | 0.25 | 7.15 | 24.7 | 0.007 |
| Sex × brood size | 1.45 | 32.5 | 0.12 | 0.00 | 42.3 | 0.49 | 0.07 | 40.5 | 0.40 | 0.04 | 41 | 0.12 | 6.58 | 35.3 | 0.007 |

^a Denominator degrees of freedom (DDF) given in table. Numerator degrees of freedom (NDF) are 1 for all analyses.

and 1997, respectively. In 1996, all treatment and control nests were successful (fledged at least one young). However, two control broods and one treatment brood were reduced during the nestling period (see Table 6 for cause of death) and one treatment juvenile died shortly after fledging. Survival rates were lower for controls during the nestling period, but differences were not significant. We were unable to detect a difference in survival rates between groups from hatching–fledging ($\chi^2 = 0.196$, $df = 1$ and 1 , $P = 0.66$), fledging through the end of the experiment ($\chi^2 = 1.182$, $df = 1$ and 1 , $P = 0.28$), or over the duration of the study ($\chi^2 = 0.038$, $df = 1$ and 1 , $P = 0.85$; Table 7). When brood was the experimental unit, survival of treatment nestlings was higher than controls, although we were unable to detect a significant difference between groups (Fisher's exact test, $P = 0.5$; Table 7).

In 1997, three control broods failed (i.e. fledged no young), and two broods were reduced by one young during the nestling period (see Table 6 for cause of death). All treatments nests were successful in 1997. Survival rate of treatment juveniles was significantly higher than that of controls during the nestling period and over the duration of the study ($\chi^2 = 10.774$, $df = 1$ and 1 , $P = 0.001$), but survival rates did not differ between treatment and controls during the fledgling period (Table 7). Using brood as the experimental unit, survival of treatment nestlings was still significantly higher than that of control nestlings (Fisher's exact test, $P = 0.04$; Table 7).

DISCUSSION

Size and mass of goshawks.—Following supplemental feeding, adult females from treatment nests were significantly heavier than controls. Those results were consistent with Ward and Kennedy (1996) and Wiehn and Korpimäki (1997), suggesting that supplemental food probably allowed the female to meet her energetic requirements, as well as that of her brood. An increase in mass for supplementally fed females may be explained in two ways. First, because treatment females were more sedentary (i.e. located closer to their nests), their energy expenditures probably were reduced. Second, females were observed eating the quail, so they

TABLE 3. Proportion of locations in the nest area for treatment and control adult female goshawks for five phases of brood rearing in the Uinta Mountains of Utah in 1996 and 1997.

| Phase ^a | Treatment | | | Control | | |
|--------------------|------------------|---------------------------|-------------------------------|------------------|---------------------------|-------------------------------|
| | $\bar{x} \pm SE$ | No. of birds ^b | No. of locations ^c | $\bar{x} \pm SE$ | No. of birds ^b | No. of locations ^c |
| Phase 1 | 1.0 \pm 0 | 13 | 77 | 1.0 \pm 0 | 13 | 68 |
| Phase 2 | 0.97 \pm 0.01 | 12 | 115 | 0.88 \pm 0.07 | 13 | 85 |
| Phase 3 | 0.91 \pm 0.06 | 12 | 85 | 0.79 \pm 0.06 | 10 | 57 |
| Phase 4 | 0.60 \pm 0.06 | 11 | 107 | 0.40 \pm 0.07 | 9 | 76 |
| Phase 5 | 0.18 \pm 0.11 | 9 | 67 | 0 \pm 0 | 9 | 47 |

^a Duration of each phase is as follows: phase 1, days 0 to 10; phase 2, days 11 to 28; phase 3, days 29 to 42; phase 4, days 43 to 65; and phase 5, days 66 to study termination. Rationale for phases is defined in the text.

^b Number of adult females for which data were collected. Sample size decreases over time because females without radio transmitters or whose nests failed were not located.

^c Total number of locations used in the analysis.

might have also increased their food consumption rates.

Treatment juveniles were significantly heavier, but except for tarsal length, not significantly larger than controls. The result for mass is consistent with our observations of deaths due to starvation and siblicide in controls: mortalities that generally indicate food stress or poor nesting condition.

As expected, effect due to nestling age was significant for most morphometric measurements. Although we attempted to measure all nestlings when they were between 25 to 30 days of age, that was not possible for several reasons. First, goshawk young hatch asynchronously and in some broods the youngest nestling was up to 10 days younger than its closest sibling. Because we measured nestlings only once, we scheduled measurements for when most of the brood was within 25 to 30 days. Occasionally one of the siblings was older or younger than this age. Second, assessing nestling age from the ground with binoculars and a photographic key proved to be difficult par-

ticularly because most nest stands were in relatively flat terrain that offered few good vantage points of the nest. As a result, nestling age was occasionally underestimated and some young were older than anticipated when measured. The variation in age necessitated adding age as a covariate to the ANOVA model. Despite accounting for age, the large amount of variation in measurements may have obscured major differences if they existed between groups.

The significant gender effect for most morphometric measures was a result of sexual size dimorphism. Lack of a significant effect due to gender for culmen length is probably due to low statistical power. Significant treatment \times year effect for mass, culmen length, and tarsal length is due to the fact that control nestlings were heavier and had larger measurements in 1996 than in 1997, whereas treatments were heavier and larger in 1997. That suggests that the treatment had more of an effect in 1997, perhaps because it was a poor prey year relative to 1996 (discussed in more detail below).

TABLE 4. Results of *F*-tests for logistic regression model comparing proportion of locations in the nest area for treatment and control adult female goshawks from the Uinta Mountains of Utah during three phases^a of brood rearing in 1996 and 1997.

| Source | Phase ^a 2 | | | Phase 3 | | | Phase 4 | | |
|-------------------------|-----------------------|-----------------|----------|-----------------------|-----------------|----------|-----------------------|-----------------|----------|
| | <i>F</i> ^b | df ^c | <i>P</i> | <i>F</i> ^b | df ^c | <i>P</i> | <i>F</i> ^b | df ^c | <i>P</i> |
| Treatment | 3.804 | 22 | 0.032 | 6.058 | 19 | 0.12 | 6.473 | 17 | 0.011 |
| Year | 0.713 | 22 | 0.204 | 6.379 | 19 | 0.10 | 0.228 | 17 | 0.319 |
| Treatment \times year | 2.56 | 22 | 0.062 | 4.524 | 19 | 0.02 | 3.180 | 17 | 0.046 |

^a Duration of each phase is as follows: phase 2, days 11 to 28; phase 3, days 29 to 42; phase 4, days 43 to 65. Rationale for phases is defined in the text.

^b Based on Type III *F*.

^c DDF given in table. NDF are 1 for all analyses.

TABLE 5. Mean distance (m) treatment and control adult female goshawks were located from their nests for five phases of brood rearing in the Uinta Mountains, Utah during 1997.

| Phase ^a | Treatment | | | Control | | |
|--------------------|------------------|---------------------------|-------------------------------|------------------|---------------------------|-------------------------------|
| | $\bar{x} \pm SE$ | No. of birds ^b | No. of locations ^c | $\bar{x} \pm SE$ | No. of birds ^b | No. of locations ^c |
| Phase 1 | 0 ± 0 | 7 | 43 | 0 ± 0 | 7 | 41 |
| Phase 2 | 12.3 ± 4.3 | 7 | 59 | 37.3 ± 6.8 | 6 | 42 |
| Phase 3 | 36.2 ± 5.0 | 7 | 48 | 135.2 ± 35.0 | 4 | 24 |
| Phase 4 | 160.1 ± 37.0 | 6 | 64 | 814.5 ± 283.8 | 3 | 29 |
| Phase 5 | 585.4 ± 214.4 | 5 | 29 | 1746.1 ± 284.7 | 3 | 11 |

^a Duration of each phase is as follows: phase 1, days 0 to 10; phase 2, days 11 to 28; phase 3, days 29 to 42; phase 4, days 43 to 65; and phase 5, days 66 to study termination. Rationale for phases is defined in the text.

^b Number of adult females for which data were collected. Sample size decreases over time because females without radio transmitters or whose nests failed were not located.

^c Total number of locations used in the analysis.

Significant interaction between brood size and treatment for tarsal length was due to smaller tarsal length measurements for nestlings in broods of two and larger measurements for broods of three. A greater proportion of females (the larger sex) made up the sample of nestlings in broods of three and that may have resulted in longer tarsal length measurements for broods of three. Similarly, the significant brood-size effect for culmen length also may have resulted from the greater proportion of females in broods of three.

Table 8 summarizes results of avian supplemental feeding experiments that investigated influence of food on nestling mass, size, or both. Five of 13 studies reviewed also found a significant positive influence of food on mass; in two of those studies, control mortalities were primarily the result of siblicide, cannibalism, or

suicide (Simons and Martin 1990, Wiebe and Bortolotti 1995). Three studies observed a non-significant positive influence of the treatment on mass of fed nestlings (Yom-Tov 1974, Högestedt 1981, and Ward and Kennedy 1996); one reported a nonsignificant positive influence one year and a nonsignificant negative influence the second year (Gende and Willson 1997); and two detected a nonsignificant negative influence of the supplemental feeding on mass (Korpimäki 1989, Wiehn and Korpimäki 1997). Of the remaining studies, one did not detect an effect of supplemental feeding on mass until the young were 32 days of age (Cook and Hamer 1997) and the other found a significant negative effect on mass (Svensson and Nilsson 1995). Only five studies examined the influence of food on nestling size (Table 8). Four of these studies (including this study) found that nestling size was similar between treatment and control groups, and Simons and Martin (1990) found that treatments were structurally larger than controls.

Despite numerous efforts to determine effect of supplementary food on mass and size of nestling birds, the answer is unresolved. Why do different studies show such different responses to extra food? Several explanations are plausible. First, food is probably not limiting every year, or for every species or in every location. Natural prey levels are dynamic, varying temporally and spatially. Results of supplemental feeding experiments may be confounded if conducted when natural food is abundant. Second, morphometric measurements may be imperfect measures of the treatment effect. For example, Wiehn and Korpimäki

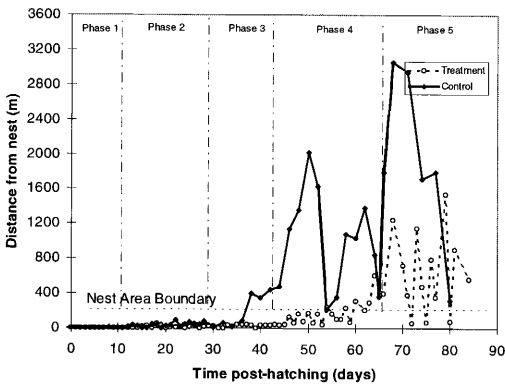


FIG. 2. Mean distance (meters) treatment and control adult female goshawks were located from their nests throughout brood rearing in 1997. The phases are defined in the text.

TABLE 6. Causes of death for treatment and control juvenile goshawks from the Uinta Mountains of Utah in 1996 and 1997.

| Year | Territory | Treatment group | Age (days) | Cause of death ^a | Evidence |
|------|-----------|-----------------|------------|-----------------------------|--|
| 1996 | CUB | Control | ~18 | Unknown | remains below nest; possibly siblicide |
| 1996 | CC | Control | ? | Unknown | remains found in nest; possibly siblicide |
| 1996 | IRS | Treatment | 45 | Predation | recovered carcass |
| 1996 | WFE | Treatment | ~19 | Accident | necropsy; multiple fractures |
| 1997 | SNK | Control | ~20 | Siblicide | observed female carrying bloody body from nest, body not recovered |
| 1997 | SNK | Control | ~20 | Unknown | recovered remains near nest; possibly siblicide/cannibalism |
| 1997 | SNK | Control | ~22 | Unknown | nest empty |
| 1997 | LGD | Control | ~23 | Siblicide | necropsy; rib fractures and internal injuries, observed nestling being forced from nest by sibling |
| 1997 | LGD | Control | ~26 | Starvation | necropsy; emaciated |
| 1997 | WHS | Control | ~25 | Blood loss | necropsy |
| 1997 | WHS | Control | ~20? | Starvation | recovered remains |
| 1997 | ALN | Control | ~20? | Starvation | recovered remains |

^a When necropsies were not performed to determine cause of death, we assumed that the disappearance of one or more nestlings (but not the entire brood) was due to either starvation or siblicide. We attributed the death to starvation if recovered remains were found away from the nest, suggesting that an adult goshawk had removed the dead nestling from the nest but not consumed it (after Simons and Martin 1990). We ruled the death a siblicide event (or a possible event) if the remains were found at the base of the tree or in the nest itself and appeared to have been partially or completely plucked or consumed in a manner consistent with goshawk feeding. This assumption was supported by our observations of a siblicide event in which one nestling forced its sibling out of the nest tree and its body was recovered at the base of the tree (Estes et al. 1999). Inspection of the body revealed that feathers had been removed by the sibling during aggressive attacks. If all nestlings disappeared from the nest between visits, it was considered a predation event (after Ward and Kennedy 1996). We did not consider an empty nest a predation event if the loss of nestlings occurred over several visits and if the other deaths were attributable to food stress.

mäki (1997) suggest that mass may not clearly indicate nestling quality because supplemented nestlings may have more mature tissue with a lower water content. Fed birds in better condition would therefore appear no different from unsupplemented birds in terms of mass. Cook and Hamer (1997) observed that parents of supplementally fed puffin chicks (*Fratercula arctica*) compensated for the extra food by mak-

ing less-frequent food deliveries. As a result of reduced provisioning, the total amount of food consumed by supplementally fed puffins was similar to that of the controls. Wiehn and Korpimäki (1997) also observed a reduction in food delivery rates by the adult female, but not the male. Lack of an effect on mass in other studies could be explained by those phenomena if one physiological response nullifies another or if

TABLE 7. Survival estimates for juvenile goshawks from the Uinta Mountains of Utah for the nestling period, fledgling period, and duration of the study in 1996 and 1997.

| Survival interval | Treatment | | | Control | | | Effect size |
|------------------------------|-----------|-----------|-------|----------|-----------|----------|---------------------|
| | <i>n</i> | \hat{S} | SE | <i>n</i> | \hat{S} | SE | Difference \pm SE |
| 1996 | | | | | | | |
| Nestling period | 15 | 0.93 | 0.074 | 18 | 0.89 | 0.07 | +0.04 \pm 0.11 |
| Nestling period ^a | 6 | 0.83 | 0.15 | 6 | 0.67 | 0.19 | +0.16 \pm 0.25 |
| Fledgling period | 14 | 0.93 | 0.08 | 16 | 1.0 | 0.55E-08 | -0.07 \pm 0.08 |
| Duration of study | 15 | 0.87 | 0.1 | 18 | 0.89 | 0.07 | -0.02 \pm 0.75 |
| 1997 | | | | | | | |
| Nestling period | 19 | 1.0 | 0 | 18 | 0.56 | 0.12 | +0.44 \pm 0.12 |
| Nestling period ^a | 7 | 1.0 | 0 | 7 | 0.57 | 0.19 | +0.43 \pm 0.19 |
| Fledgling period | 19 | 1.0 | 0 | 10 | 1.0 | 0 | 0 \pm 0 |
| Duration of study | 19 | 1.0 | 0 | 18 | 0.56 | 0.12 | +0.44 \pm 0.12 |

^a Brood is experimental unit.

TABLE 8. Summary of the effects of supplemental food on offspring size and mass (+ + indicates significant positive effect, -- indicates significant negative effect, + indicates a nonsignificant positive effect, and - indicates a nonsignificant negative effect) in several avian species with respect to timing of food addition.

| Species | Timing of food addition ^a | Effect on offspring size | Effect on offspring mass | Source |
|--|--------------------------------------|--------------------------|--------------------------|---------------------------|
| <i>Accipiter gentilis</i> | N, F | + / - ^b | + + | This study |
| <i>Accipiter gentilis</i> | N, F | + | + | Ward and Kennedy 1996 |
| <i>Aegolius funereus</i> | P, L | | - | Korpimäki 1989 |
| <i>Campylorhynchus brunneicapillus</i> | N | + + ^c | + + ^c | Simons and Martin 1990 |
| <i>Corvus corone</i> | L, N | | + | Yom Tov 1974 |
| <i>Falco sparverius</i> | P | | + + | Wiebe and Bortolotti 1995 |
| <i>Falco tinnunculus</i> | N | + / - ^d | - | Wiehn and Korpimäki 1997 |
| <i>Fratercula arctica</i> | N | + / - ^e | + + ^f | Cook and Hammer 1997 |
| <i>Haliaeetus leucocephalus</i> | I, N | | + / - ^g | Gende and Willson 1997 |
| <i>Melospiza melodia</i> | B | | + + | Arcese and Smith 1988 |
| <i>Parus caeruleus</i> | P, L | | -- | Svensson and Nilsson 1995 |
| <i>Pica pica</i> | P, L, I | | + | Högstedt 1981 |
| <i>Pica pica</i> | Y | | + + ^h | Dhindsa and Boag 1990 |

^a P = prelaying period, L = laying period, I = incubation period, N = nestling period, F = fledgling period, B = throughout breeding season, Y = year round.

^b Results equivocal; mean culmen and hallux length smaller for treatments, mean tarsal length and width larger for treatments.

^c Effect was significant for only 1 year of the study.

^d Results equivocal; mean wing length longer for treatments, mean tarsal length smaller for treatments.

^e Results equivocal.

^f Effect after age 32 days.

^g Results equivocal; positive for one year of the study and negative for the other.

^h Effect after age 8 days.

the response is actually behavioral rather than physiological. Similarly, size measurements may be poor indicators of a treatment effect if physical size is strongly determinate. Moss (1979) studied growth rates of nestling sparrowhawks (*Accipiter nisus*) and observed that weight gain varied more between broods than size measurements, suggesting that size may be less influenced by short-term variations in food availability than weight. Third, small sample sizes may result in low statistical power of tests leading to nonsignificant results, particularly if variance associated with measurements is high, (e.g. Ward and Kennedy 1996). Of the studies we reviewed (Table 8), only Ward and Kennedy (1996) reported the statistical power of their tests. To achieve 90% power with $\alpha = 0.1$, our *a priori* power analyses indicated that a 10% difference in some size measurements between treatment groups was necessary. Most differences were <10%, and the fact that we were unable to detect a difference in size measurements between treatment groups may be a Type II error. Finally, study design limitations may lead to spurious results as suggested by Nakamura and Kubota (1998). We measured two control nestlings postmortem. Although we did not include those nestlings in

the analysis, they were considerably lighter and smaller than treatment juveniles of similar age, suggesting that the weak effect of the treatment on mass may have been a result of the timing of measurement collection. During lean times, it is likely that, rather than having an entire brood of poor-quality nestlings that all eventually die, the young in poorest condition are eliminated through starvation or siblicide at an early age. Nestlings that live are of average size and, because smaller young are not included in the analyses, the effect of the treatment appears minimal. Nonsignificant results in other studies may be due to this phenomenon if measurements were collected only once and after a number of young died, (e.g. Ward and Kennedy 1996).

Patterns of female nest attendance.—Diurnal patterns of female nest attendance were similar for treatment and control groups during the early part of the nestling period, strongly suggesting that food availability does not influence the female's brooding behavior when the young cannot thermoregulate. After young were homeothermic, treatment females stayed closer to the nest and, on average, did not range as far from the nests as the controls, which were presumably foraging. Female behavior during

those phases of brood rearing was clearly adjusted in response to food. Cadiou and Monnat (1996) observed a similar plasticity in attendance behavior of adult kittiwakes (*Rissa tridactyla*) that was related to food availability. However, unlike this study, predation losses were heavy at unattended kittiwake nests. Although predation was not an important mortality factor for young goshawks during the two years of this study, it is possible that plasticity in female nest attendance behavior is related to perceived predation risk.

Nestling and postfledging survival.—The survival rate of control nestlings was higher in 1996 than in 1997. Although we did not quantify natural food supplies, the variation in effect of supplemental food on juvenile survival rates is probably related to variation in natural prey levels. Snowfall during the winter preceding the 1997 breeding season was 200% of normal in some parts of our study area, and the snowpack persisted a month later in the spring than it did the previous year (Natural Resource Conservation Service Snotel Data 1998). Based on that and on fewer field observations of some prey species (S. Dewey unpubl. data), it is likely that natural prey levels were higher in 1996 than in 1997.

Ward and Kennedy (1996) documented similar annual variation in survival rates for nestling goshawks in New Mexico indicating that the influence of food on goshawk reproduction varies temporally and spatially. Temporal variability in the influence of food on avian reproduction has been documented in both long-term correlative studies (e.g. Steenhof et al. 1997, Herrera 1998) and in experimental manipulations of food abundance (e.g. Boutin 1990, Rodenhouse and Holmes 1992). Those results suggest that food does not limit avian reproductive success in temperate environments on an annual basis as suggested by Fretwell (1972) and Wiens (1977).

Predation on nestling goshawks was low during this study. In two breeding seasons, only one juvenile died from predation, and the event occurred shortly after fledging. Most deaths were either the direct result of low food availability (i.e. starvation) or an indirect result through sibling competition and siblicide. In contrast, most of the juvenile losses in New Mexico (Ward and Kennedy 1996) were attributed to predation. Such variability in cause of

death suggests that the mechanism by which food influences juvenile survival may vary temporally and spatially.

Habitat quality can vary temporally if prey populations are cyclic (as discussed above), or spatially if management activities or natural processes influence forest structure which in turn influences predator or prey abundance across a landscape. Most nests in the Utah study site were in lodgepole pine habitat types, whereas the predominant habitat type in the New Mexico study area was ponderosa pine. Ponderosa pine may support a more diverse community of potential predators, prey species, or both. Avian communities in ponderosa pine tend to be richer and more abundant than those in lodgepole pine (Finch and Ruggiero 1993, Paulin et al. 1999). Greater number and diversity of potential prey might lead to higher predator populations and could result in higher predation rates. Long-term predation rates also may not actually be higher in the New Mexico study area. Given the stochastic nature of predation, it would be conceivable to document two years of low predation. Predation rates for many species are known to fluctuate over time, and such fluctuations are most often related to the densities of predators and prey and availability of alternate prey species (Wiens 1989, Caughley and Sinclair 1994).

Influence of supplemental food on siblicide.—Siblicide was the cause of death at two nests in 1997 and suspected in several other deaths in both 1996 and 1997 (Table 6). The cause of facultative siblicide is not well understood for many raptor species, but aggressive sibling behavior is thought to be limited to times when food is in very low supply (Newton 1979). Although our experiment was not designed to examine the influence of supplemental food on brood reductions resulting from siblicide, observations collected during a related study examining the influence of food on nestling goshawk begging vocalizations (W. Estes unpubl. data) provided an opportunity to explore the link between food and occurrence of siblicide events. The details of these observations are reported in Estes et al. (1999), and the results suggest that supplemental food influenced the incidence of siblicide in goshawks, and that siblicide may be an important mortality factor when food resources are tight.

Conclusions.—Results of this study and Ward and Kennedy's (1996) experiment provide evidence that food limits reproductive success in goshawks during brood rearing, although the system appears more complex than originally hypothesized. For the population of goshawks examined in this study, food limited reproductive output, either directly through starvation or indirectly through sibling competition and siblicide. However, this limitation did not occur in both years of this study, suggesting that food does not limit avian reproductive success on an annual basis. We established a causal link between food resources and patterns of nest attendance, but not between nest attendance and deterrence of predation.

Additional experimental studies where food supplies and densities of nest predators (or perceived risk of predation) are manipulated are needed to determine the relative effect of those two processes on avian reproduction. In future food-supplementation experiments, we encourage investigators to measure background food abundance, food provisioning rates, or both, to determine if an experimental treatment occurred.

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