

APPROACHES TO INVESTIGATING FOOD LIMITATION HYPOTHESES IN RAPTOR POPULATIONS: AN EXAMPLE USING THE NORTHERN GOSHAWK

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Abstract. Food supplementation experiments have been used to demonstrate that food limits reproductive success and recruitment of a given animal population. Of the experiments that have been conducted on terrestrial vertebrates, few have been conducted on raptors. Hence, correlative evidence supporting a relationship between food availability and breeding densities of raptors may not be conclusive. We discuss the strengths and weaknesses of past supplementation experiments and detail an experiment designed to investigate this relationship for a Northern Goshawk (*Accipiter gentilis*) population in northern New Mexico. Our experiment illustrates that food supplementation experiments can be conducted on raptors throughout brood-rearing to rigorously test hypotheses concerning the effect of food availability on raptor demographics.

Key Words: *Accipiter gentilis*; dispersal; experimental design; food supplementation; juvenile survival; nestling size; Northern Goshawk.

It is commonly assumed that food often limits the reproductive success and thus, recruitment of animals into a breeding population (Lack 1954; Newton 1980, 1991). To test this relationship rigorously, a multitude of supplemental feeding experiments have been conducted on terrestrial vertebrates, including nesting birds, and have successfully increased at least one breeding parameter (Boutin 1990). Nearly all of the avian supplemental feeding experiments have been conducted on herbivores (seed eaters) and omnivores (insect and seed eaters) and have examined the influence of food on clutch size and hatching success where supplemental feeding was discontinued after hatching. Advanced laying date and/or increased clutch size as a result of supplemental food have been reported (Yom-Tov 1974, Newton and Marquiss 1981, Dijkstra et al. 1982, Hochachka and Boag 1987, Arcese and Smith 1988) and some experiments demonstrated an increase in nestling and fledgling survival as a result of supplemented diets (Yom-Tov 1974, Hansen 1987, Simons and Martin 1991). However, results of the studies have been variable, and very few studies have been conducted with non-passerines such as raptors. Newton (1980, 1991) noted that only correlative relationships between food abundance and raptor densities have been established. As a result, current evidence supporting a relationship between food availability and breeding densities of raptors is not conclusive.

Another limitation of past avian supplementation experiments is that only three studies have initiated supplemental feeding after hatching (Hochachka and Boag 1987, Simons and Martin 1991, Kenward et al. 1993), so knowledge about the effects of additional food on the post-hatching period and particularly its influence on off-

spring growth, survival and recruitment is scarce for all birds, and nonexistent for raptors. In three experiments on raptors (Newton and Marquiss 1981, Dijkstra et al. 1982, Hansen 1987), birds were not provided additional food after hatching. Since Boutin's (1990) review, Kenward et al. (1993) conducted a study examining causes of dispersal, providing excess food to goshawk young from three weeks post-fledging until independence (a period of ca. 30 days).

The transition from dependent fledgling to independent juvenile is assumed to be one of the most critical periods for avian survival (Richner 1992). High avian juvenile mortality rates attributed to starvation have been reported during this time (Southern 1970, Hiron et al. 1979, Newton et al. 1982, Korpimäki 1988, Sullivan 1989). Further, both Newton et al. (1982) and Sullivan (1989) speculated that adequate food may be available to the young during the fledgling dependency period, but that juveniles may starve because they are inexperienced and inefficient foragers.

Most of the aforementioned studies were controlled experiments; however, most failed to measure the magnitude of the treatment, supplying unquantified amounts of excess food (but see Yom-Tov 1974, Hogstedt 1981, Dijkstra et al. 1982, Hansen 1987, Hochachka and Boag 1987, Kenward et al. 1993). We believe it is important to quantify the treatment to know how much excess food needs to be provided to yield a true treatment effect. There further exists a need for experimentation on a larger spatial scale over longer periods of time (Boutin 1990).

We are currently examining the potential effects of increased food availability on (1) the size of nestling Northern Goshawks (*Accipiter gentilis*), (2) the time of goshawk fledging, (3) the

TABLE 1. ESTIMATES OF AGE-SPECIFIC ENERGY REQUIREMENTS FOR JUVENILE NORTHERN GOSHAWKS (KELLY AND KENNEDY 1993:TABLE A2.1). AVERAGE AGE OF DISPERSAL FOR TREATMENT JUVENILE GOSHAWKS WAS 12 WEEKS; FOOD SUPPLEMENTATION ENDED AT 22 WEEKS

Age (weeks)	Formula ¹	Energetic requirement (kJ/day)	No. of quail required/day ²	Total no. of quail required
0–2	0.3E* ⁿ	239.1	0.3	4.2
3–5	E* ⁿ	797.0	1.0	21.0
6–7	0.7E* ⁿ	557.9	0.7	9.8
8–22	0.5E* ⁿ	398.5	0.5	45.5

¹ E*ⁿ = peak energy expenditure of an altricial nestling.

² Assimilated energy intake of 150 g quail = 792 kJ (based on methods in Kennedy [1991]).

time of goshawk dispersal, and (4) juvenile goshawk survival. In this paper, we discuss our experimental design as an example of an approach that can be used to evaluate the influence of increased food availability on post-hatching reproductive success and juvenile survival in raptors.

METHODS

STUDY AREA

The experiment was conducted from mid-April to mid-October during the 1992 breeding season and is ongoing for 1993, on a goshawk population in the Jemez Mountains and the adjacent Pajarito Plateau in north-central New Mexico. The majority of the goshawk nests in this area were on land managed by the USDA Forest Service, Santa Fe National Forest. The study area elevation ranges from 1200–3900 m, and the average elevation of the goshawk nests was 2493 m. The mountains are characterized by steep terrain dominated by typical southwestern montane habitat types such as ponderosa pine (*Pinus ponderosa*) and mixed-conifer forests. The Pajarito Plateau, a table-like extension of the eastern flank of the Jemez Mountains, is cut into numerous, narrow, finger-like mesas by southeast-trending, intermittent streams. The mesas are dominated by pinyon-juniper woodland. The drainages contain riparian habitats dominated by ponderosa pine or cottonwood (*Populus* spp.) stands and flow into the Rio Grande. See Kennedy (1988) for a detailed description of the study area.

ENERGETIC CALCULATIONS

To maximize the effect of the treatment, we designed the experiment to supply at least 100% of the broods' (excluding adults) energy requirements at treatment nests. Kennedy (1991) developed an allometric equation describing the relationship between peak energy expenditure of altricial nestlings (E*ⁿ, measured in Watts) and adult biomass (M, measured in g), where E*ⁿ = 53.578M^{0.757}. We used this equation to determine the peak energy expenditure for a nestling goshawk. Peak energy expenditure of nestling males and females was estimated to be 730 kJ/day (where M = 800 g) and

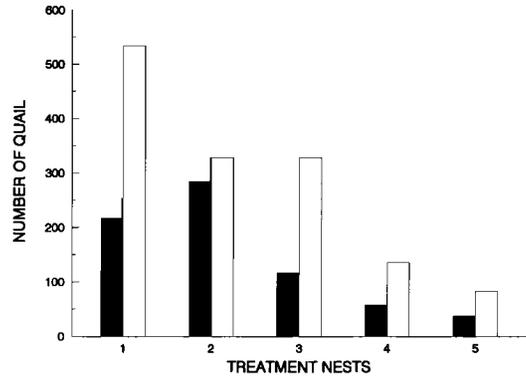


FIGURE 1. Number of quail required (solid bars) to meet 100% of the energetic requirements of the treatment goshawk broods (based on brood size and sex ratio), and the number of quail provided (open bars) at each treatment nest (1–5) during the 1992 experiment.

864 kJ/day (where M = 1000 g), respectively. The average of these two estimates, 797 kJ/day, was used as the estimate of E*ⁿ. The energetic requirements for young goshawks over the rest of the breeding season can then be calculated as a percentage of E*ⁿ. The age-specific energetic requirements are not yet known for the goshawk. However, energetic requirements have been estimated for the Cooper's Hawk (*Accipiter cooperi*), a smaller accipiter that also breeds in the study area (Kelly and Kennedy 1993). We used a modification of the method described by Kelly and Kennedy (1993:Table A2.1) to estimate the age-specific energetic requirements for nestling goshawks (Table 1).

The treatment broods were supplemented with Japanese quail (*Coturnix* sp.) that weighed 120–150 g. The assimilated energy of one 150-g quail is estimated to be about 792 kJ (based on methods used by Kennedy [1991] to estimate assimilated energy of avian prey). According to the age-specific energy requirement calculations, one goshawk offspring required 73.5 quail to meet its daily energy requirements from hatching until mid-October. To maximize the treatment effect, we put out as many quail as the brood would take in addition to the amount provided to meet 100% of the offsprings' estimated energetic requirements. Hence the amount provided at each nest varied with how much excess food the birds would take, and with the number of young at each nest (Fig. 1).

FOOD SUPPLEMENTATION

Twelve of 14 known nest sites were active in 1992; six of the 12 active goshawk nests were randomly assigned as treatments and the remaining six were controls. Sixteen active nests were located in 1993, with eight randomly assigned as treatments and eight as controls. We observed the behavior of the incubating adult bird to determine date of hatching. After hatching, the adult bird on the nest would remain relatively still, except for frequent jerking motions caused by the newly hatched young. It is likely that the hatchlings do

not cause this behavior until they are a few days old. However, since we used the same behavior protocol to determine date of hatching at all nests, any error in age estimation should be equal for all nests.

Food supplementation began the day after hatching was observed (late April) and ended when most birds had dispersed (mid-October). When Newton and Marquiss (1981) provided extra food to sparrowhawks (*Accipiter nisus*), they placed food on or near a regularly used plucking post, and the birds could not remove the food. We modified this technique, placing quail on a podium about 1.5 m tall, located within 10 m of the active nest where the incubating adults could always see the food while on the nest. To entice the birds to take the supplemental food, we initially provided daily 1–2 live quail tethered to the podium. After the live quail were regularly taken, we provided dead quail every other day. In all cases, the quail could be removed by the hawk from the podium. To avoid attracting potential nocturnal predators such as the Great Horned Owl (*Bubo virginianus*), each feeding podium had a motorized cover activated by a solar cell that covered the food by sunset and exposed it by sunrise the following morning. Feeding podiums were also placed at control nests, and were visited every other day to equalize the amount of disturbance at each nest. Each treatment podium was observed 2–3 times during the experiment from sunrise to sunset from a blind approximately 15 m from the feeding podium to verify that the adults, and later, the juvenile goshawks from that territory, were taking the quail. Individual birds were identified by unique alpha-numeric coded color bands.

DATA COLLECTION

Size of nestling goshawks

Morphometric measurements were taken for culmen and hallux length, tarsometatarsus width and length, and weight on 29 21-day-old nestling goshawks (16 controls, 13 treatments) in 1992, and 13 nestling goshawks (10 treatments, 3 controls) in 1993. A single observer (JMW) collected all measurements to eliminate observer variability in measurement technique.

Time of fledging and dispersal

When the morphometric measurements were taken, tarsal-mounted transmitters with mortality switches (Advanced Telemetry Systems, Inc., Isanti, MN) were attached to the nestling goshawks. To minimize the impact of transmitter attachment to the offspring, the transmitters were designed to drop off after 3–4 months. After transmitter attachment, the birds were relocated at least once every two days either from the ground or from an airplane. By mid-October the majority of the juvenile birds could not be relocated because they had dispersed, or their transmitter had dropped off or failed prematurely, and the experiment was terminated.

Fledging was defined a priori as the first observation of young perching on a branch (we assume the same fledging date for all young in a nest), and dispersal was defined a priori as the first time a juvenile spent more than a week at least two km away from the nest. Kenward et al. (1993) used a similar definition of dispersal for goshawks in Sweden, defining dispersal as the first

day that a hawk was not within 1.5 km of the nest and did not return for at least two days.

RESULTS AND DISCUSSION

The food supplementation experiment was successful, with all treatment birds eating quail. None of the adult birds ate immediately, but all ate within 3–5 days after the experiment was initiated. Adult females and fledgling goshawks were observed taking quail at every treatment nest. However, adult males were never observed taking quail from the podium. In 1992, when the experiment was terminated in mid-October, both adult females and juvenile birds were still taking the supplemental food. On several occasions while delivering quail, we observed goshawks perching on the podium. We also regularly observed molted adult feathers at the base of the podium, and quail feathers were frequently observed at goshawk plucking posts and at the base of frequently used perches. Although we recorded the number of quail taken from the podium, we do not know how many of these quail were eaten by the young and by the adults. Since both parents continued to hunt and were rarely seen in the nest stand during the fledgling-dependency period, we surmise that the young ate most of the quail during this period. The amount of quail eaten varied by nest, which we expected because parental care, habitat quality, and the number of offspring differed at each nest. In 1992, the family that ate the most quail had three offspring and removed 86% of the supplemented quail, whereas the family that consumed the fewest number of quail had one offspring and ate only 22% of the quail.

On several occasions, the podiums were knocked over by black bears (*Ursus americanus*) but the bears did not regularly take quail. There was no evidence of other mammalian predators taking quail. At two of the treatments, Gray Jays (*Perisoreus canadensis*) and Steller's Jays (*Cyanocitta stelleri*) regularly picked at the quail. Also, yellowjackets (Hymenoptera: Vespidae) were an unexpected consumer, sometimes eating the entire quail and leaving only the skeleton. We never observed other avian predators taking food from the podium, which was not surprising since goshawks are such vigorous defenders of their territories. If this technique is used for a less aggressive species or in areas where other consumers are more of a problem, the podium may have to be modified (e.g., metal sheeting placed around the base) to prevent consumption of the supplemental food by other animals.

Although our experiment is an improvement on past supplemental feeding studies (for reasons stated in the introduction), our design also had

some flaws that should be corrected in future experiments. Our sample size is probably not large enough to provide meaningful comparisons of survival of treatment versus control offspring, a common problem in raptor studies. Also, when calculating the energetic requirements of the offspring, the requirements of the adults should be accounted for if the excess food is available to the adults. Another weakness of our experiment is measuring offspring's morphometrics at only one age, the expected time of maximum growth (Kennedy 1991). It is possible that significant differences may be found in the mass of treatment versus control offspring after they reach independence, when the controls have to capture their food and the treatments are still being supplemented. Finally, the fates of goshawk offspring need to be monitored for a longer period of time. We chose tarsal-mounted transmitters because we thought backpack transmitters would adversely affect survival, a parameter we were measuring. The drawback of tarsal-mounts is their short battery life (about 4 months). We suggest using Kenward et al.'s (1993) approach of recapturing fledglings prior to independence and replacing the tarsal-mounted transmitters with backpacks.

This experiment demonstrates the feasibility of conducting food supplementation experiments on birds of prey. We hope our work will encourage other raptor researchers to employ rigorous experiments to demonstrate causality when investigating questions about birds of prey, rather than observational studies that only describe correlative relationships. Possible future research regarding the question of raptor population regulation and food availability may be to conduct an experiment for one part of the breeding season (e.g., courtship) at some nests and another part of the breeding season (e.g., fledgling-dependency period) at other nests during the same year. This would determine if food is limiting during all of the breeding season or only for a portion of it. Other useful experiments would be to provide excess food during the winter when food availability may have a greater influence on raptor survival than during the breeding season. Experimental manipulations of food availability are logistically challenging, but we believe they are necessary to answer conclusively questions regarding food limitation and population regulation in birds of prey.

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