EFFECTS OF SUPPLEMENTAL FOOD ON SIZE AND SURVIVAL OF JUVENILE NORTHERN GOSHAWKS

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ABSTRACT.—In 1992 and 1993, 28 Northern Goshawk (*Accipiter gentilis*) broods in north-central New Mexico were used in a supplemental-feeding experiment to determine if there was a causal relationship between food availability and survival of young goshawks. We randomly assigned 28 nests as treatments or controls. Every two days (from hatching [late April] until juvenile dispersal [mid-October]) we visited control nest stands and provided food at treatment nest stands. We measured morphological characteristics and attached tarsal-mounted transmitters with mortality switches to 42 nestling Northern Goshawks when they were 21 days old. In both 1992 and 1993, we relocated birds via telemetry every other day until mid-August. We located birds at least once a week from mid-August until mid-October in 1992, and until late-November 1993. There were no significant differences in nestling size. Treatment birds had a significantly higher survival rate during the nestling period in 1993, but not in 1992. Because most control nestlings died from predation, we attribute higher nestling survival to increased time spent in nest stands by adult females, whose presence probably deterred predators. *Received 25 April 1995, accepted 20 August 1995.*

LACK (1954) PROPOSED that food often limits reproductive success and, thus, recruitment of animals into a breeding population (Newton 1980, 1991). Many supplemental-feeding experiments have tested this relationship on terrestrial vertebrates, including nesting birds, and have successfully manipulated at least one breeding variable (Boutin 1990). Most avian supplemental-feeding experiments have been conducted on passerines and have examined the influence of food on clutch size and hatching success. Supplemental food has resulted in advanced laying dates and/or larger clutch sizes, increases in size of nestlings, and increases in nestling and fledgling survival (Yom-Tov 1974, Newton and Marquiss 1981, Dijkstra et al. 1982, Hansen 1987, Hochachka and Boag 1987, Arcese and Smith 1988, Meijer et al. 1988, Korpimäki 1989, Hörnfeldt and Eklund 1990, Simons and Martin 1990, Hochachka and Smith 1991, Aparicio 1994).

The transition from dependent fledgling to independent juvenile may be a stage critical for avian survival (Richner 1992). High avian juvenile mortality rates during this period have been attributed to starvation (Southern 1970, Hirons et al. 1979, Newton et al. 1982, Husby 1986, Korpimäki and Lagerström 1988, Sullivan 1989). Newton et al. (1982) and Sullivan (1989) have speculated that, although adequate food may be available to young during the fledgling-dependency period, juveniles starve because they are inexperienced and inefficient foragers.

Knowledge about effects of additional food on the posthatching period, particularly on fledgling and juvenile survival, is scarce for all birds and virtually nonexistent for avian predators. In most experiments, supplemental feeding was discontinued after hatching. Only 2 of 58 avian experiments cited by Boutin (1990) initiated feeding after hatching (Hochachka and Boag 1987, Simons and Martin 1990), and neither was conducted on a predator. Kenward et al. (1993) conducted an experiment on Northern Goshawks (*Accipiter gentilis*) in which they began feeding during the postfledgling period. No supplemental-feeding experiments have initiated feeding at hatching and continued until the end of brood rearing.

Raptors are useful organisms for studying the relationship of food availability to reproductive success after fledging because they have a long fledgling-dependency period. Parents may not be able to provide enough food for the entire fledgling-dependency period, and high mortality rates caused by starvation are expected (Newton 1991). We provided supplemental food to Northern Goshawks from hatching until dis-

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persal to test the prediction that increased food availability will directly reduce juvenile mortality caused by starvation. We chose the Northern Goshawk as our study organism because recent management guidelines for this species (Reynolds et al. 1992) emphasize managing habitat for its prey. These guidelines are based on the untested assumption that Northern Goshawk demographics, particularly reproductive success and recruitment, is limited by food availability. We also measured potential indirect effects of excess food on survival by measuring how supplemental food influenced nestling size, and evaluated the utility of this indirect measure for predicting survival by examining its relationship to actual survival rates of juvenile Northern Goshawks.

METHODS

Food supplementation.—This experiment was conducted from mid-April to mid-October 1992 and 1993 on a Northern Goshawk population in the Santa Fe National Forest (35°30′00″–36°30′00″N, 106°00′00″– 107°00′00″W) in north-central New Mexico. Our experimental methods are briefly described below (details are provided in Ward and Kennedy 1994).

Twelve of 14 known Northern Goshawk nest sites were active (defined as an adult bird observed in incubating posture) in 1992. Six of the 12 active nests were randomly assigned as treatments and six as controls (Table 1). Sixteen active nests were located in 1993, with eight randomly assigned as treatments and eight as controls (Table 1). Approximately 7 to 10 days prior to the estimated hatching date (P. L. Kennedy unpubl. data), we observed behavior of the incubating adult bird daily for about 0.5 h from an observation blind located 30 m from the nest to determine hatching date. Food supplementation began the day after hatching in 1992 and about one week before we estimated hatching would occur in 1993 (late-April), and ended when most control birds left the study area (mid-October). Dead Japanese Quail (*Coturnix coturnix*) were provided every other day on feeding podiums located 10 m from the nest; podiums also were placed at control nests and visited every other day (for detailed description of podium, see Ward 1994). During each visit to experimental nest stands, we recorded number of young and adults present (nest-stand visits ca. 0.5 h). To maximize the treatment effect, we provided as many quail as treatment broods would take in addition to the amount required to meet 100% of the offspring's estimated daily energetic requirements.

Data collection.—Morphological measurements were taken, and tarsal-mounted transmitters with mortality switches (Advanced Telemetry Systems, Isanti, Minnesota) were attached to 42 nestling Northern Goshawks at approximately 21 days of age (13 treatments and 16 controls in 1992; 10 treatments and 3 controls in 1993). At this same time, we also attempted to trap (using dho-gaza method described in Kennedy et al. 1994) and weigh unbanded adults (nine females [six in 1992, three in 1993]; seven males [three in 1992, four in 1993]) at experimental nest stands. Adults banded in previous years were not retrapped. After transmitter attachment, birds were relocated at least once every two days from the ground to monitor survival. By mid-August the birds started moving long distances; we continued to try to locate birds every other day on the ground, and also tracked their movements and survival from an airplane at least once a week until mid-October 1992, and through November 1993.

DATA ANALYSIS

Body size.—We used a mixed-model analysis of variance (SAS Institute 1987) to test for differences in each measurement between treatment and control offspring. A reduced model with source terms treatment, year, sex, nest (treatment), and nest (treatment) × sex interaction was used. The nest (treatment) term measured variation between nests within treatment and control groups. Sex × treatment and year × treatment interaction terms were nonsignificant in the full model. In the reduced model, nest was a random effect and treatment and year were fixed effects. Resulting type III sums of squares were generated to test for variation between nests. For our analyses, we assumed all young were about the same age, so one treatment nestling and four control nestlings of unknown ages (nests located after hatching, which prevented accurate age determination) were removed from the data analyses. The experiment was designed to determine the effects of supplemental food on young Northern Goshawks; therefore, adult Northern Goshawk mass was analyzed *a posteriori*. We conducted these analyses to determine if there was also a physiological response by adult Northern Goshawks to extra food in the nest stand in addition to the behavioral response we observed. Nest was the sampling unit for each test and an α of 0.05 was used for all statistical tests. We report $\bar{x} \pm$ SD unless otherwise specified.

Offspring survival.—Survival rates of Northern Goshawk offspring were analyzed separately for each year using procedure LIFETEST (SAS Institute 1987), which allows for right censoring of data points. When experiments measuring survival terminate, some animals are still alive, and these observations are right censored. Both censored and uncensored data need to be included for accurate calculation of survival rates. Five offspring from 1992 of unknown ages were included in survival analyses because variation in estimated age did not change the outcome of these analyses. If we could not determine cause of death when dead birds were recovered, we conducted necropsies

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TABLE 1. Summary of Northern Goshawk nests used in supplemental-feeding experiment conducted in north-central New Mexico in 1992 and 1993.

Nest	Adult territory occupancy	1992		1993	
		Experimental assignment	Final status	Experimental assignment	Final status
BAC	Same female both years, male unknown	Control	Successful[a]	Treatment	Successful[a]
BAR	Different female each year, male unknown	Control	Successful[a]	Treatment	Failed during incubation
CPA	n/a[b]	—	—	Control	Failed during incubation
CPE	Same adults both years	Treatment	Successful[a]	Treatment	Successful[a]
CPL	n/a[b]	—	—	Control	Failed during nestling period
GAR	n/a[c]	Control	Successful[a]	n/a[c]	—
GUA	Same female both years, male unknown	Control	Successful[a]	Treatment	Failed during incubation
HSH	Female unknown, same male both years	Treatment	Failed during nestling period	Control	Failed during nestling period
JOA	n/a[b]	—	—	Treatment	Failed during incubation
LCH	n/a[b]	—	—	Treatment	Successful[a]
MAL	n/a[b]	—	—	Control	Failed during nestling period
MGU	n/a[b]	—	—	Control	Successful[a]
PON	Same female both years, male unknown	Treatment	Successful[a]	Control	Failed during incubation
RED	Same adults both years	Treatment	Successful[a]	Control	Successful[a]
SJU	n/a[c]	Control	Successful[a]	n/a[c]	—
STA	Same adults both years	Control	Successful[a]	Treatment	Successful[a]
TEL	Same female both years, male unknown	Treatment	Failed during nestling period	Control	Failed during incubation
WAT	Same female both years, different male each year	Treatment	Successful[a]	Treatment	Successful[a]

[a] Fledged at least one young.
[b] Territory discovered in 1993.
[c] Territory not relocated in 1993.

TABLE 2.   Average of measurements taken in 1992 and 1993 on 21-day-old female and male Northern Goshawks from Jemez Mountains in New Mexico, and 95% confidence interval (CI) associated with difference in mean.

Measurement	Treatment	Control	Difference ± 95% CI[c]
Female[a]			
Mass (g)	682 ± 76	676 ± 14	6 ± 176
Culmen length (cm)	1.9 ± 0.1	1.9 ± 0.7	0.1 ± 1.4
Hallux length (cm)	2.2 ± 0.2	2.2 ± 0.1	0.1 ± 1.6
Tarsometatarsus width (cm)	0.8 ± 0.1	0.7 ± 0.1	0.1 ± 0.2
Tarsometatarsus length (cm)	7.5 ± 0.5	7.4 ± 0.2	0.1 ± 1.4
Male[b]			
Mass (g)	590 ± 49	541 ± 80	49 ± 252
Culmen length (cm)	1.8 ± 0.1	1.7 ± 0.2	0.1 ± 0.6
Hallux length (cm)	2.1 ± 0.2	2.0 ± 0.2	0.1 ± 0.6
Tarsometatarsus width (cm)	0.7 ± 0.1	0.6 ± 0.1	0.1 ± 0.2
Tarsometatarsus length (cm)	7.3 ± 0.3	7.1 ± 0.4	0.2 ± 1.4

[a] n = eight treatment females; n = 6 control females.

[b] n = 14 treatment males; n = 9 control males.

[c] Column illustrates estimated power of statistical test for each variable measured (e.g. variable with large CI had low power for statistical test performed).

after the experiment was terminated (n = 2 in 1992, n = 1 in 1993).

Presence of adults in nest stand.—We used procedure GENMOD, which fits a generalized linear model to data by maximum-likelihood estimation (SAS Institute 1987) to compare the number of times adult females were recorded in treatment nest stands to the number of times adult females were recorded in control nest stands. We did not compare the number of times adult males were seen in treatment and control nest stands because they were rarely seen in either treatment or control nest stands. We also compared female attendance in the nest stand at successful nests between the two years of the experiment. Because our experiment was not designed to detect changes in adult behavior, our analyses of adult attendance in nest stands was conducted *a posteriori*. We conducted these analyses to attempt to explain why predation, and not starvation, was the primary mortality factor for nestling Northern Goshawks.

RESULTS

Body size.—The supplemental-feeding experiment was successful, with all treatment birds eating quail. For a detailed evaluation of the success of our feeding technique, see Ward and Kennedy (1994). Treatment nestlings tended to be heavier and structurally larger on average than controls (Table 2), but all differences were nonsignificant (Table 3). As expected, sex significantly effected all measurements and was a result of sexual size dimorphism. The significant nest (treatment) effect for hallux length, tarsometatarsus width, and tarsometatarsus

length was probably a result of the natural variation between nests, which may be attributed to differences in parental care, habitat quality, and number of offspring. The significant year effect for tarsometatarsus width was due to a small measurement on a 1993 treatment nestling. Culmen growth of each sex was different at each nest; males at one treatment nest had some of the largest culmens, while their sisters had the smallest, which probably resulted in the significant nest (treatment) × sex interaction effect for this measurement (Table 3).

Adult females at treatment nest stands were about 30 g heavier ($\bar{x}$ = 1,007 ± 24 g, n = 6) than adult females at control nest stands ($\bar{x}$ = 975 ± 47 g, n = 3). Adult males at treatment nest stands were also heavier (689 ± 39 g, n = 5) than adult males at control nest stands (660 ± 0.0 g, n = 2). Adult masses were not statistically compared due to small sample sizes and large standard deviations associated with adult mass.

Survival.—In 1992, all six control nests were successful (all eggs hatched and young fledged). At two treatment nests all nestlings died (for causes of death, see Table 4), and another treatment brood ate supplemental food only occasionally (Ward and Kennedy 1994). The survival rate of treatment birds ($\bar{x}$ = 80 ± 10%, n = 15) did not differ significantly from the survival rate of control birds ($\bar{x}$ = 100 ± 0%, n = 16) from hatching until fledging (Wilcoxon test, X^2 = 3.43, df = 1, P = 0.06), or from fledging until

TABLE 3. P-values from mixed model ANOVA ($n = 10$ treatment nests and 6 control nests) of measurements taken in 1992 and 1993 on 21-day-old control and treatment Northern Goshawk nestlings from Jemez Mountains in New Mexico.

Source	Mass	Culmen length	Hallux length	Tarsometa-tarsus width	Tarsometa-tarsus length
Treatment	0.28	0.17	0.68	0.58	0.47
Sex	<0.01	<0.01	<0.01	<0.01	0.01
Year	0.07	0.36	0.31	0.04	0.42
Nest (treatment)	0.10	0.32	0.01	0.02	0.02
Nest (treatment) × sex	0.30	0.04	0.82	0.94	0.73

experiment termination (treatment survival, $\bar{x}$ = 91 ± 9%, n = 12; control survival, $\bar{x}$ = 93 ± 6%, n = 15; Wilcoxon test, X^2 = 0.08, df = 1, P = 0.78).

In 1993, three of eight control nests failed to hatch eggs, and all nestlings died at three other control nests (for causes of death, see Table 4). Three of eight treatment nests failed prior to hatching, and the remaining five were successful. The survival rate of treatment birds ($\bar{x}$ = 90 ± 10%, n = 10) was significantly higher than the survival rate of control birds ($\bar{x}$ = 37 ± 17%, n = 8; Wilcoxon test, X^2 = 6.62, df = 1, P = 0.01) from hatching until fledging. Because most nestling deaths were caused by predation (Table 4), the fate of individual nestlings may not have been independent events. When nest was the experimental unit, survival of treatment nestlings was higher ($\bar{x}$ = 80 ± 18%, n = 5), but not significantly different from survival of con-

trol nestlings ($\bar{x}$ = 40 ± 22%, n = 5; Fisher's exact test, P = 0.26).

One treatment fledgling was last known to be alive on 15 September 1993 when its transmitter failed. The remaining eight treatment birds survived to the end of the experiment (feeding ended 25 October and locating birds terminated 30 November 1993), and one of three remaining control birds died from unknown causes within a week after fledging. Survival of treatment birds ($\bar{x}$ = 100 ± 0%, n = 9) was not significantly higher than controls ($\bar{x}$ = 67 ± 27%, n = 3) from fledging until experiment termination (Wilcoxon test, X^2 = 2.66, df = 1, P = 0.10).

Presence of adults in nest stand.—In 1992, adult females from treatment nests were seen in the nest stand significantly more times ($\bar{x}$ = 85 ± 11%, n = 4) than controls ($\bar{x}$ = 58 ± 17%, n = 5; X^2 = 16.02, df = 1, n = 9, P < 0.001) during the

TABLE 4. Cause of death of treatment and control Northern Goshawk young from Jemez Mountains in New Mexico in 1992 and 1993.

Year	Experimental assignment	Age (days)	Cause of death (evidence)
1992	Treatment	29	Disease[a] (tissue analysis)
1992	Treatment	22	Unknown[b] (recovered body)
1992	Treatment	22	Predation[c] (not in nest)
1992	Control	54	Predation[d] (recovered remains)
1992	Treatment	51	Accident[e] (necropsy)
1993	Treatment	33	Spinal injury (necropsy)
1993	Control	15	Predation[c] (nest empty)
1993	Control	15	Predation[c] (nest empty)
1993	Control	17	Predation (recovered remains[d])
1993	Control	29	Predation (recovered remains[d])
1993	Control	29	Unknown[f] (recovered remains)
1993	Control	51	Unknown[b] (recovered remains)

[a] Two organisms (*Chlamydia tsittaci, E. coli*) caused severe fibrinous pericarditis on heart, which led to heart failure.
[b] Could not determine cause of death from recovered remains or necropsy.
[c] Nestling not seen in nest; assume predation is cause of death.
[d] Recovered remains (feather pile) and pellets suggest avian predator.
[e] Fledgling had internal injuries and a broken humerus.
[f] Found body at base of nest tree; probably fell when sibling taken by predator.

nestling period (ca. three weeks; each nest visited ca. 25 times). A similar pattern was observed for the duration of the experiment; adult females were seen in nest stands significantly more times ($\bar{x}$ = 51 ± 9.0%, n = 4) than control adult females ($\bar{x}$ = 32 ± 10%, n = 4; X^2 = 16.99, df = 1, n = 8, P < 0.001 [each nest visited ca. 45 times]). High nest-failure rates in 1993 (Table 1) prevented statistical comparison of adult female presence in nest stands. In 1993, all nestlings at three of five control nests died from predation. At all three depredated nests, the adult female was not seen during the last two visits (n = 10 visits) made before nestlings died from predation, whereas adult females at the two remaining control nests were seen during 96 and 72% of 25 visits made during the first two weeks after hatching. These rates were similar to, or higher than the average percentage of times treatment females were seen during this same time ($\bar{x}$ = 78 ± 12%, n = 4; each nest visited ca. 25 times), and predation did not occur at either control nest.

Three nests that successfully fledged young both years, were each randomly assigned as a treatment one year and a control another (BAC, RED, STA; Table 1). Two other nests (CPE, WAT; Table 1) were randomly assigned as treatments both years (same adult female present both years at all five nests; Table 1). The female at the WAT nest (treatment assignment both years), was seen for a very high percentage of nest visits made during both nestling periods (95% in 1992, 92% in 1993; for both years, brood size = 3). Female presence at the CPE nest (treatment assignment both years) during the nestling period also was consistently high both years (89% in 1992 [brood size = 4]; 69% in 1993 [brood size = 2]). At the BAC nest, adult female presence in the nest stand during the nestling period was 44% (brood size = 2) when assigned as a control in 1992, which increased to 65% when the nest was assigned as a treatment in 1993 (brood size = 3). The same pattern was observed at the STA nest, where adult female presence in the nest stand during the nestling period was 52% (brood size = 2) when assigned as a control in 1992, and increased to 77% (brood size = 1) when assigned as a treatment in 1993. At the RED nest, adult female presence in the nest stand during the nestling period was 82% (brood size = 1) when assigned as a treatment in 1992, which decreased to 60% when the nest was assigned as a control in 1993 (brood size = 2).

DISCUSSION

Size and survival of juveniles.—Although treatment offspring were nonsignificantly heavier and structurally larger, we predicted a significant mass difference between treatments and controls because we maximized the treatment effect and our *a priori* estimate of the power of the statistical test was high (1 $-$ β = 0.97, based on 5% difference in mass of treatments and controls, n = 20 nests, SE = 1,000). However, variance associated with measurements was greatly underestimated, so actual power of the statistical test for each measurement was probably low (Table 2). We attribute the large variation in measurements to differences in brood size, parental quality, and timing of measurement (peak growth). Hatching day was not known exactly, so rapidly growing nestlings only a few days apart in age may have varied greatly in size. Furthermore, young in a large brood or with "inexperienced" parents may not receive as much food and may have a slower growth rate than would nestlings with "experienced" parents or in a smaller brood. Given the variability in size of nestling Northern Goshawks at this age and small sample size, our failure to reject the null hypothesis may be a Type II error. However, no control young were emaciated or showed outward signs of nutritional stress, and we did not attribute any nestling control deaths directly to starvation, suggesting the null hypothesis may not be false.

Heavier nestlings may have a higher probability of survival under conditions of food stress; however, conflicting results have been reported about this relationship. Magrath (1991) cited 14 studies that found a positive relationship between nestling mass and juvenile survival (Great Tits [*Parus major*] were subjects in 6 of 14 studies), and 10 studies that found no relationship between these variables. Further, mass may not be an accurate measure of fat content, which is assumed to be the major factor influencing postfledgling survival (Thompson et al. 1993). Nestling mass is an index to probability of nestling survival when starvation is the primary cause of death, but may not accurately predict nestling survival when other mortality factors such as predation are important.

Influences of adult behavior on nestling survival.—Higher survival rates of treatment nestlings in 1993 were not a direct result of starvation, but of differences in predation rates (Ta-

bles 3 and 4). We propose excess food indirectly affected Northern Goshawk young survival by altering the adult female's behavior. Adult females appeared to exhibit a short-term response (change in allocation of time to foraging or guarding) to changes in food availability (Martin 1992). Northern Goshawks practice biparental care; males provide most of the food, and females generally remain at the nest and protect the young. When nestlings are about three weeks old, adult females often leave the nest stand and hunt to help males meet energetic demands of nestlings, which are at their peak (Ward and Kennedy 1994). The superabundant food supplies at treatment nests probably enabled the adult female to meet her physiological demands and those of her brood and, hence, remain in the nest stand and deter potential predators. While both adult males and females were heavier at treatment nest stands compared to adults at control nest stands, only adult female behavior appeared to change with addition of extra food in the nest stand. Adult males rarely were seen at either control or treatment nest stands, and were never observed taking quail from the podium, whereas the female at every treatment nest was seen taking quail (Ward and Kennedy 1994). Males also continued to deliver prey to treatment broods (J. M. Ward unpubl. data). Our observations suggest the Northern Goshawk's parenting strategy allows females to alter their behavior with fluctuating food availability, whereas adult male behavior did not appear to change. Males continued to hunt even when food was superabundant in the nest stand. Our experiment, however, was not designed to detect changes in adult behavior with addition of food, and adult males at treatment nest stands may have altered their behavior in a manner undetected by our observations (i.e. lower prey delivery rates and/ or increased perching away from nest stand). Radio-tracking of adult birds combined with another supplemental feeding experiment would be an interesting test of our hypotheses regarding alteration of adult Northern Goshawk behavior when food is superabundant in the nest stand.

Similar conclusions about adult presence near nests and resulting reduced predation have been made from other supplemental-feeding experiments. Arcese and Smith (1988) reported reduced nest parasitism in food-supplemented nests of Song Sparrows (*Melospiza melodia*) and

suggested it was the result of increased guarding time. However, they did not find significant differences in nest predation between supplemented and control nests. Yom-Tov (1974) reported that increased food abundance near nests of Carrion Crows (*Corvus corone*) reduced predation and increased nesting success. Högstedt (1981) reported the same relationship for Black-billed Magpies (*Pica pica*) and attributed increased nesting success to reduced predation. Martin (1992) pointed out that, under natural conditions, increases in food abundance may be confounded by increases in predator density or predator search intensity, and reported that only one experiment has manipulated both food abundance and predation (Simons 1988). We concur with Martin (1992) that more experiments are needed that manipulate both food and predation, and determine the relationship between food availability and survival through changes in adult behavior and predation rates.

Although we did not measure prey availability, nestling survival may have been high for both experimental groups in 1992 because there may have been more food available in the environment, allowing control females to remain in their nest stands often enough to deter predators. In 1992, a treatment brood of one offspring rarely took supplemental food (29 of 136 quail eaten), whereas in 1993 two treatment broods of one offspring both regularly took quail (237 of 311, and 283 of 322 quail eaten), suggesting less food may have been available in 1993 (Ward and Kennedy 1994). Also, there may have been fewer predators and/or more available alternate prey for potential predators of Northern Goshawk nestlings in 1992.

Conclusions.—Results of our experiment support the hypothesis that Northern Goshawks are food limited from hatching until juvenile independence. However, the nonsignificant survival difference during the nestling stage in 1992 (versus significantly higher treatment survival in 1993) suggests that the degree to which Northern Goshawks are food limited is variable. Furthermore, we propose that excess food did not directly decrease nestling starvation rates in 1993, but indirectly affected nestling survival by altering the behavior of the adult female, whose increased presence in the nest stand may have deterred predators. We suggest Northern Goshawks respond behaviorally and/or physiologically to increased food availability, and either response may influence survival de-

pending upon the amount and duration of increased food availability. Altering behavior allows the Northern Goshawk to respond immediately to short-term increases in food availability, whereas a physiological improvement (e.g. mass gain) may result from long-term increases in food availability. Hence, directly decreased starvation rates in response to increased food availability may be less common than indirect decreases in predation rates for the Northern Goshawk. However, it is unlikely that food availability and predation rates are independent of one another. For example, control nestlings were not significantly smaller than treatment nestlings, but it is possible that control birds were hungrier and attracted predators by begging loudly (Perrins 1965). Survival differences likely are due to a combination of both direct and indirect effects of food availability.

Experiments designed to detect changes in adult behavior with addition of food in the nest stand are needed to test our hypothesis regarding the interactions of food availability, adult behavior, and predation. Further, we did not monitor recruitment of the juvenile Northern Goshawks into a breeding population, and encourage future researchers to do so.

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