AN ABSTRACT OF THE THESIS OF

Katherin L. Haley for the degree of Master of Science in Wildlife Science presented on January 31, 2002. Title: The Role of Food Limitation and Predation on Reproductive Success of Burrowing Owls in Southern California.

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Abstract approved _____

Daniel K. Rosenberg

The temporal and spatial variation in reproductive success exhibited by burrowing owls (*Athene cunicularia hypugaea*) facilitates the testing of mechanisms influencing this parameter. I predicted that food supplementation would increase reproductive success through one of two means: (1) directly, through increasing food availability and decreasing the effects of brood reduction, resulting in higher growth and survival of the youngest owlets, or (2) indirectly, through increasing nest attendance and decreasing predation rates of eggs and owlets, demonstrating the relationship between food availability and nest predation. Food limitation on reproductive success would also be evident if supplementation resulted in increased parental condition.

I tested for the effects of food limitation and predation on the reproductive success of burrowing owls by conducting experimental food supplementation studies at the Sonny Bono Salton Sea National Wildlife Refuge from April - July, 1999 and 2000. Food supplemented nests had higher reproductive success, female condition, owlet growth, and owlet survival, demonstrating direct food limitation at the level of the individual. Male condition was not affected by food supplementation possibly indicating a lack of reproductive costs or a fixed paternal effort due to trade-offs between future survival and reproduction. Nest attendance was greater in supplemented nests although attendance was

not associated with higher reproductive success, probably because predation rates on eggs and owlets were low. In nests not supplemented with food, brood size was reduced through poor growth and survival of later-hatched owlets, suggesting brood reduction is an adaptive response to fluctuating food availability. This study provides strong support for the hypothesis that burrowing owl reproduction is food-limited in the study area.

The Role of Food Limitation and Predation
on Reproductive Success of Burrowing Owls in Southern California.

by
Katherin L. Haley

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Katherin L. Haley, Author

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INTRODUCTION

Avian reproductive success can be affected by a multitude of factors, including food, nest predation, habitat quality, and parental experience or condition. Nest predation and food availability are often the two most influential factors (Ricklefs 1969) and Martin (1992) proposed that these factors have an interacting relationship. Food availability may influence the amount of time parents attend the nest, thus influencing the probability of nest predation (Martin 1992). Time spent foraging is time not spent attending the nest, making the nest more susceptible to predation. This relationship has also been suggested by several researchers studying the effects of food supplementation on reproductive success. Food-supplemented pairs had higher reproductive success, a result of decreased nest predation (Yom-Tov 1974, Högstedt 1981, Ward and Kennedy 1996) or nest parasitism (Arcese and Smith 1988). The change in parental behavior that may have resulted in higher nesting success was not assessed. Without understanding the role of parental behavior, these studies failed to provide evidence for an interacting relationship between food availability and predation (Martin 1992).

Food availability can indirectly affect reproductive success by influencing parental behavior. Ward and Kennedy (1996) attributed the higher reproductive success of food-supplemented northern goshawks (*Accipiter gentilis*) to greater nest attendance because food-supplemented females were more frequently found at the nest. The cause of nestling death further supported this hypothesis; nestlings from nests without

supplemental food were more often preyed upon. Likewise, Yom-tov (1974) found that food supplementation to nesting carrion crows (*Corvus corone*) decreased the number of nestlings preyed upon by conspecifics, a response attributed to the greater nest attendance of food-supplemented pairs.

Food supplementation experiments have demonstrated that reproductive success can be directly influenced by food availability because energetic constraints often limit the number of young a pair can raise (Boutin 1990). Species with asynchronous hatching respond to food supplementation by raising more young, due to less brood reduction (Arcese and Smith 1988). Asynchronous hatching results in a hierarchy among siblings, thus facilitating brood reduction; older nestlings are most likely to be fed and survive, whereas younger nestlings survive only when food availability is high (Lack 1954, Ricklefs 1965). Brood reduction is often correlated with decreased growth and survival of later-hatched young (Osorno and Drummond 1995, but see Krebs 1999), a pattern which is thought to ensure efficient brood reduction because the parents do not allocate resources to young that are unlikely to survive (Husby 1986). If food limitation exists, supplemental food should reduce the effects of brood reduction, resulting in higher growth and survival of younger nestlings.

I investigated the effects of supplemental food on components of reproductive success for western burrowing owls (*Athene cunicularia hypugaea*). Burrowing owls exhibit temporal and spatial variation in reproductive success, with 0 - 10 young raised per nesting attempt (Haug, Millsap, and Martell 1993), thus facilitating testing causal factors. I predicted that food supplementation would increase reproductive success

through one of two means: (1) directly, through increasing food availability and decreasing the effects of brood reduction, resulting in higher growth and survival of the youngest owlets, or (2) indirectly, through increasing nest attendance and decreasing predation rates on eggs and owlets, demonstrating the relationship between food availability and nest predation. Either result would be strong support for the hypothesis that food can limit reproductive success in this species.

METHODS

STUDY SPECIES AND AREA

The western burrowing owl is a small, burrow-nesting raptor that inhabits grasslands, deserts, and agricultural areas throughout western North America (Haug, et al. 1993). Burrowing owls lay large clutches (avg. 7 - 9, range 4 - 12 eggs [Bent 1938, Haug et al. 1993]) that hatch asynchronously within a span of up to 7 days (Wellicome 2000, Rosenberg and Haley, in press). Like other asynchronously hatching species, brood reduction has been documented in the burrowing owl (Botelho 1996, Wellicome 2000). Reproductive success in burrowing owls is often dynamic due to variation in food, weather conditions, and nest predation (Green and Anthony 1989, Wellicome 2000). Burrowing owls actively defend nests against potential predators and conspecifics (Botelho 1996) and males are thought to actively guard the nest (Coulombe 1971). These characteristics make the burrowing owl ideally suited to test the relationship between food availability and nest predation.

The study area was located on the Sonny Bono Salton Sea National Wildlife Refuge and adjacent land in southeastern California (33°1'N. 115°3'W). The habitat was characterized by agricultural fields that were framed by an irrigation system. Burrowing owl nesting habitat was primarily limited to the linear tracts of land between irrigation systems, roads, and fields (Rosenberg and Haley, in press). The owls included in this study nested in constructed boxes ("artificial burrows;" for description see Trulio 1995). In 1999, pairs nesting in natural nests outside of the Refuge boundary were also included.

FOOD SUPPLEMENTATION EXPERIMENT

After clutch completion, I assigned nests to food-supplemented (treatment) or non-supplemented (control) groups alternately, with the initial assignment determined randomly. Each week I checked nest chambers with an infrared probe (Sandpiper Technologies, Manteca, CA). Once eggs were seen, I checked the nest chamber at four-day intervals. A clutch was defined as complete when the number of eggs did not increase during 72 hours (normal laying interval is 36 hours; Botelho 1996).

Nests in the treatment group were supplemented with dead laboratory-bred mice in excess of the energy requirements for all the individuals in a nest. I estimated the energy requirements of adults and owlets based on Wijnandts (1984) estimates for long-eared owls (*Asio otus*). The allometric equation for BMR of Strigiformes is $BMR = 1.435\ M_b^{0.759}$, where M_b is body mass in grams and BMR is basal metabolic rate in kJ/day (Wijnandts 1984). I estimated an average mass of 160 g for adult burrowing owls (Haley, unpub. data), which resulted in an estimated average BMR of 67.57 kJ/day. Wijnandts (1984) estimated that the energy requirements of long-eared owls were 2.6 X BMR for females during the incubation and brood-rearing periods and 2.7 X BMR and 3.0 X BMR for males during the incubation and brood-rearing periods, respectively. Thus, I used the same multiples of BMR to estimate the energy requirements of adult burrowing owls during incubation and brood-rearing. For owlets, I estimated daily energy expenditure (DEE) as 73% of the estimate for long-eared owlets, as the BMR of adult burrowing owls was 73% of the BMR of long-eared owls (Wijnandts 1984). The amount of mice (g/day) that I used to supplement treatment nests was calculated by dividing the DEE for all the

individuals in a nest (kJ/day) by the caloric content (CC) of the mice after accounting for the metabolizable energy coefficient (MEC) of the mice (average MEC = 0.77, average CC = 8.0 kJ/g [Wijnandts 1984]).

Due to the inaccessibility of natural nests, I estimated the number and age of owlets to calculate the amount of supplemental food to provide. I used clutch size as a liberal estimate of the number of owlets in a nest. The age of owlets was estimated based on hatch date of the first owlet. I monitored nests with the infrared probe at 2-day intervals, beginning 3 weeks after clutch completion until newly-hatched owlets were observed (approx. incubation period 23 days; Botelho 1996). For supplementation purposes, all of the owlets were assigned the same age as the oldest owlet in the nest.

Every day (1999) or every other day (2000), I provided supplemental food to nests in the treatment group. Food supplementation began within 7 days of clutch completion. Mice were placed in the nest entrance, ensuring that only the intended owls would receive the food, as burrowing owls actively defend nest sites from conspecifics (Coulombe 1971). Control nests were visited for the same amount of time to account for disturbance effects. I assumed that all treatment nests were food-supplemented in excess of their energy requirements because partially eaten mice were often found in the entrance and inside the nest. I ceased feeding owls at unsuccessful nests once failure was determined. I gradually decreased food supplementation at the end of the study to avoid the effect of an immediate change in food supply.

REPRODUCTIVE SUCCESS

To estimate reproductive success, I monitored nests from clutch completion to the date owlets were 28 d post-hatch or the nest failed. I ceased monitoring at 28 days of age because owlets can move into nearby natural burrows after this age. Nests were monitored with an infrared probe during incubation and by opening the box during brood-rearing. Natural nests were not monitored for success during incubation but were monitored during brood-rearing through observations of the nests with binoculars or a spotting scope from a vehicle at a distance of ≥80 m.

I included hatching success (eggs hatched/eggs laid), the proportion of eggs that survived to 28 d owlets, and productivity (number of owlets alive at 28 d) in the analysis of reproductive success. Productivity was further estimated as number of owlets/nest attempt and number of owlets/nest that hatched ≥1 owlet. The latter estimate of productivity excludes nests that failed during the incubation period. I suspected that failure during incubation was influenced by different mechanisms than failure during post-hatching, so I separated these periods in order to better understand factors that may be influential. For natural nests, productivity was estimated as the maximum number of owlets 20 - 28 d post-hatch seen simultaneously during four 30-min observation periods.

These parameters of reproductive success were examined for differences between treatment groups and year. Hatching success and the proportion of hatchlings that survived to 28 d owlets were evaluated with logistic regression. Productivity was evaluated with analysis of variance. Prior to analysis, I developed a suite of models with a combination of treatment and year as explanatory variables. I also included a null model

where only an intercept was estimated, allowing for the possibility of no treatment or year

effects. Models were compared with an information-theoretic approach (see Model

Selection).

NEST ATTENDANCE

I observed nests to estimate attendance rates during incubation and brood-rearing.

I observed nests 3 times per week for 30 min each time. Observations were completed

during a 5-hr period that began one-half hour after sunset (typically 2000 to 0100 hours).

I observed the nest from a vehicle at a distance ≥ 80 m with binoculars and a spotlight

(Able2 Products, SHO-ME 100 M CP Spotlight). The light did not appear to disturb the

owls' behavior. I considered a nest attended if an adult was in the nest or within 10 m of

the nest entrance. If only one member of the pair was seen throughout any 30-min

observation period, I used the infrared probe to determine whether the nest chamber was

occupied. During incubation, nest attendance was estimated as the proportion of time

both adults were present, because the female was incubating and food supplementation

would only be expected to alter the male's behavior, unless the female was not receiving

adequate food (Martin 1987). During brood-rearing, attendance was the proportion of

time either sex was present because both were expected to forage for the young (Haug et

al. 1993) and treatment might alter the behavior of both adults.

Because early nest failure during either the incubation or brood-rearing periods

caused an unequal sampling duration of nest attendance among nests, I evaluated the

effect of missing data prior to analysis. A temporal effect on nest attendance could bias

the estimated nest attendance rate for nests that failed early. Depending on the direction of the temporal effect, these early failing nests could have higher or lower estimates of nest attendance than nests that were sampled throughout the entire period. Plots of nest attendance through time, however, did not show any relationship and thus I assumed that missing data from nests that failed early resulted in negligible bias.

I examined annual and treatment group differences for nest attendance in both the incubation and brood-rearing periods with analysis of variance. I used analysis of variance weighted by the number of observations to account for the different number of observations among nests. I developed models *a priori* that allowed nest attendance to differ by year, treatment, or both factors. I also included a null model for evaluation of no differences in nest attendance between years or treatment groups.

GROWTH

I estimated growth rate by measuring owlets every 3 days (1999) or every other day (2000) from hatching to 28 d post-hatch. I measured mass to the nearest 0.1 g and tarsus and wing chord length to the nearest 0.1 mm. Newly-hatched owlets were banded with elastic thread or plastic-coated wire, which did not cause abrasion to the tarsus and could be adjusted as the owlets grew. I also clipped a nail on each owlet to identify it from the other owlets in the nest. Once the tarsi were sufficiently long (approx. 10 - 14 d post-hatch), I banded owlets permanently with a U.S. Fish and Wildlife Service aluminum band (No. 4) and with an alpha-numeric rivet band (Acraft Sign and

Nameplate Co., Ltd., Edmonton, Alberta, Canada). Growth could not be estimated for

owlets at natural nests due to the inaccessibility of the nest chambers.

I ranked owlets according to hatching sequence in order to compare growth rates

between treatment groups for first- and last-hatched owlets. The differences in growth

between treatments in these hatch orders would most effectively provide evidence for the

effects of brood reduction. Frequently more than one owlet hatched on the same day;

therefore, I estimated hatch rank based on body measurements. Owlets with greater mass

and tarsus or wing chord length were assigned an older rank than smaller owlets.

Growth rate was estimated as the slope of the linear regression of mass on age.

Plots of mass on age showed that a linear function was a useful approximation of most

owlets' growth although a few individuals deviated from this pattern. Deviation from a

linear rate could bias estimates of treatment effects on growth rates. In particular, owlets

that died soon after hatching may have had a higher growth rate than owlets measured

over the entire time interval if growth rate declined with age. Growth rates for individuals

that died were not higher than those that lived (mean $\pm$ SE; lived: 4.11 ± 0.21, n $= 27$;

died: 3.89 ± 0.85, n $= 14$); thus, I assumed growth rates from owlets that died early

resulted in negligible bias.

For both first- and last-hatched owlets, the effect of year and treatment group on

growth rate was evaluated with analysis of variance. Before analysis, I developed a set of

models that included a combination of year and treatment as explanatory variables. I also

evaluated variables that may have confounded growth rate: hatch rank relative to brood

size and brood size over time. Hatch rank relative to brood size was included because

owlets originated from broods of different sizes and growth of an individual could be influenced by brood size. For example, a first-hatched owlet in a brood of eight would be given a hatch rank relative to brood size value of 0.125. I also included brood size over time, which I defined as the rate of loss of owlets over time for each nest. I estimated rate of loss as the slope of the regression of brood size from hatching to 4 weeks of age, based on estimates of brood size at weekly intervals. Owlets from nests with a high rate of owlet loss (large negative slope of brood size over time) may grow at a faster rate because the energy requirements of the brood are reduced and parents may be able to supply food at a higher rate to the remaining owlets. I also included a null model to allow for no effects.

PARENTAL CONDITION

I evaluated adult body condition after the owlets hatched and after the female was first regularly seen outside of the nest (ca. 5 days post-hatch). Adults were captured with spring-net traps (Rosenberg and Haley, in press) and two-way burrow traps (Botelho and Arrowwood 1995). I recorded sex, mass, tarsus, and wing chord length.

I examined differences in parental condition between treatment groups and years with linear regression. Analyses were performed separately for males and females to account for the sexual differences in parental roles. The response variable was mass and the explanatory variables included tarsus and wing chord length to account for variation in body size (Brown 1996) and a combination of treatment group and year. Models without treatment or year were also included to account for no differences due to these

factors. In addition, analyses were performed with and without the covariate of average age of owlets. As adults were captured when their owlets were different ages, it was necessary to evaluate this factor as a possible confounding variable.

OWLET SURVIVAL

I used mark-recapture data to estimate the survival rate of owlets from hatching to 28 d post-hatch. Nest boxes were opened every 3 days (1999) or every other day (2000) to ascertain if owlets were alive, dead, or missing. Missing owlets were assumed dead on the first day missing if they were not seen for a duration of 3 days with at least 4 observations, either visual nest observations or opening the nest box, after the disappearance. Because I had extensive knowledge of these nests and never observed owlets presumed dead based on these criteria at a later date, I considered the criteria sufficient.

I performed an analysis to test whether owlet recapture probabilities were similar between treatments, as I was interested in relative survival between treatment groups, not actual survival. Similar recapture probabilities would allow me to exclude this parameter, thereby increasing precision of the estimates (Skalski and Robson 1992). I fit modified Cormack-Jolly-Seber models to the capture history of all owlets with Program MARK (White and Burnham 1999). I allowed survival and recapture probability to vary by treatment, age, or a linear relationship with age (age trend). A linear relationship with age would show that probability of survival increased or decreased as the owlets aged. I also included models that allowed for an additive relationship between treatment and age and

interactive relationships with treatment and age, either as age-specific or as a linear relationship. Each year was analyzed separately due to the difference in sampling interval between years.

I used known fate models to evaluate factors affecting survival (White and Burnham 1999) because recapture probability was high and similar between treatments (0.96 vs. 0.99). The capture histories of owlets that were temporarily missing but later found alive were modified to reflect their survival (n = 9 owlets). Data from 1999 and 2000 were combined and survival from hatch to 28 d was estimated at 4-day intervals. I allowed survival to vary by treatment, year, age, or as a linear relationship with age. I also included models that allowed for both an additive and an interactive relationship between treatment, year, and a linear relationship with age. In a similar analysis, I evaluated the influence of growth rate on survival. These analyses were performed separately because I was not able to estimate growth rate for all owlets and hence analyses had different sample sizes. In addition to the models included in the survival analysis described previously, I included models with growth rate (g/d) as an explanatory variable. Both analyses included a null model in the suite of models considered to account for similar survival rates among all individuals.

I evaluated cause of owlet death to distinguish brood reduction from predation. In order to increase the probability of finding owlet remains if brood reduction occurred, I collected pellets during each visit to the nest in 2000. Other researchers have found evidence of owlet remains in pellets, including feathers, bones, and bands, when brood reduction occurred (Wellicome 2000). I also performed a test to estimate the probability

of finding bands in pellets. Fifty bands were placed on mice and fed to members of a nest

that were not included in the food supplementation experiment, but were fed similarly to

the food-supplemented nests. I estimated the probability of finding bands in pellets as the

proportion of bands found in pellets collected 10 days after the last supplementation of

banded mice.

MODEL SELECTION

For all analyses, a set of models was developed *a priori* in order to evaluate

factors influencing the response variable. All models considered for each analysis are

referenced in tables within the Results section. For most analyses, the fit of the most

parameterized (global) model was assessed by adding interaction terms to the model

(extra sum of squares F-test, Ramsey and Shafer 1997). If the model with interaction

terms was not a significant (p≥0.10) improvement, I assumed the global model without

interaction terms fit the data. Excluding interactions kept the number of models I assessed

small; this was important because too many models or overly-complex models could not

be supported by small sample sizes (Burnham and Anderson 1998). For logistic

regression with individual covariates, I used the Hosmer and Lemeshow goodness of fit

test (Allison 1999). I also used χ^2 goodness of fit tests to assess model fit (Allison 1999).

Goodness of fit was p≥0.10 unless reported otherwise.

Akaike's information criteria with small sample bias adjustment (AICc) was used

to evaluate each set of models (Burnham and Anderson 1998). I ranked models with this

information-theoretic approach according to their ability to explain the data relative to the

suite of models considered (Franklin 2000). AIC model selection allowed me to consider

multiple models in analyses and provided a means to assess the strength of evidence

between models (Burnham and Anderson 1998). Akaike weights (w_i), a relative measure

of the likelihood of the model from the set of models considered, estimated the

uncertainty in the models used for inferences (Burnham and Anderson 1998). Models

best supported by the data have the lowest AICc and the highest Akaike weight. Although

all models were considered for inferences, competing models, defined as models with an

AICc value close to the lowest, were given the most consideration.

RESULTS

REPRODUCTIVE SUCCESS

Food supplementation influenced several parameters of reproductive success between treatments and years. Hatching success (hatchlings/egg laid) differed between groups (Table 1), although the large variance combined with small sample size resulted in weak evidence for a treatment effect (Table 2). The apparent treatment effect was in part due to one food-supplemented nest that failed for reasons other than nest predation or food supply. All of the eggs in this nest failed to develop. Exclusion of this nest resulted in little (6%) difference in hatching success between treatments as well as selection of the year effect model over the treatment effect model. This supports the lack a treatment effect on hatching success. Predation was a cause of failure but appeared to be unrelated to treatment; predation occurred at one treatment and one control nest in 1999 and one treatment nest in 2000. Partial hatching failure within a nest comprised the remainder of egg losses.

The proportion of hatchlings that survived to 28 d post-hatch owlets varied by year and treatment (Table 1). The differences between groups were greater in 1999, the year with the overall lower survival (Table 2). Hatchlings in treatment nests had ca. 55% greater probability of survival to 28 d owlets in 1999 than control nests, although in 2000 the probability of survival was only ca. 25% greater (Table 2).

Food-supplemented nests consistently had higher productivity than control nests, although the pattern was most pronounced in 1999. There was no clear treatment effect

Table 1. Comparison of models relating food supplementation (treatment) and year to different parameters of reproductive success for burrowing owls in 1999 and 2000. Analyses with hatchlings are limited to nest boxes.

Reproductive parameter	Model	k	AICc	ΔAICc	w_i
Hatchlings/egg laid (n = 28)					
	null	2	214.18	2.17	0.16
	treatment	3	212.01	0.00	0.47
	year	3	215.25	3.24	0.09
	treatment + year	4	213.11	1.10	0.27
Owlets 28 d/hatchlings (n = 23)					
	null	2	184.98	25.32	0.00
	treatment	3	166.18	6.52	0.04
	year	3	180.30	20.64	0.00
	treatment + year	4	159.66	0.00	0.96

Note: The model best supported by the data has the lowest AICc and the highest Akaike weight (w_i), a relative measure of the likelihood of the model from the set of models considered (Burnham and Anderson 1998). k is the number of estimable parameters in the model.

Table 2. Comparison of burrowing owl reproductive success between food-supplemented (treatment) and control nests in 1999-2000. Analyses with hatchlings are limited to nests in nest boxes.

		Hatchlings/egg				Owlets 28 d/hatchlings				Owlets 28 d/nest				
Year	Group	n	Mean	SE	Range	n	Mean	SE	Range	n	No. failed	Mean	SE	Range
1999	Treatment	5	0.63	0.17	0.0 - 1.0	6	0.72	0.19	0.20 - 1.0	8	2 (25%)	3.3	1.0	0 - 7
	Control	6	0.73	0.15	0.0 - 1.0	9	0.15	0.10	0.0 - 0.40	9	3 (33%)	1.7	0.5	0 - 4
2000	Treatment	9	0.70	0.14	0.0 - 1.0	7	0.82	0.10	0.33 - 1.0	9	2 (22%)	3.7	0.9	0 - 7
	Control	8	0.84	0.07	0.5 - 1.0	8	0.55	0.08	0.25 - 0.83	8	0 (0%)	3.4	0.5	1 - 5

Table 2. Continued

	Owlets 28 d/nest ≥1 hatch		
n	Mean	SE	Range
6	4.3	1.0	3 - 7
8	1.9	0.5	2 - 4
7	4.7	0.6	2 - 7
8	3.4	0.5	1 - 5

on productivity when all nest attempts were considered (Table 3), but the pattern was clear for nests with at least one hatchling. There was strong evidence of treatment and year effects on the number of owlets raised in nests that succeeded in hatching at least one egg (Table 3). When including all nest attempts, treatment nests produced 50% more 28 d owlets in 1999 (1.6 more owlets/nest, 95% CI: -0.7 to 3.9) and 10% more owlets in 2000 (0.3 more owlets/nest, 95% CI: -2.0 to 2.6; Table 2) than control nests. In nests with at least one hatchling, the number of owlets in food-supplemented nests was greater than control nests by 56% in 1999 (2.5 more owlets/nest, 95% CI: 0.2 to 4.7) and 28% in 2000 (1.3 more owlets/nest, 95% CI: -0.3 to 3.0; Table 2). Overall, productivity tended to be higher in treatment nests than control nests, particularly in 1999 when productivity was considerably lower for control nests.

NEST ATTENDANCE

Food supplementation increased nest attendance rates during both incubation and brood-rearing (Fig. 1). There was evidence of a treatment effect on nest attendance during incubation, although the null model was competing to explain the data (Table 4). Treatments differed by 5.0% attendance in 1999 (95% CI: -10.0 to 20.0) and 15.0% attendance in 2000 (95% CI: -7.0 to 37.0), with the food-supplemented group having the greater attendance. There was strong evidence of a treatment effect and some evidence of a year effect on nest attendance during brood-rearing (Table 4). Owls from the food-supplemented group attended nests on average 13.0% more of the time than the control nests in both years (95% CI: 0.0 to 26.0 [1999] and 0.0 to 27.0 [2000]; Fig. 1).

Table 3. Comparison of models relating food supplementation (treatment) and year to different parameters of reproductive success for burrowing owls in 1999 and 2000. Productivity is the number of owlets to survive to 28 d post-hatch from all nest attempts and from nest attempts with at least one hatchling, excluding nests that failed during the incubation period.

Reproductive parameter	Model	R^2	k	AICc	ΔAICc	w_i
Productivity of all nests (n = 34)						
	null	0.00	2	58.50	0.00	0.31
	treatment	0.01	3	59.13	0.64	0.23
	year	0.08	3	58.68	0.18	0.28
	treatment + year	0.09	4	59.60	1.10	0.18
Productivity of nests with ≥ 1 hatchling (n = 29)						
	null	0.00	2	44.47	5.00	0.04
	treatment	0.23	3	39.47	0.00	0.49
	year	0.07	3	44.80	5.33	0.03
	treatment + year	0.29	4	39.72	0.25	0.43

Note: The model best supported by the data has the lowest AICc and the highest Akaike weight (w_i), a relative measure of the likelihood of the model from the set of models considered (Burnham and Anderson 1998). k is the number of estimable parameters in the model.

A. Incubation
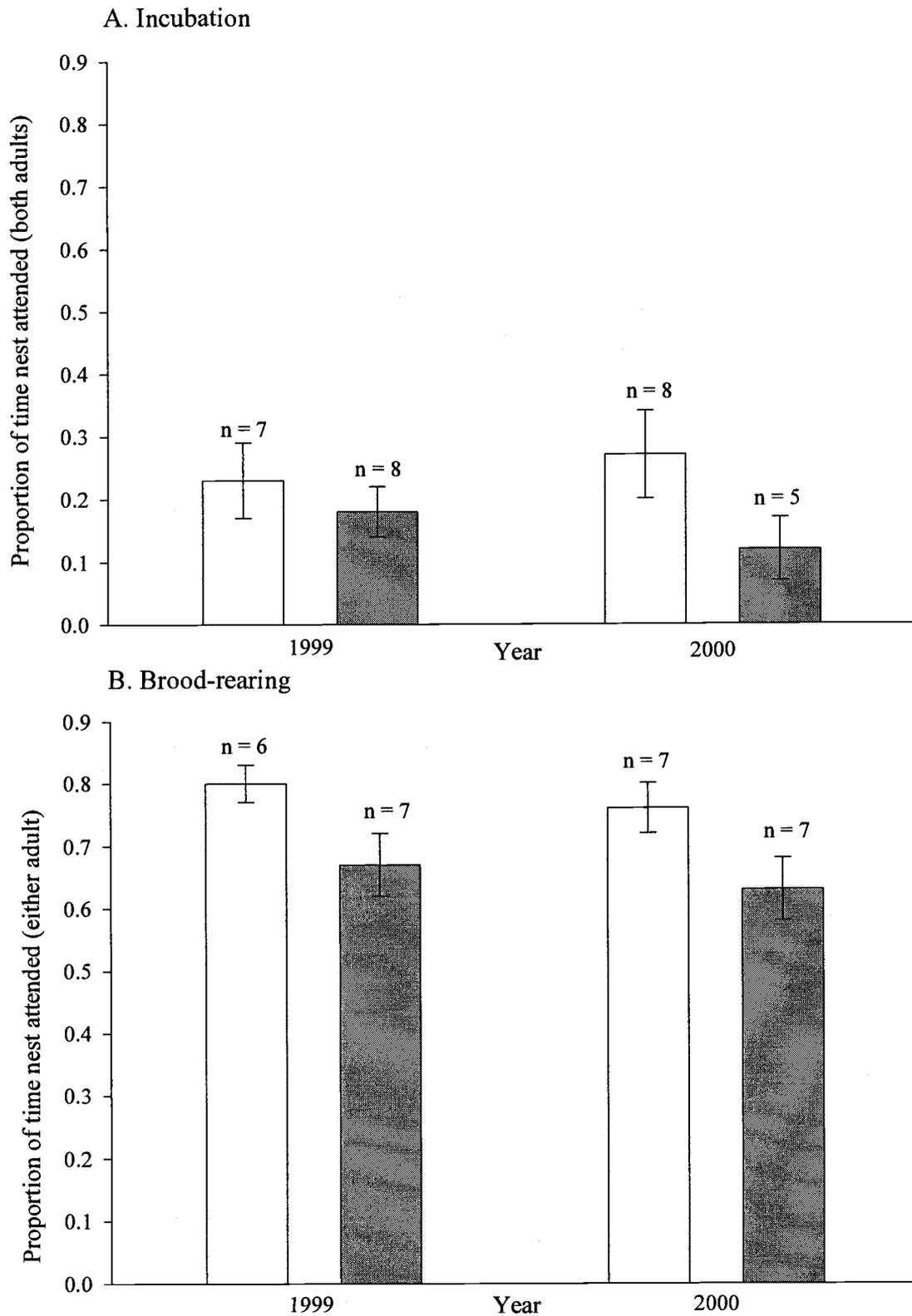
B. Brood-rearing

Figure 1. Mean (± standard error) nest attendance rates for food-supplemented (white) and control (gray) burrowing owls during incubation (A) and brood-rearing (B). Nest attendance rate is the number of minutes a nest was attended during a 30-min observation period.

Table 4. Comparison of models relating food supplementation (treatment) and year to nest attendance in the incubation and brood-rearing periods for burrowing owls in 1999 and 2000.

Stage	Model	R^2	k	AICc	ΔAICc	w_i
Incubation (n = 28)						
	null	0.00	2	-55.84	1.47	0.25
	treatment	0.13	3	-57.31	0.00	0.53
	year	0.00	3	-53.42	3.89	0.08
	treatment + year	0.13	4	-54.59	2.72	0.14
Brood-rearing (n = 27)						
	null	0.00	2	-39.36	4.61	0.06
	treatment	0.23	3	-43.98	0.00	0.59
	year	0.05	3	-38.12	5.86	0.03
	treatment + year	0.28	4	-42.74	1.24	0.32

Note: The model best supported by the data has the lowest AICc and the highest Akaike weight (w_i), a relative measure of the likelihood of the model from the set of models considered (Burnham and Anderson 1998). k is the number of estimable parameters in the model.

GROWTH

Although variation in growth rates among individual owlets was high, treatment influenced growth rates of last but not first-hatched owlets (Fig. 2, Table 5). Growth of first-hatched owlets was similar between treatment groups; owlets in the treatment group grew an average of 0.3 g/day less in 1999 (95% CI: -5.5 to 4.9) and 0.9 g/day less (95% CI: -1.8 to 0.1) in 2000 than the control nests. Growth rates of last-hatched owlets, however, differed by year and treatment (Table 5). Growth rates of food-supplemented last-hatched owlets were 0.4 g/day greater in 1999 (95% CI: -2.2 to 3.1) and 3.1 g/day greater in 2000 (95% CI: 0.9 to 5.2) than owlets in the control nests. Models that included possible confounding variables (i.e., hatch rank relative to brood size, brood size over time) were not selected as influential on growth rate for either first- or last-hatched owlets (Table 5).

PARENTAL CONDITION

Factors affecting parental condition were sex-specific. Females in the treatment group weighed more after controlling for differences in body size than those in the control group (Fig. 3). There was strong evidence of a treatment and year effect on female mass (Table 6). Females from food-supplemented nests weighed on average 20.1 g more than females from the control nests (95% CI: 10.6 to 29.5). There was also a 15.9 g difference between years in average female body mass, with females in 2000 weighing less (95% CI: -26.0 to -5.7 g). Average age of owlets at the time when adult females were weighed was not influential in model weights (Table 6).

A. First-hatched
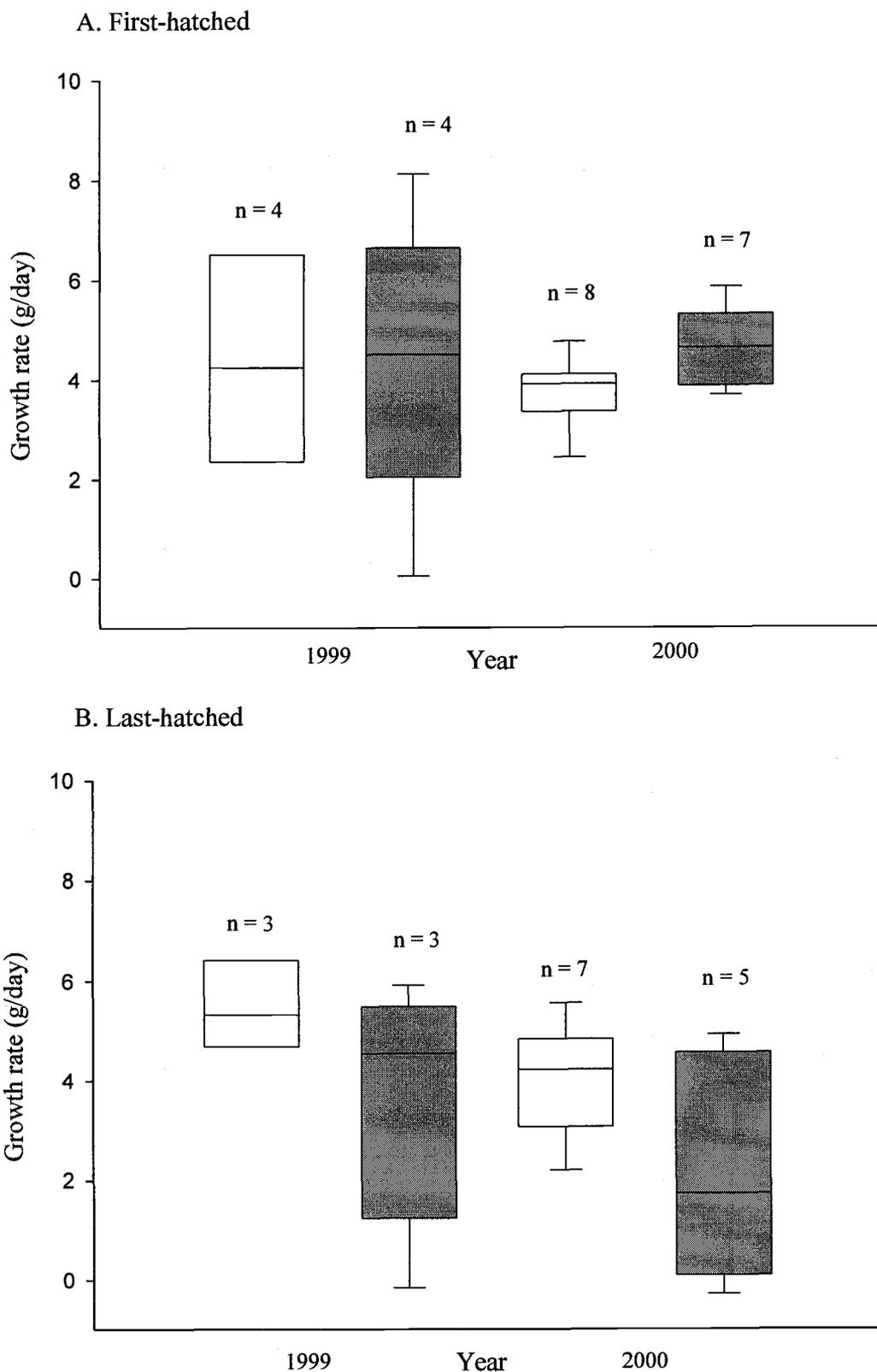
B. Last-hatched

Figure 2. Boxplots of burrowing owl growth rates for first- (A) and last-hatched (B) owlets in food-supplemented (white) and control (gray) nests. The line through the box represents the median growth rate. The tails represent the 5th and 95th percentiles.

Table 5. Comparison of models relating food supplementation (treatment) and year to owlet growth (g day^{-1}) for first- and last-hatched burrowing owlets in 1999 and 2000. Confounding variables are included in the analysis: hatch rank and brood size over time.

Hatch order	Model	R^2	k	AICc	ΔAICc	w_i
First (n = 23)						
	null	0.00	2	29.31	0.00	0.47
	year	0.01	3	31.77	2.47	0.14
	treatment	0.04	3	30.86	1.55	0.22
	treatment + year	0.05	4	33.52	4.21	0.06
	treatment + hatch rank	0.06	4	33.47	4.16	0.06
	treatment + brood size over time	0.05	4	33.70	4.39	0.05
Last (n = 18)						
	null	0.00	2	33.83	8.91	0.01
	year	0.34	3	29.24	4.31	0.10
	treatment	0.19	3	33.06	8.13	0.01
	treatment + year	0.57	4	24.93	0.00	0.87
	treatment + hatch rank	0.20	4	36.13	11.21	0.00
	treatment + brood size over time	0.21	4	35.85	10.93	0.00

Note: The model best supported by the data has the lowest AICc and the highest Akaike weight (w_i), a relative measure of the likelihood of the model from the set of models considered (Burnham and Anderson 1998). k is the number of estimable parameters in the model.

A. Female

B. Male
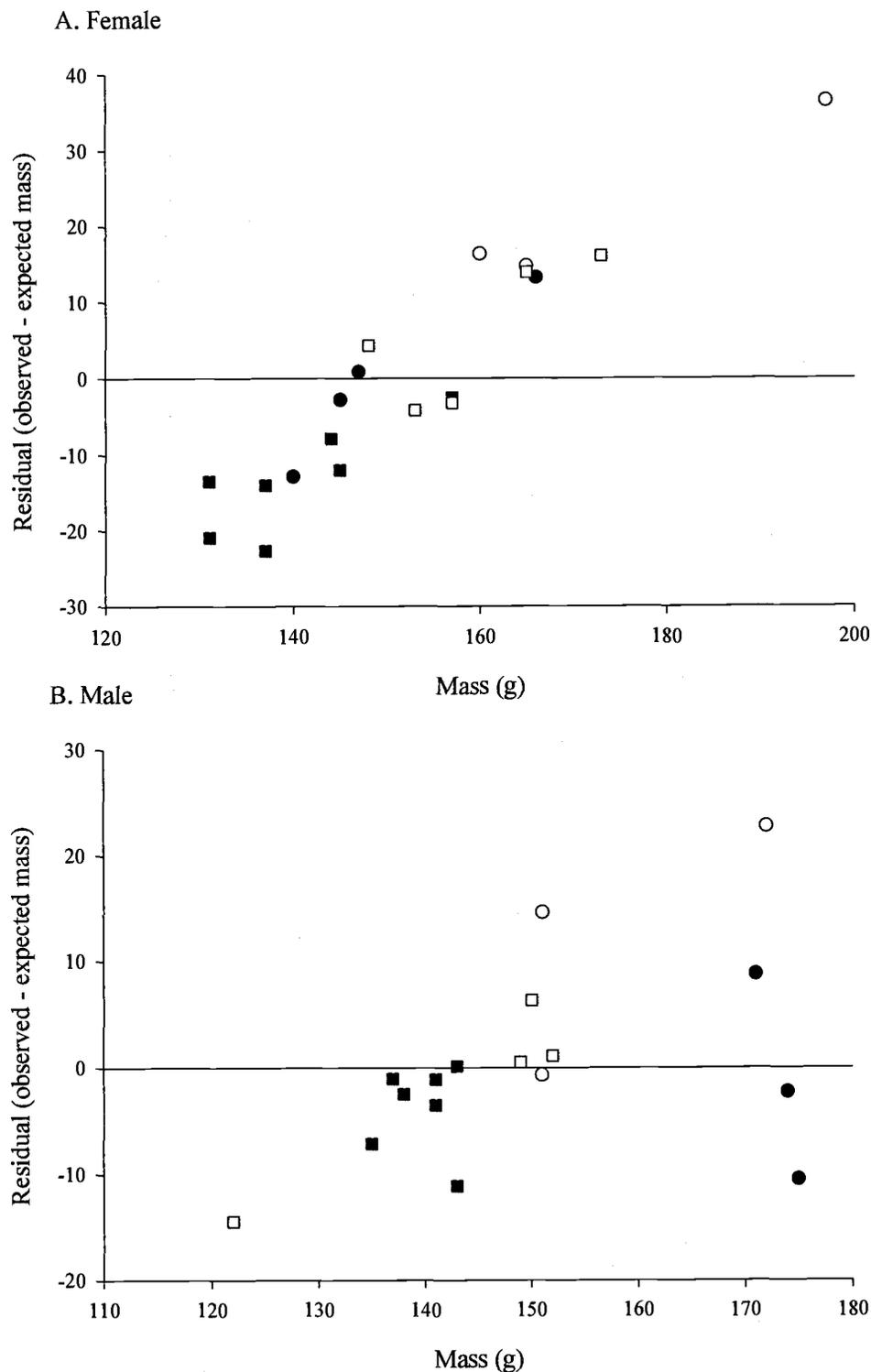
Figure 3. Scatterplots of adult female (A) and male (B) burrowing owl condition in both food-supplemented (unfilled) and control (filled) nests in 1999 (circle) and 2000 (square). Body mass is plotted against the residual (observed mass minus expected mass [mass based on tarsus and wing chord length]). Sample sizes for food-supplemented and control nests, respectively: Female: (1999) n= 3, n=4, and (2000) n=5, n=7; Male: (1999) n=3, n=3, and (2000) n=4, n=7.

Table 6. Comparison of models relating food supplementation (treatment) and year to parental mass for burrowing owls in 1999 and 2000. Average age of owlets at time of capture is included as a confounding variable.

Sex	Model	k	AICc	ΔAICc	w_i
Females (n = 19)					
	mass = tarsus + wing	4	113.47	14.87	0.00
	mass = tarsus + wing + treatment	5	105.42	6.81	0.03
	mass = tarsus + wing + year	5	111.50	12.90	0.00
	mass = tarsus + wing + treatment + year	6	98.61	0.00	0.85
	mass = tarsus + wing + age	5	117.04	18.43	0.00
	mass = tarsus + wing + treatment + age	6	108.48	9.87	0.01
	mass = tarsus + wing + age + year	6	115.85	17.24	0.00
	mass = tarsus + wing + treatment + year + age	7	102.68	4.07	0.11
Males (n = 17)					
	mass = tarsus + wing	4	85.87	0.00	0.25
	mass = tarsus + wing + treatment	5	86.90	1.03	0.15
	mass = tarsus + wing + year	5	86.00	0.13	0.24
	mass = tarsus + wing + treatment + year	6	88.04	2.17	0.09
	mass = tarsus + wing + age	5	87.05	1.19	0.14
	mass = tarsus + wing + treatment + age	6	88.70	2.83	0.06
	mass = tarsus + wing + age + year	6	88.72	2.85	0.06
	mass = tarsus + wing + treatment + year + age	7	91.62	5.76	0.01

Note: The model best supported by the data has the lowest AICc and the highest Akaike weight (w_i), a relative measure of the likelihood of the model from the set of models considered (Burnham and Anderson 1998). k is the number of estimable parameters in the model.

There were no apparent differences in year or treatment for male condition (Table 6), although a few males from the food-supplemented group were heavier than control males (Fig. 3). There was some support for effects of year being influential on male mass, although the null model, which included only factors accounting for body size, was the highest-ranked model (Table 6). Average male mass differed by 8.7 g between years, with males in 2000 weighing less (95% CI: 0.5 to -18.0 g).

OWLET SURVIVAL

Owlet survival rate, estimated as survival from one 4-day age interval to the next, was influenced by hatch order, age, treatment, and year. All first-hatched owlets survived in 2000 (n = 15) and thus they could not be included in analyses. In 1999, first-hatched owlet survival was most strongly influenced by age with no evidence of a treatment effect (Table 7; Fig. 4). There was evidence of a linear relationship of survival with age for last-hatched owlets (Table 7; Fig. 4). The probability of survival for last-hatched owlets increased as they aged. Last-hatched owlets had similar survival between groups in 1999 (survival estimates from model treatment*year; treatment: 0.36, 95% CI: 0.19 to 0.58; control: 0.42, 95% CI: 0.09 to 0.85), whereas survival in 2000 was higher for food supplemented nests (0.72, 95% CI: 0.34 to 0.93) than for control nests (0.02, 95% CI: 0.00 to 0.28).

Table 7. Comparison of models relating food supplementation (treatment) and year to survival of first- and last-hatched owlets for burrowing owls in 1999 and 2000. Survival from hatch to 28 d post-hatch was estimated at 4-day intervals. All first-hatched owlets survived in 2000 and thus were not included in the analysis. The number of parameters was lower than expected for the model with age because all owlets survived at some age intervals and thus survival rate could not be estimated.

Hatch order	Model	Model description	k	AICc	ΔAICc	w_i
First (n = 8)						
	null	Similar among individuals	1	42.28	6.06	0.04
	treatment	Varies by treatment	2	43.69	7.47	0.02
	age trend	Linear function of age	2	44.32	8.11	0.01
	age trend + treatment	Varies by treatment with a common linear age effect	3	45.89	9.67	0.00
	age	Varies by age interval	3	36.21	0.00	0.91
	age trend * treatment	Effect of age is linear and varies by treatment	4	48.20	11.99	0.00
Last (n = 23)						
	null	Similar among individuals	1	134.28	17.13	0.00
	treatment	Different for treatments	2	130.96	13.81	0.00
	year	Different for years	2	131.62	14.47	0.00
	age trend	Linear function of age	2	119.51	2.36	0.15
	treatment * year	Treatment effect varies by year	4	127.52	10.37	0.00
	age trend + treatment * year	Varies by treatment and year, with a common linear age effect	5	117.15	0.00	0.48
	age	Varies by age interval	5	122.45	5.30	0.03
	age trend * treatment * year	Effect of age is linear and varies between treatments and years	8	117.96	0.81	0.33

Note: The model best supported by the data has the lowest AICc and the highest Akaike weight (w_i), a relative measure of the likelihood of the model from the set of models considered (Burnham and Anderson 1998). k is the number of estimable parameters in the model.
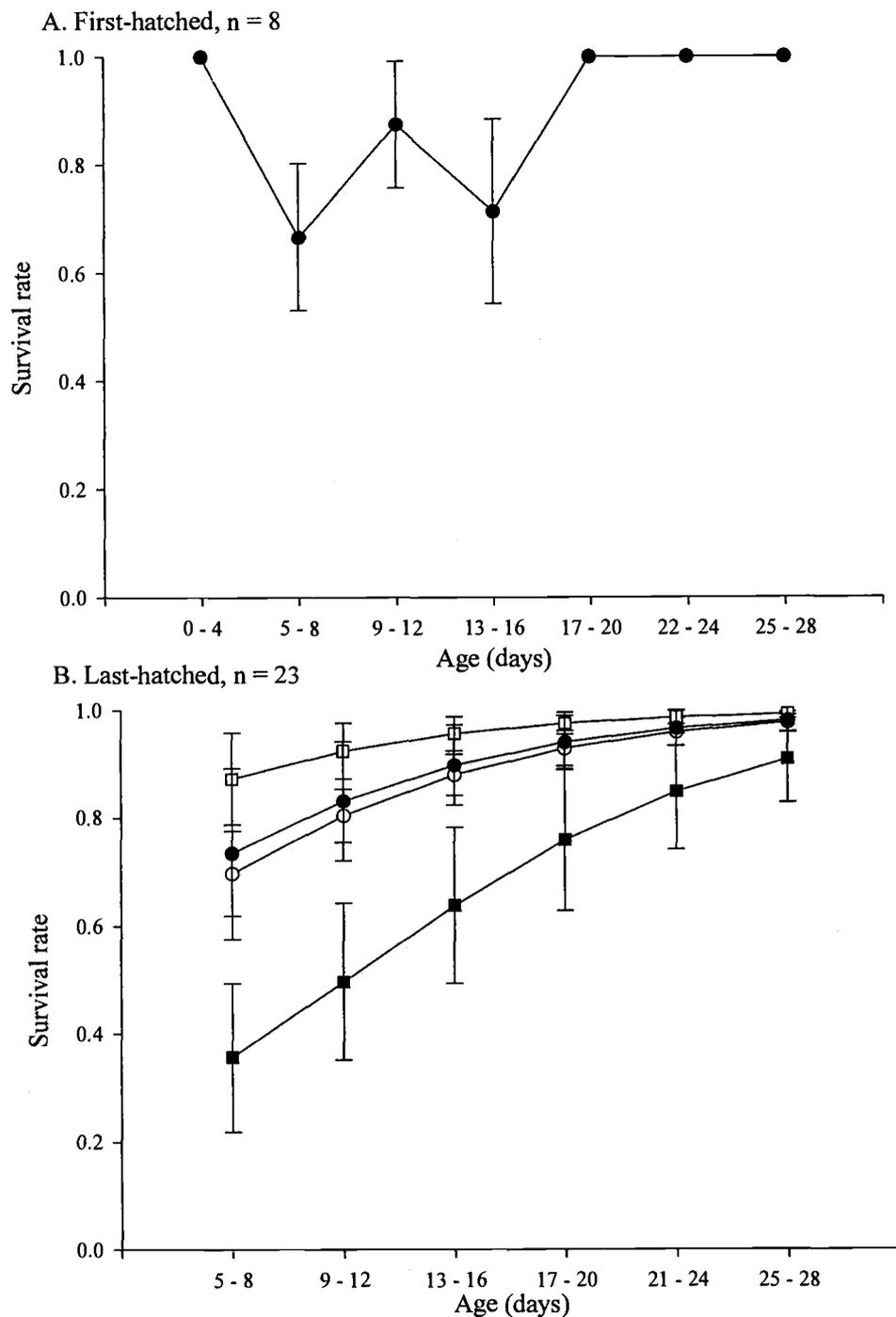
Figure 4. Survival rates estimated as the survival from one age interval to the next for first (A) and last-hatched (B) owlets. Estimates are from the models selected as best through AIC model selection, S (age) for first-hatched owlets and model S (age trend+treatment*year) for last-hatched owlets. The survival probability for last-hatched owlets increased as they aged. For last-hatched owlets, food-supplemented (unfilled) and control (filled) owlets in 1999 (circle) and 2000 (square) are represented.

I found little support for the hypothesis that survival was associated with growth rates of either first or last-hatched owlets. As with the previous analyses, age, treatment, year, and a linear relationship with age were influential for survival of first and last-hatched owlets (Table 8).

A total of 49 owlets died of various suspected causes (Table 9). Mortality of food-supplemented owlets was low in both years; the primary causes for owlet mortality were predation and exposure. Owlet predation occurred at few nests in either treatment group and therefore was most likely a chance event and unrelated to treatment. As predicted, brood reduction was the primary cause of death for owlets from control nests. Because owlet carcasses were rarely found, death from brood reduction was determined by the pattern of weight change prior to death. Control owlets showed weight loss or declines in weight gain prior to death (n = 15). The death of an additional 15 control owlets and one treatment owlet that died before they could be measured more than once was attributed to brood reduction. These owlets were frequently the last- or penultimate-hatched of the brood a pattern that follows the brood reduction strategy.

My attempt to identify owlets lost to brood reduction by finding remains of owlets in pellets was not successful. From the bands placed on mice and fed to owls, I found the probability of detecting a band in pellets was very low (4%). There was some evidence of owlet feathers in pellets but owlet bands were never found. Furthermore, it was difficult to distinguish burrowing owl remains from the remains of other birds in pellets. Birds can be an important component of burrowing owl diets in this area and occur frequently in pellets (Rosenberg and Haley, in press).

Table 8. Comparison of models relating growth rate, food supplementation (treatment), and year to survival of first- and last-hatched owlets for burrowing owls in 1999 and 2000. Survival from hatch to 28 d post-hatch was estimated at 4-day intervals. All first-hatched owlets survived in 2000 and thus were not included in the analysis. The number of parameters was lower than expected for the model with age because all owlets survived at some age intervals and thus survival rate could not be estimated.

Hatch order	Model	Description of survival	k	AICc	ΔAICc	w_i
First (n = 8)	null	Similar among individuals	1	42.28	6.06	0.04
	treatment	Varies by treatment	2	43.69	7.47	0.02
	growth rate	Varies by growth rate	2	41.40	5.18	0.06
	age trend	Linear function of age	2	44.32	8.11	0.01
	age trend + treatment	Varies by treatment with a common linear age effect	3	45.89	9.67	0.01
	treatment + growth	Varies by treatment with a common effect of growth rate	3	43.67	7.46	0.02
	age trend * treatment	Effect of age is linear and varies by treatment	4	48.20	11.99	0.00
	age	Varies by age interval	3	36.21	0.00	0.83
Last (n = 16)	null	Similar among individuals	1	78.44	2.39	0.08
	treatment	Different for treatments	2	79.55	3.50	0.04
	year	Different for years	2	78.54	2.48	0.08
	age trend	Linear function of age	2	78.46	2.41	0.08
	growth rate	Varies by growth rate	2	80.41	4.36	0.03
	treatment * year	Treatment effect varies by year	3	76.05	0.00	0.27
	growth rate + year	Varies by year with a common effect of growth rate	3	80.21	4.16	0.03
	growth rate + treatment	Varies by treatment with a common effect of growth rate	3	81.62	5.57	0.02
	age trend + treatment * year	Varies by treatment and year with a common linear age effect	4	76.89	0.84	0.18
	growth rate + treatment * year	Varies by treatment and year with a common growth rate effect	4	78.10	2.04	0.10
	age	Varies by age interval	5	82.30	6.25	0.01
	age trend * treatment * year	Effect of age is linear and varies by treatment and year	6	78.32	2.27	0.09

Note: The model best supported by the data has the lowest AICc and the highest Akaike weight (w_i), a relative measure of the likelihood of the model from the set of models considered (Burnham and Anderson 1998). k is the number of estimable parameters in the model.

Table 9. Number and causes of mortality for owlets in food-supplemented (treatment) and control burrowing owl nest boxes, 1999-2000. Sample size represents number of nests. The percentage of owlets that died is a minimum because only owlets with known fate were included.

Year	Group	n	No. owlets			Cause of mortality			
			Total	Known fate	Died	Predation	Exposure	Brood reduction	Unknown
1999	Treatment	4	20	18	5 (28%)	3 (60%)	0 (0%)	1 (20%)	1 (20%)
	Control	5	27	24	21 (88%)	6 (28%)	0 (0%)	14 (67%)	1 (5%)
2000	Treatment	7	39	39	6 (15%)	1 (17%)	4 (67%)	0 (0%)	1 (17%)
	Control	8	49	48	21 (44%)	1 (5%)	2 (9%)	17 (81%)	1 (5%)

DISCUSSION

RELATIONSHIP BETWEEN FOOD LIMITATION AND PREDATION

Food supplementation resulted in greater nest attendance by burrowing owls

during both incubation and brood-rearing. Other avian studies have also shown that food

supplementation altered parental behavior. Wiehn and Korpimäki (1997) found that food

supplementation decreased prey delivery rate and hunting effort in female Eurasian

kestrels (*Falco tinnunculus*), although reproductive success was still higher for the food-

supplemented pairs. In contrast, Boland, Heinsohn, and Cockburn (1997) found that food-

supplemented white-winged choughs (*Corcorax melanorhamphos*) increased feeding

rates to nestlings, which also resulted in increased reproductive success. Although the

nestlings were rarely fed the supplemental food, the addition of food increased the

foraging effort of the parents and indirectly resulted in more food provisioned to

nestlings. These studies demonstrated how food supplementation changed parental

behavior, although the increase in reproductive success was not always attributable to the

change in behavior.

Nest attendance was altered by food supplementation in the present study, but

attendance was not conclusively associated with increased hatching success as evident

from the similar success between the groups. Similar to other studies of burrowing owls

(Botelho 1996, Wellicome 2000), partial hatching failure was common with at least one

egg of most clutches failing to hatch. Predation on eggs occurred infrequently (9% of

nests) and always resulted in the loss of all eggs in a clutch. Additional causes of hatching

failure may have been due to inexperience of either or both members of a pair, although this factor is difficult to assess. Causes of individual variation in reproductive success have been investigated in other species of birds (e.g., Wendeln and Becker 1999 for common terns), although causes may be difficult to assess for the burrowing owl because it is a comparatively short-lived species.

Reproductive success was also not associated with increased nest attendance during the brood-rearing period. Had nest attendance been influential, I would have expected owlet mortality as a result of predation to be higher in the control group due to lower parental nest attendance. Owlet mortality due to predation was infrequent (9% of owlets, 5 nests) and appeared to be unrelated to treatment, although there are several issues that may confound this finding. First, reported predation rates are only minimums because a few causes of owlet death remain unknown. Also, I suspect predation-related mortality was underestimated when owlets were very young; it is doubtful that remains would be detectable. Likewise, certain predators (e.g., snakes) would leave little evidence of their presence. Further confounding this issue, starvation may make nestlings more vulnerable to predation by resulting in behaviors, e.g., increased begging, that increase the likelihood of detection by a predator (Newton 1998). As weight loss prior to death was one of my criteria for determining a death that resulted from brood reduction, death from predation could have been incorrectly attributed to brood reduction. I think any underestimation of predation would be slight, however, because it was frequently the last- and penultimate-hatched owlets that died, a pattern that follows the brood reduction strategy.

Three experimental studies have provided evidence for the relationship between food and predation proposed by Martin (1992). In these studies, parental behavior changed in response to food supplementation, resulting in increased reproductive success through decreased predation rates. In a colony of lesser black-backed gulls (*Larus fuscus*), Bukaciński, Bukacińska, and Spaans (1998) found that food-supplemented females decreased the length of feeding trips and increased feeding rates to chicks. The decreased amount of time when chicks could wander into an adjacent pair's territory lowered predation rates on food-supplemented chicks. Simons (1988) found that food-supplemented cactus wren (*Campylorhynchus brunneicapillus*) pairs increased nest defense and were more responsive to a model of a predator. She attributed the lower predation rates for the food-supplemented nests to these factors. Soler and Soler (1996) found that food supplementation increased the density of jackdaw (*Corvus monedula*) nests. This increase in density was coupled with increased nest attendance and increased group defense, which deterred predation by ravens.

Dewey and Kennedy (2001) found results similar to the present study; food-supplemented female northern goshawks (*Accipiter gentilis*) increased nest attendance, but predation on nestlings was very low in both treatment and control nests. They attributed their inability to detect a relationship between food availability and nest predation to several factors, including the stochastic nature of nest predation. The low level of predation also confounded finding a relationship between food availability and nest predation in this study. But given that food-supplemented nests had higher nest

attendance rates, predation would presumably be lower if burrowing owls were able to defend their nests from potential predators.

FOOD LIMITATION ON REPRODUCTIVE SUCCESS

Food limitation was evident as reproductive success was positively influenced by supplemental food. Wellicome (2000) also found positive effects of supplemental food on the number of owlets burrowing owls were able to raise. Owlets from control nests often died of brood reduction through cannibalism or starvation (Wellicome 2000). In addition, he found that food supplementation increased the size of owlets at fledging. In Newton's (1998) review of food supplementation studies, all studies that supplemented food during the brood-rearing stage resulted in increased number of young produced. It is particularly interesting that, although the number of young raised always increased, the weight or growth rate of young did not always increase.

Low nestling growth rate is often reported as evidence of food limitation (Newton 1998). In this study, growth of first-hatched owlets in both treatment groups was similar, but growth of last-hatched owlets was higher for food-supplemented than for control nests in both years. This difference in growth rate can best be explained by the brood reduction strategy frequently employed by burrowing owls. A within-brood hierarchy in body size was evident in this study (Rosenberg and Haley, in press), and sibling competition probably resulted in poor growth of last-hatched owlets from control nests. In food-supplemented nests, the satiation of the first-hatched owlets probably permitted the last-hatched to receive food, resulting in higher growth rates. Similar to this study,

Boland et al. (1997) found that first-hatched chough nestlings in both food-supplemented and control nests were similar in weight, but last-hatched nestlings in control nests had lower weights than those in food-supplemented nests. They found that food-supplemented parents selectively fed the last-hatched nestlings. In contrast, Krebs (1999) found that nestling growth in crimson rosellas (*Platycercus elegans*) did not differ with hatching order but later-hatched nestlings were more likely to die. Krebs cited parental refusal to feed certain nestlings, not food limitation as a result of sibling competition, as the cause of nestling death because many nestlings died before receiving any feedings. It is unknown in the present study whether last-hatched owlets were selectively fed or if it was the satiation of the older owlets that allowed the younger owlets to be fed. Regardless, it is clear from the low growth rates that the last-hatched owlets from control nests did not receive adequate food.

Similar to growth rates, survival of last-hatched owlets from control nests was very low, particularly 2000, whereas the survival of first-hatched owlets was comparable to the food-supplemented nests. It is evident that food limitation was responsible for the lower survival of the owlets from control nests. In contrast, Stoleson and Beissinger (1997) found little difference in survival of last-hatched nestlings between supplemented and control nests. Rather than food limitation as a mechanism, they attributed the equivalent survival to unequal food distribution that resulted from a size hierarchy among siblings. This hierarchy, a consequence of asynchronous hatching, resulted in a discrepancy in feeding rates among nestlings; earlier-hatched nestlings were fed daily, whereas later-hatched nestlings would often go a day without feeding. Further

exemplifying the role of hatching asynchrony in reproductive success, Wiebe and

Bortolotti (1995) found that, of food-supplemented nests, later-hatched nestlings from

asynchronously hatched nests had a lower survival than nestlings from synchronous

nests. Like Stoleson and Beissinger (1997), they cited unequal food distribution as a

result of sibling competition, not food limitation, as the cause of the poor survival.

Although unequal food distribution may play an important role in brood reduction, I

hypothesize that food limitation, not a hierarchy among siblings, is the proximate cause

of the low survival of last-hatched owlets in the control nests. Hatching asynchrony and a

within-brood size hierarchy was evident in this study (Rosenberg and Haley, in press),

but supplemental food increased survival for both first- and last-hatched owlets. This

hypothesis would best be tested by an experiment similar to that of Wiebe and Bortolotti

(1995), where both hatching pattern and food were manipulated.

Despite the lower growth and survival of last-hatched owlets from control nests, I

found little evidence of an effect of growth rate on survival. This finding may be the

result of the high variation in growth rates and my inability to include in this analysis

several owlets that died early. Consistent with the brood reduction strategy, studies of

hatching asynchrony have found lower growth and survival of last-hatched nestlings

(Lago, Johnson, and Albrecht 2000). Nisbet, Spendelow, and Hatfield (1995) found that

survival of roseate tern *(Sterna dougallii)* chicks was influenced by growth rate and hatch

order; first-hatched chicks had high growth rates and survival, whereas second-hatched

chicks had lower growth rates and survival. They attributed the survival of

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second-hatched chicks to parental quality. Higher quality parents laid larger eggs and laid earlier in the breeding season.

Food limitation was also supported because female condition was positively affected by supplemental food. It is well known that the sexes often carry out different roles in raising young and incur different costs in reproduction (Moreno 1989). Different gender roles may explain why female condition was strongly affected by supplemental food but not male condition. Only female burrowing owls incubate and brood young. Shortly after hatching, the female joins the male in foraging for the owlets (Haug et al. 1993). Moreno (1989) suggested that females have a time trade-off between self-maintenance and brooding or feeding young. As a result of this trade-off, females may experience mass loss and depend on fat reserves when raising young. Wijnandts (1984) found that successful parental care in long-eared owls (*Asio otus*) was dependent upon the female maintaining fat reserves until the young hatched. Although I did not measure change in mass over the incubation and brood-rearing periods, food-supplemented females were heavier than expected for their size in comparison to control females. Thus, supplemental food allowed females to maintain better body condition.

Male condition was not related to food supplementation, year, or age of the brood. Other studies also have found that males did not respond to supplemental food. Garcia, Merkle, and Barclay (1993) found that the mass of male mountain bluebirds (*Sialia currucoides*) did not change under different levels of food supplementation, a finding they attributed to the lack of reproductive costs for males. Moreno (1989) suggested that males do not experience mass loss because there is no trade-off between survival and

reproduction as in females. Wiehn and Korpimäki (1997) found that males did not adjust their parental effort, as measured by hunting effort and prey delivery rates, or increase mass in response to supplemental food. They hypothesized that males may be working at an optimum level that maximizes fitness regardless of current food availability. They cited unpredictable food conditions and hence, unpredictable survival of young as the primary reason for males to work at a level that promotes their own future survival. Either of these two hypotheses may describe my findings, although further information about future reproduction and survival would be needed to test these hypotheses.

CONCLUSION

This investigation provided experimental evidence for the role of food limitation in reproductive success of burrowing owls. Brood sizes were reduced through the poor growth and survival of later-hatched owlets in control nests, suggesting that brood reduction is an adaptive response to a fluctuating environment. I did not find evidence for a relationship between food availability and nest predation, a relationship that may have been obscured by low predation rates on both eggs and owlets. Food supplementation influenced parental condition for females but not for males, possibly reflecting different gender roles in raising young. The results of this study emphasize the importance of food supply as a factor affecting reproductive success via brood reduction.

LITERATURE CITED

Allison, P.D. (1999) Logistic Regression using the SAS System: Theory and Application. SAS Institute Inc., Cary, North Carolina.

Arcese, P. & Smith, J.N.M. (1988) Effects of population density and supplemental food on reproduction in song sparrows. Journal of Animal Ecology, 57, 119-136.

Bent, A.C. (1938) Life histories of North American birds of prey. U.S. National Museum Bulletin, No. 170.

Boland, C.R.J., Heinsohn, R. & Cockburn, A. (1997) Experimental manipulation of brood reduction and parental care in cooperatively breeding white-winged choughs. Journal of Animal Ecology, 66, 683-691.

Botelho, E.S. (1996) Behavioral ecology and parental care of breeding western burrowing owls (*Speotyto cunicularia hypugaea*) in southern New Mexico. PhD dissertation, New Mexico State University, Las Cruces, New Mexico, USA.

Botelho, E.S. & Arrowwood, P.C. (1995) A novel, simple, safe, and effective trap for burrowing owls and other fossorial animals. Journal of Field Ornithology, 66, 380-384.

Boutin, S. (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Canadian Journal of Zoology, 68, 203-220.

Brown, M.E. (1996) Assessing body condition in birds. Current Ornithology, vol. 13 (eds V. Nolan, Jr. and E. D. Ketterson), pp 67-135. Plenum Press, New York.

Bukaciński, D., Bukacińska, M. & Spaans, A.L. (1998) Experimental evidence for the relationship between food supply, parental effort and chick survival in the lesser black-backed gull *Larus fuscus*. Ibis, 140, 422-430.

Burnham, K.P. & Anderson, D.R. (1998) Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, New York, USA.

Coulombe, H.N. (1971) Behavior and population ecology of the burrowing owl, *Speotyto cunicularia*, in the Imperial Valley of California. Condor, 73, 162-176.

Dewey, S.R. & Kennedy, P.L. (2001) Effects of supplemental food on parental-care strategies and juvenile survival of northern goshawks. Auk, 118, 352-365.

Franklin, A.B., Anderson, D.R., Gutiérrez, R.J. & Burnham, K.P. (2000) Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs, 70, 539-590.

Garcia, P.F.J., Merkle, M.S. & Barclay, R.M.R. (1993) Energy allocation to reproduction and maintenance in mountain bluebirds (*Sialia currucoides*): a food supplementation experiment. Canadian Journal of Zoology, 71, 2352-2357.

Green, G.A. & Anthony, R.G.(1989) Nesting success and habitat relationships of burrowing owls in the Columbia Basin, Oregon. Condor, 91, 347-354.

Haug, E.A., Millsap, B.A. & Martell, M.S. (1993) Burrowing owl (*Speotyto cunicularia*). The Birds of North America, No. 61 (eds A. Poole and F. Gill). Philadelphia: The Academy of Natural Sciences; Washington, D. C.: The American Ornithologists' Union.

Högstedt, G. (1981) Effects of additional food on reproductive success in the magpie (*Pica pica*). Journal of Animal Ecology, 50, 219-229.

Husby, M. (1986) On the adaptive value of brood reduction in birds: experiments with the magpie *Pica pica*. Journal of Animal Ecology, 55, 75-83.

Krebs, E.A. (1999) Last but not least: Nestling growth and survival in asynchronously hatching crimson rosellas. Journal of Animal Ecology, 68, 266-281.

Lack, D. (1954) The Natural Regulation of Animal Numbers. Oxford University Press, Oxford.

Lago, K., Johnson L.S. & Albrecht, D.J. (2000) Growth of late-hatched, competitively disadvantaged nestling House Wrens relative to their older, larger nestmates. Journal of Field Ornithology, 71, 676-685.

Martin, T.E. (1987) Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics, 18, 453-487.

Martin, T.E. (1992) Interaction of nest predation and food limitation in reproductive strategies. Current Ornithology, vol. 9 (ed D. M. Power), pp 163-197. Plenum Press, New York.

Moreno, J. (1989) Strategies of mass change in breeding birds. Biological Journal of the Linnean Society, 37, 297-310.

Newton, I. (1998) Population Limitation in Birds. Academic Press, Inc., San Diego.

Nisbet, I.C.T., Spendelow, J.A. & Hatfield, J.S. (1995) Variations in growth of roseate tern chicks. Condor, 97, 335-344.

Osorno, J.L. & Drummond, H. (1995) The function of hatching asynchrony in the blue-footed booby. Behavioral Ecology and Sociobiology, 37, 265-273.

Ramsey, F.L. & Schafer, D.W. (1997) The Statistical Sleuth: A Course in Methods of Data Analysis. Duxbury Press, California.

Ricklefs, R.E. (1965) Brood reduction in the curve-billed thrasher. Condor, 67, 505-510.

Ricklefs, R.E. (1969) An analysis of nesting mortality in birds. Smithsonian Contributions in Zoology, 9, 1-48.

Rosenberg, D.K. & Haley, K.L. In press. The ecology of burrowing owls in the agroecosystem of the Imperial Valley, California. Studies in Avian Biology.

Simons, L.S. (1988) Experimental studies in the reproductive ecology of cactus wrens. PhD dissertation, Arizona State University, Tempe, Arizona.

Skalski, J.R. & Robson, D.S. (1992) Techniques for Wildlife Investigations: Design and Analysis of Capture Data. Academic Press, Inc., San Diego.

Soler, M. & Soler, J.J. (1996) Effects of experimental food provisioning on reproduction in the jackdaw, *Corvus monedula*, a semi-colonial species. Ibis, 138, 377-383.

Stoleson, S.H. & Beissinger, S.R. (1997) Hatching asynchrony, brood reduction, and food limitation in a Neotropical parrot. Ecological Monographs, 67, 131-154.

Trulio, L.A. (1995) Passive relocation: a method to preserve burrowing owls on disturbed sites. Journal of Field Ornithology, 66, 99-106.

Ward, J.M. & Kennedy, P.L. (1996) Effects of supplemental food on size and survival of juvenile northern goshawks. Auk, 113, 200-208.

Wellicome, T.I. (2000) Effects of food on reproduction in burrowing owls (*Athene cunicularia*) during three stages of the breeding season. PhD dissertation, University of Alberta, Edmonton, Alberta.

Wendeln, H. & Becker, P.H. (1999) Effects of parental quality and effort on the reproduction of common terns. Journal of Animal Ecology, 68, 205-214.

White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. Bird Study, 46 Supplement, 120-138.

Wiebe, K.L & Bortolotti, G.R. (1995) Food-dependent benefits of hatching asynchrony in American kestrels (*Falco sparverius*). Behavioral Ecology and Sociobiology, 36, 49-57.

Wiehn, J. & Korpimäki, E. (1997) Food limitation on brood size: experimental evidence in the Eurasian kestrel. Ecology, 78, 2043-2050.

Wijnandts, H. (1984) Ecological energetics of the long-eared owl (*Asio otus*). Ardea, 72, 1-92.

Witter, M.S. & Cuthill, I.C. (1993) The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences, 340, 73-92.

Yom-Tov, Y. (1974) The effects of food and predation on breeding density and success, clutch size and laying date of the crow (*Corvus corone* L.). Journal of Animal Ecology, 43, 479-498.