J. Raptor Res. 47(4):365–376

INFLUENCE OF FOOD LIMITATION ON REPRODUCTIVE PERFORMANCE OF BURROWING OWLS

KATHERIN L. HALEY[1]
Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331 U.S.A.

DANIEL K. ROSENBERG[2]
Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331 U.S.A., and Oregon Wildlife Institute, Corvallis, OR 97339 U.S.A.

ABSTRACT.—Reproductive strategies of birds are shaped by patterns of food supply, yet empirical evidence of the consequences and mechanisms of food limitation on reproductive performance is inconsistent, probably due to variable responses from species of differing life-history strategies. We tested the hypothesis that food supplementation would increase reproductive rates of a nonmigratory population of Burrowing Owls (*Athene cunicularia*) via direct and indirect pathways. We predicted increasing food availability would directly increase growth and survival of the youngest nestlings and would indirectly decrease predation rates of eggs and nestlings by increasing nest attendance. We experimentally supplemented food from clutch completion through brood-rearing during two breeding seasons (April–July 1999 and 2000) in the agricultural matrix of the Imperial Valley, in southeastern California. In both years, hatching success (hatchlings/egg laid) was similar between supplemented and non-supplemented nests, but the proportion that survived to 28 d was higher in food-supplemented nests. Growth rates and survival rates of last-hatched young were lower in non-supplemented than supplemented nests in only one year of the study. A greater proportion of hatchling deaths were attributed to starvation in non-supplemented nests. Nest attendance was greater in supplemented nests although low predation for supplemented and non-supplemented nests resulted in no effects on reproductive success. Our results were consistent with the brood-reduction hypothesis that predicts that food supplementation would result in a greater number of fledglings by increasing survival of the youngest nestlings through increased growth rates when hatching asynchrony exists and food is limited.

KEY WORDS: *Burrowing Owl*; Athene cunicularia; *asynchronous hatching*; *brood reduction*; *food limitation*; *nest attendance*; *population ecology*; *reproductive performance*.

INFLUENCIA DE LA LIMITACIÓN DE ALIMENTO EN EL DESEMPEÑO REPRODUCTIVO DE *ATHENE CUNICULARIA*

RESUMEN.—Las estrategias reproductivas de las aves están moldeadas por los patrones de suministro de alimento; sin embargo, la evidencia empírica de las consecuencias y mecanismos de la limitación de alimento en el desempeño reproductivo es inconsistente, probablemente debido a las respuestas variables de especies con estrategias de historias de vida diferentes. Probamos la hipótesis de que la suplementación de alimento incrementa las tasas reproductivas de una población no migratoria de *Athene cunicularia* a través de vías directas e indirectas. Predijimos que el incremento de la disponibilidad de alimento aumentaría directamente el crecimiento y la supervivencia de los pichones más jóvenes y disminuiría indirectamente las tasas de depredación de huevos y pichones al intensificar la atención del nido por parte de los padres. Suplementamos comida experimentalmente desde el final de la puesta y a lo largo la cría de la nidada durante dos épocas reproductivas (abril–julio de 1999 y 2000) en la matriz agrícola del Valle Imperial, en el sureste de California. En ambos años, el éxito de eclosión (pichones eclosionados/huevos puestos) fue similar entre nidos con suplementos y sin él, pero la proporción que sobrevivió 28 días fue superior en los nidos con suplementación de alimento. Las tasas de crecimiento y supervivencia de los pichones que eclosionaron últimos fue menor en los nidos sin suplemento que en los nidos con

[1] Present address: Florida Fish and Wildlife Conservation Commission, 620 South Meridian Street, Tallahassee, FL 32399 U.S.A.
[2] Email address: dan@oregonwildlife.org

suplemento en sólo un año del estudio. Una mayor proporción de muertes de pichones recién eclosionados se atribuyó a la inanición en nidos no suplementados. La atención al nido fue mayor en nidos suplementados, aunque la baja depredación en nidos suplementados y no suplementados no tuvo efectos en el éxito reproductivo. Nuestros resultados fueron consistentes con la hipótesis de la reducción de la nidada que predice que la suplementación de alimento resulta en un mayor número de volantones al incrementar la supervivencia de los pichones más jóvenes a través del incremento de las tasas de crecimiento, cuando existe la asincronía de eclosión y el alimento es limitado.

[Traducción del equipo editorial]

Avian food-supplementation experiments have demonstrated that food availability influences reproductive output directly through energetic constraints that limit the number of young that parents can raise (Martin 1987, Boutin 1990, Wiehn and Korpimäki 1997). Food availability may also affect productivity indirectly by limiting the time parents spend attending the nest rather than foraging. The majority of studies on avian reproductive food limitation tested hypotheses on the effects of food availability prior to and through egg-laying (Newton 1998:145, Boutin 1990). Earlier laying, larger eggs, and/or increased clutch size and number of clutches were most commonly reported (Martin 1987, Boutin 1990, Newton 1998:145, Arnold 2011). Food supplementation studies conducted during the nestling period, when energy needs are likely greatest for altricial birds (Walsberg 1983, Monaghan and Nager 1997, Woodburn and Perrins 1997), have reported divergent responses. Not surprisingly, effects were often year-dependent (Simons and Martin 1990, Wiebe and Bortolotti 1995, Ward and Kennedy 1996, Hipkiss et al. 2002), presumably due to changes in food availability (Boutin 1990, Simons and Martin 1990). In most cases, nestlings from food-supplemented nests were larger and had greater nestling survival rates than nestlings from non-supplemented nests (Simons and Martin 1990, Wiebe and Bortolotti 1995, Wiehn and Korpimäki 1997, Hipkiss et al. 2002, Arnold 2011). In other cases, increased reproductive performance during the period of food supplementation was not found. Rather, energy was allocated to the parents' condition, particularly to females (Garcia et al. 1993, Wiehn and Korpimäki 1997, Brommer et al. 2004), through lower provisioning rates from parents to young (Wiehn and Korpimäki 1997, Dawson and Bortolotti 2002). In the case of the long-lived Ural Owl (*Strix uralensis*), food-supplemented females had earlier and larger clutches in the breeding season following the nesting season in which food was supplemented (Brommer et al. 2004).

Food availability can indirectly affect reproductive success by influencing parental behavior. Martin (1992) proposed that nest predation and food limitation have an interactive relationship through effects on nest attendance, which has been empirically demonstrated (Dewey and Kennedy 2001, Chalfoun and Martin 2007, Vergauwen et al. 2012). Time spent foraging is time not spent attending the nest, making the nest more susceptible to predation (Martin 1992). 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. Likewise, because food-supplemented female Northern Goshawks (*Accipiter gentilis*) were more frequently found at the nest in comparison to those not supplemented, Ward and Kennedy (1996) attributed the higher reproductive success of food-supplemented pairs to greater nest attendance. Similarly, Dewey and Kennedy (2001) found greater nest attendance of female Northern Goshawks that were food-supplemented but low predation rates for both food-supplemented and non-supplemented nests prevented them from finding the relationship between food, attendance, and predation proposed by Martin (1992).

We experimentally examined reproductive food limitation on a nonmigratory population of Burrowing Owls (*Athene cunicularia*), a species with high fecundity (as high as 14 eggs/clutch; Todd and Skilnick 2002) and periodic peaks of food supply (Poulin et al. 2001, Gervais et al. 2006). Burrowing Owls exhibit high temporal, spatial, and individual variation in clutch size and in the number of fledglings (0–10 young raised per nesting attempt; Ronan 2002, Gervais and Anthony 2003, Rosenberg and Haley 2004, Wellicome 2005, Conway et al. 2012), will rarely produce second broods (Millsap and Bear 1990, Gervais and Rosenberg 1999), and will frequently nest again following nest failure, with reports of up to four clutches laid within a single nesting season (Catlin and Rosenberg 2008). These

traits, coupled with their relatively low annual survival rate (e.g., 0.6; Rosenberg and Haley 2004), suggests the optimal strategy may be one of high allocation of energy toward maximum number of young in a given year. Clutches of Burrowing Owls hatch asynchronously, independent of food supply, within a span of up to 8 d (Wellicome 2000, 2005; Haley 2002, Rosenberg and Haley 2004, Conway et al. 2012) and as in other asynchronously hatching species, partial-brood loss is common (Botelho 1996, Haley 2002, Rosenberg and Haley 2004, Wellicome 2005). Together, these traits suggest that Burrowing Owls should be sensitive to reproductive food limitation. We predicted that food supplementation during incubation and brood-rearing would increase reproductive performance by decreasing partial-brood loss (*sensu* Mock 1994) via increased growth and survival of the youngest nestlings and by decreasing predation of nestlings via higher parental nest attendance.

METHODS

Study Area. The study was conducted on the Sonny Bono Salton Sea National Wildlife Refuge and adjacent land in southeastern California, U.S.A. (33°1′N, 115°3′W). Agricultural fields framed by an irrigation system consisting of delivery ditches, canals, and drains characterized the landscape. Nesting habitat was primarily limited to the linear tracts of land between irrigation systems, roads, and fields (Rosenberg and Haley 2004). The owls included in this study nested in constructed boxes (''artificial burrows''; for description see Trulio [1995]).

Food Supplementation. We assigned nests to food-supplemented or non-supplemented treatments, alternately by clutch completion date, with the initial assignment determined randomly. Thirty-four nests were included in the study from April through July in 1999 (eight supplemented, nine non-supplemented) and 2000 (nine supplemented, eight non-supplemented). Every day (1999) or every other day (2000), we provided supplemental food to nests in the treatment group. Food supplementation began within 7 d of clutch completion. A clutch was defined as complete when the number of eggs did not increase during 72 hr, which fit most of the patterns of egg-laying intervals reported at our study area (Conway et al. 2012). We supplemented nests in the manipulated group with dead laboratory-bred mice (*Mus musculus*) in excess of the energy requirements for all the individuals in a nest. Haley (2002) estimated the energy requirements of adult and nestling Burrowing Owls, based on Wijnandts' (1984) estimates for Long-eared Owls (*Asio otus*), to be an average of 30 g mouse/day for every owl in the nest. We placed mice in the nest entrance, increasing the likelihood that only the intended owls would receive the food, because Burrowing Owls actively defend nest sites from conspecifics (Coulombe 1971, Fisher et al. 2004). We visited food-supplemented and non-supplemented nests for the same amount of time to account for disturbance effects. We assumed that all manipulated nests were food-supplemented in excess of their energy requirements because numerous partially eaten mice were consistently found in the entrance and inside the nest. Caches of food were rarely found in non-supplemented nests.

Hatching Success and Nest Productivity. To estimate reproductive performance, we monitored nests from clutch completion to the date the youngest nestlings were 28 d post-hatch or the nest failed. We ceased monitoring at 28 d of age because nestlings are capable of short flights (Poulin et al. 2011) and often move into nearby burrows after this age (D. Rosenberg unpubl. data). We monitored nests with an infrared scope (Sandpiper Technologies, Manteca, CA) during incubation and by opening the box during brood-rearing. Measures of reproductive performance included hatching success (eggs hatched/eggs laid) and the proportion of hatchlings that survived to 28 d. We used the proportion of hatchlings rather than the total number of hatchlings to estimate the change in productivity of individual nests because of the large variation in the number of hatchlings/nest in Burrowing Owl nests (Rosenberg and Haley 2004, Poulin et al. 2011). We evaluated food supplementation and year effects with logistic regression models.

Nest Attendance. We observed nests to estimate attendance rates during incubation and brood-rearing. Nests were observed three times per week for a 30-min period each time; the observation periods took place during the time from 0.5 hr after sunset until 5 hr later. We observed nests from a vehicle at a distance ≥80 m with binoculars and a spotlight (Able2 Products, SHO-ME 100 M CP Spotlight, Cassville, Missouri, U.S.A.). The light did not appear to disturb the owls' behavior. We 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 during any 30-min observation period, we used the infrared scope to determine whether the nest chamber was occupied. During incubation, we defined nest attendance as the duration of time both

adults were present because the female was incubating and food supplementation would be expected to primarily alter only the male's behavior. During brood-rearing, we defined nest attendance as the duration of time at least one parent was present because both were expected to forage for the nestlings and supplementation might alter the behavior of both adults. For each nest, the estimate reported is the mean proportion of time the nest was attended during each nesting phase (i.e., incubation and brood-rearing). We evaluated food supplementation and year effects on nest attendance during the incubation and brood-rearing periods with ANOVA models.

Growth Rate. We estimated growth rates because low nestling growth rate is often reported as evidence of food limitation (Newton 1998) and may be more sensitive to food availability than survival rates. We estimated growth rate by weighing nestlings every 3 d (1999) or every other day (2000) from hatching to 28 d post-hatch, prior to when growth is expected to reach an asymptote (>30 d post-hatch; Landry 1979, Olenick 1990). We measured mass to the nearest 0.1 g using a portable digital scale. We banded newly hatched nestlings with elastic thread or plastic-coated wire. We clipped the tip of a talon on each nestling to identify it from the other nestlings in the nest. Once the tarsi were sufficiently long (approx. 10–14 d post-hatch), we banded nestlings with a U.S. Fish and Wildlife Service aluminum band and with an alpha-numeric rivet band (Acraft Sign and Nameplate Co., Ltd., Edmonton, Alberta, Canada).

We ranked nestlings according to hatching sequence. Frequently, more than one nestling hatched on the same day; therefore, we based hatch rank on mass at first measurement. Of those that may have been hatched on the same day, we assigned an older rank to the larger nestling.

We estimated growth rate 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 nestlings' growth for the age span we investigated (Haley 2002). Nestlings that died prior to a second measurement of mass were excluded from the growth analysis. We evaluated hatch rank relative to brood size and brood size through time as factors that may have influenced growth rate. We defined hatch rank relative to brood size as the ratio of the hatching order to brood size (i.e., the rank of a first-hatched nestling would be 1/5 for a brood size of five young). We included this covariate because we expected that different brood sizes would influence growth for first and last-hatched nestlings differently. We estimated brood size over time, defined as the rate of nestling loss over time for each nest, as the slope of the regression of brood size from hatching to 4 wk of age, based on estimates of brood size at weekly intervals. We included this as a covariate in the analysis because nestlings from nests with a high rate of brood loss may grow at a faster rate than predicted from their initial brood size. We evaluated these factors, in addition to food supplementation and year effects, with ANOVA models.

Nestling Survival. We uniquely marked nestlings to estimate age-specific survival from hatching to 28 d post-hatch. We opened nest boxes every 3 d (1999) or every other day (2000) to ascertain if nestlings were alive, dead, or missing. We later pooled observations to a 4-d interval to include both years in the analysis. Missing nestlings were assumed dead on the first day missing (Haley 2002).

We estimated survival with known-fate models in Program MARK (White and Burnham 1999) because recapture probability was high and similar between food-supplemented and non-supplemented nests (0.96 vs. 0.99, Haley 2002), and because we were interested in relative survival between owlets from food-supplemented and non-supplemented nests. Similar recapture probabilities would allow us to exclude this parameter, thereby increasing precision of the estimates (Skalski and Robson 1992). Because there were few ($n = 9$) nestlings that were temporarily missing but later found alive, we modified their capture histories to reflect their survival, which allowed us to use known fate models. We developed models *a priori* that allowed survival to vary by food supplementation, year, age class, or as a linear relationship with age class. We compared models that allowed for both an additive and an interactive relationship between supplementation, year, and a linear relationship with age class, as well as a null model of no effects.

We classified nestling mortality into three presumed causes: exposure, food limitation, and predation. We classified mortality as exposure for nestlings that were consistently found outside of the burrow in a lethargic state prior to death, but that did not show signs of weight loss. We classified the cause of mortality as food limitation when evidence suggested starvation and possible infanticide and/or siblicide. Because nestling carcasses were rarely found, death from food limitation was determined by the pattern of weight change prior to death. We

Table 1. Reproductive performance and nest attendance of Burrowing Owls in food-supplemented and non-supplemented nests during 1999 and 2000, Imperial Valley, California. Hatching success was estimated as the proportion of hatchlings/egg laid; the proportion of nestlings was estimated as the proportion of hatchlings that survived to 28 d; and nest attendance was estimated as the proportion of observations when both adults (during incubation) or at least one adult (during brood-rearing) were observed. Nestlings measured only one time were not included in the growth rate analyses. Sample size (n) is the number of nests.

		Non-supplemented				Supplemented			
Reproductive Parameter	Year	n	Mean	SE	90% CI	n	Mean	SE	90% CI
Hatching success	1999	6	0.71	0.14	0.48–0.94	5	0.63	0.17	0.35–0.91
	2000	8	0.84	0.07	0.72–0.96	9	0.70	0.14	0.47–0.93
Proportion nestlings	1999	5	0.27	0.19	0.0–0.58	4	0.72	0.19	0.41–1.03
	2000	8	0.55	0.08	0.42–0.68	7	0.82	0.10	0.66–0.98
Nest attendance (incubation stage)	1999	8	0.18	0.04	0.11–0.25	7	0.23	0.06	0.13–0.33
	2000	5	0.12	0.05	0.04–0.20	8	0.27	0.07	0.15–0.39
Nest attendance (brood-rearing stage)	1999	7	0.67	0.05	0.59–0.75	6	0.80	0.03	0.75–0.85
	2000	7	0.63	0.05	0.55–0.71	7	0.76	0.04	0.69–0.83
Growth rate (first-hatched)	1999	4	4.71	1.72	1.88–7.54	4	4.44	1.25	2.38–6.50
	2000	7	4.67	0.3	4.18–5.16	8	3.77	0.32	3.24–4.30
Growth rate (last-hatched)	1999	3	5.27	0.40	4.61–5.93	3	5.7	0.87	4.27–7.13
	2000	5	0.93	0.91	−0.57–2.43	7	3.98	0.48	3.19–4.77

classified mortality as predation when there was an obvious disturbance to the nest, which often was accompanied by partially eaten nestlings or feathers near the burrow entrance.

Model Selection. We developed a set of models *a priori* in order to evaluate factors affecting hatching success, proportion of hatchlings that survived to 28 d, nest attendance, and nestling growth and survival (Appendix). We evaluated each set of models with Akaike's Information Criteria with small sample bias adjustment (AICc; Burnham and Anderson 2002). We used Akaike weights (w_i) as a relative measure of the likelihood of the model from the set of models considered (Burnham and Anderson 2002). Models best supported by the data had the lowest AICc and the highest Akaike weight. We report ΔAICc, the difference between AICc of a given model to that of the model with the lowest AICc.

RESULTS

Food supplementation influenced reproductive performance during brood-rearing but not during incubation. Although the best model included supplementation (Appendix), hatching success (hatchlings/egg laid) was similar between supplemented and non-supplemented nests, with extensive overlap between 90% CI's (Table 1). Predation, resulting in the loss of the entire clutch, appeared to be unrelated to supplementation; predation occurred at one food-supplemented and one non-supplemented nest in 1999 and one food-supplemented nest in 2000. Partial hatching failure within a nest, due to unknown causes, made up the majority of reproductive loss at the egg stage, but was unrelated to food supplementation.

The proportion of hatchlings that survived to 28 d was affected by food supplementation and year. Difference of the proportion of hatchlings that survived between food-supplemented and non-supplemented nests was greater in 1999 than in 2000 (Table 1).

Food supplementation tended to increase nest attendance rates. There was only weak evidence of a supplementation effect on nest attendance during incubation (Appendix), with only 13% of the variation explained by the model with treatment effects. Although attendance during incubation at supplemented nests was on average substantially higher in both 1999 and 2000 at supplemented than non-supplemented nests, 90% confidence intervals overlapped (Table 1), providing only weak evidence of effects. However, there was strong evidence of a supplementation effect on nest attendance during brood-rearing (Appendix), with an average 0.13 increase in the proportion of time the nest was attended by at least one adult (Table 1). However, only 23% of the variation was explained by the food-supplemented model; the addition of year in the model only contributing an additional 5% to explained variance.

Food supplementation influenced growth rates of last- but not first-hatched nestlings. Growth of first-hatched nestlings was similar between years and between supplemented and non-supplemented nests. Growth rates of last-hatched nestlings, however, differed by year and food regime (Table 1, Appendix). Growth rates of food-supplemented and non-supplemented last-hatched nestlings were similar in 1999, but in 2000, nestlings from supplemented nests grew an average of 3.1 g/day greater than nestlings in the non-supplemented nests, the latter having very low growth rates in 2000 relative to 1999 (Table 1). Models that included possible confounding variables of hatch rank relative to brood size and brood size over time failed to explain growth rate for either first- or last-hatched nestlings (Appendix). The best model (supplementation and year) explained 57% of the variation for last-hatched nestlings.

Nestling survival rate, estimated as survival from one 4-d age interval to the next, was influenced primarily by hatch order, with age, food supplementation, and year affecting last-hatched nestlings. All first-hatched nestlings survived in 2000. In 1999, first-hatched nestling survival was similar between groups (Fig. 1) and had no clear evidence of other effects (Appendix). The probability of survival for last-hatched nestlings increased as they aged (Fig. 1) and was higher for food-supplemented nests than for non-supplemented nests only in 2000 (Fig. 1). In 2000, survival rates for last-hatched nestlings were particularly low in nests without supplemental food (Fig. 1).

Food limitation was a predominant cause of mortality, although death from exposure and predation occurred (Table 2). Because nestling carcasses were rarely found, death from food limitation was determined by the pattern of weight change prior to death. Nestlings in non-supplemented nests showed weight loss or declines in weight gain prior to death. Food limitation as a cause of mortality included death from starvation, siblicide, or infanticide. The death of an additional 15 nestlings from non-supplemented nests and one nestling from a supplemented nest that died before they could be measured more than once was attributed to food limitation (Table 2). These nestlings were consistently the last- or penultimate-hatched of the brood.

DISCUSSION

Food limited the reproductive performance of Burrowing Owls, which was largely manifested through poor growth and ultimately lower survival of later-hatched nestlings. Young hatched asynchronously, which has been shown to be independent of food supply in Burrowing Owls (Wellicome 2000, 2005) and other species (Kontiainen et al. 2010, Arnold 2011). Hatching asynchrony resulted in variation in nestling size and development that presumably was responsible for the lower growth rates and ultimately higher mortality in last-hatched nestlings in the non-supplemented nests. Food supplementation allowed similar growth rates to occur among nestlings, and resulted in low mortality for nestlings of all hatch ranks. Our findings that growth of first-hatched nestlings in both groups was similar, but growth of last-hatched nestlings was higher for food-supplemented than for non-supplemented nests, suggest that size and/or developmental stage variation within a brood was the proximate cause that contributed to higher survival rates in the supplemented nests. In food-supplemented nests, the satiation of first-hatched nestlings and lower sibling competition for resources probably permitted last-hatched nestlings to receive food, resulting in higher growth rates. Unlike some species that demonstrate food limitation at even high ambient food resource levels (e.g., Eurasian Kestrel [*Falco tinnunculus*; Wiehn and Korpimäki 1997]), food limitation in the non-supplemented nests was most evident in only one of the two years of the study.

Effects of food supplementation on reproductive performance were year-dependent but not consistent among the various parameters we investigated. Annual variation in the magnitude of reproductive food limitation is common (Martin 1987, Boutin 1990, Newton 1998:145). Unlike Simons and Martin (1990) who attributed annual variation of reproductive performance of Cactus Wren (*Campylorhynchus brunneicapillus*) largely to differences in the density of breeding pairs and greater costs of defending territories, we found that density of Burrowing Owls nesting in our study area remained remarkably similar between years (Rosenberg and Haley 2004). Seasonal and annual prey resources can vary considerably in our study area (Rosenberg and Haley 2004), as we observed in cached prey; more bird, rodent, and butterfly remains were found in nests in 2000 than in 1999 (K. Haley unpubl. data). Making interpretation more complex, we failed to find consistent annual patterns in the reproductive parameters we estimated. In general, 1999 had lower numbers of fledged young than in 2000 in non-supplemented nests (Haley 2002) as well as in nests throughout the study area (Rosenberg and Haley 2004). We speculate that this was due to lower ambient food

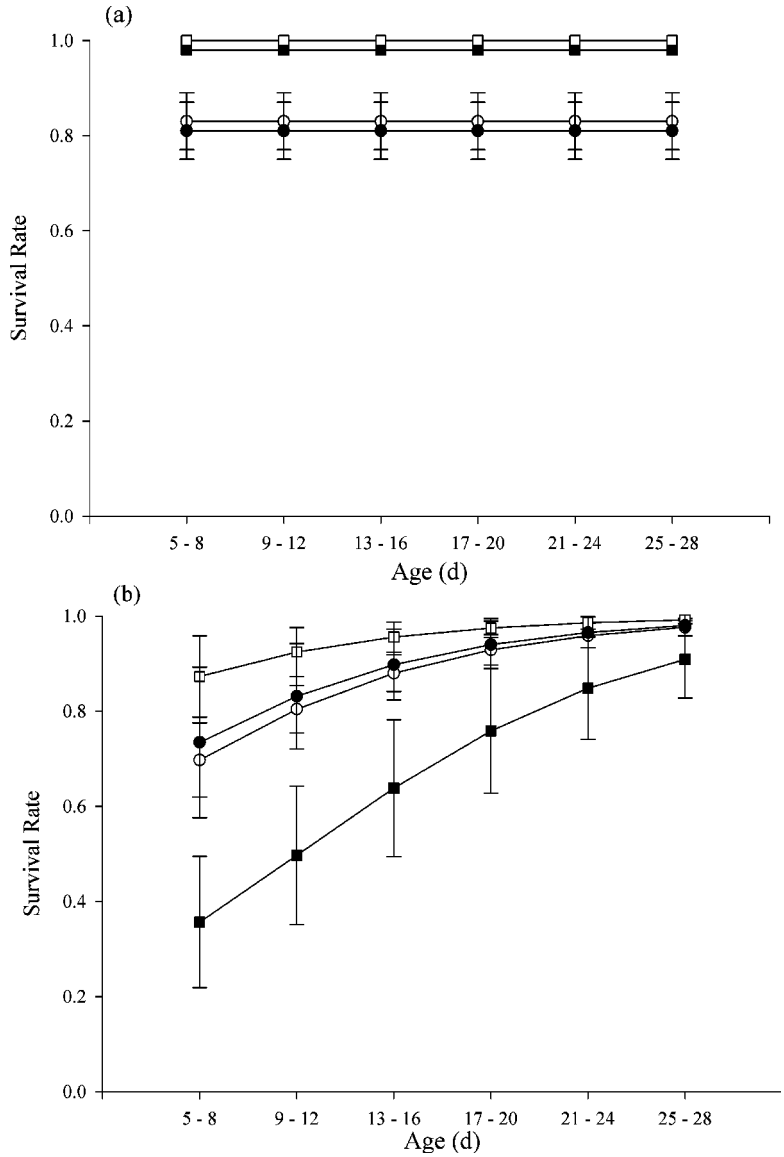

Figure 1. Survival rates estimated as the proportion of Burrowing Owls alive from one age interval to the next for first-hatched nestlings (a) and last-hatched (b) nestlings from food-supplemented (unfilled) and non-supplemented (filled) nests in 1999 (circle) and 2000 (square), Imperial Valley, California. Estimates are from the model of no effects for first-hatched nestlings and age trend + supplementation * year for last-hatched nestlings (Appendix). We also show the function for 100% survival for first-hatched nestlings in 2000. In (A), points are off-set to prevent overlap.

resources in that year. The diet of Burrowing Owls is exceptionally broad at our study area (York et al. 2002, Rosenberg and Haley 2004), making assessments of prey availability difficult. We speculate that non-supplemented last-hatched nestlings had lower survival and lower growth in 2000 than 1999 due to greater food competition of last-hatched nestlings with the larger brood size in 2000. Lower growth rates of last-hatched nestlings was not evident in 1999, potentially due, in part, to overestimating the growth rate in that year for non-supplemented last-hatched nestlings because some individuals

Table 2. Number and suspected causes of mortality for Burrowing Owl nestlings in food-supplemented and non-supplemented nest boxes, 1999–2000, Imperial Valley, California. The percentage of nestlings that died is a minimum because only nestlings with known fate were included. Nestling death attributed to food limitation included nestlings that lost weight or reduced weight gain prior to death or were frequently the last- or penultimate-hatched of the brood. Food limitation as a cause of mortality included death from starvation, siblicide, or infanticide. Sample size (n) is the number of nests.

			Number Nestlings			Cause of Mortality			
Year	Group	n	Total	Known Fate	Died	Predation	Exposure	Food Limitation	Unknown
1999	Supplement	4	20	18	5 (28%)	3 (60%)	0 (0%)	1 (20%)	1 (20%)
	Non-supplement	5	27	24	21 (88%)	6 (28%)	0 (0%)	14 (67%)	1 (5%)
2000	Supplement	7	39	39	6 (15%)	1 (17%)	4 (67%)	0 (0%)	1 (17%)
	Non-supplement	8	49	48	21 (44%)	1 (5%)	2 (9%)	17 (81%)	1 (5%)

died before a second measurement (presumably those with lower growth rates), and thus were excluded from the analysis. Interestingly, concentrations of yolk androgens in Burrowing Owl eggs laid later in the clutch were year-dependent and could affect level of sibling competition for later-hatched nestlings (Welty et al. 2012).

When food limitation on reproduction has been demonstrated during the nestling phase in altricial birds, it is often manifested in the lower survival of later-hatched nestlings when asynchronous hatching occurs. The proximate causes of lower survival differed among studies. As in our study, Stoleson and Beissinger (1997) found last-hatched Green-rumped Parrotlet (*Forpus passerinus*) nestlings had slower growth rates and a lower probability of fledging than first-hatched nestlings. Rather than food limitation as a proximate mechanism, they attributed the lower survival of last-hatched nestlings to unequal food distribution that resulted from a size hierarchy among siblings. In contrast to our study, Wiebe and Bortolotti (1995) and Wiehn and Korpimäki (1997) found that later-hatched American Kestrels (*F. sparverius*) and Eurasian Kestrels had lower mass at fledging and lower nestling survival than earlier-hatched nestlings regardless of food supplementation. Wiebe and Bortolotti (1995) speculated this might have been due to unequal distribution of food among size hierarchies, consistent with numerous studies that demonstrate dominance by siblings (e.g., Parker et al. 1989). Wiehn and Korpimäki (1997) speculated food limitation occurred because of limited availability of prey even at high ambient levels. It was clear from our study that last-hatched nestlings in one year of the study only received sufficient food when the older nestlings were satiated through supplemental feeding. We were unable to determine whether selective feeding of earlier-hatched young by the parents or sibling competition (or both) was responsible for food limitation in last-hatched nestlings in non-supplemented nests. Had a size hierarchy been the proximate cause, we would have expected to find results similar to those of Stoleson and Beissinger (1997) and Wiebe and Bortolotti (1995): low survival of last-hatched nestlings in both food-supplemented and non-supplemented nests. Regardless, it is clear from the low growth rates, lower survival rates, and mortality that was likely due to starvation that last-hatched nestlings from non-supplemented nests did not receive adequate food, likely a result of sibling competition during one of the two years of our study.

Reproductive success was not associated with increased nest attendance during incubation or brood-rearing. Had nest attendance been influential, we would have expected predation of eggs and nestlings to be higher in non-supplemented nests due to the lower parental nest attendance we observed. Predation on eggs occurred infrequently and always resulted in the loss of all eggs in a clutch. Nestling mortality due to predation was infrequent and appeared to be unrelated to food supplementation. As weight loss prior to death was one of our criteria for classifying a death due to brood reduction, death from predation could have been incorrectly attributed to brood reduction. We think any underestimation of predation would be slight, however, because it was consistently the last- and penultimate-hatched nestlings that died, a pattern that follows the brood reduction strategy. Although we did not find any relationship between food and

predation, the mechanism was present: increased food availability resulted in greater nest attendance.

We found that food supplementation increased nest attendance during brood-rearing, but our low predation rates in both food-supplemented and non-supplemented nests did not allow us to evaluate the interaction of food supplementation, nest attendance, and nest predation. In most 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 et al. (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 enter 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 Eurasian Jackdaw (*Corvus monedula*) nests. This increase in density was coupled with increased nest attendance and increased group defense, which deterred predation by Common Raven (*Corvus corax*). Dewey and Kennedy (2001) found results similar to those from our study: food-supplemented female Northern Goshawks (*Accipiter gentilis*) increased nest attendance, but predation on nestlings was very low in both food-supplemented and non-supplemented 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.

Our results, from a nonmigratory population of Burrowing Owls, are consistent with studies from a migratory population from the grasslands of southern Saskatchewan, Canada. Wellicome (1997) initially found that supplementation during the egg-laying period increased clutch and egg volume slightly, but had no effect on hatching success or the number of young fledged. However, the number of young fledged was greater when food was supplemented during the nestling period. Wellicome (2000, 2005) later found that food limitation manifested itself only during the nestling period via greater hatchling size and survival. Because food supplementation from egg-laying through nestling periods had no different response than for owls supplemented only during the nestling period, Wellicome (2005) concluded that laying females were unable to forecast post-hatch food conditions. Rather, the life-history strategies of Burrowing Owls to lay large clutches and create a size hierarchy of nestlings via hatching asynchrony allows for greater productivity when food conditions are sufficient. This has been shown empirically by Gervais and Anthony (2003) when the number of fledglings doubled during a peak vole year. Results from our study of a nonmigratory Burrowing Owl population, coupled with those from a migratory population (Wellicome 1997, 2000, 2005), provide support for the hypothesis that asynchrony in Burrowing Owls maximizes the number of young that fledge in environments with variable and unpredictable prey resources. This strategy allows for a greater number of young with little costs to parents or siblings regardless if asynchrony is an adaptation to increase the number of fledglings or is an outcome from other selective pressures.

ACKNOWLEDGMENTS

We thank J. Gervais, L. Houck, P. Kennedy, D. Roby, N. Ronan, T. Wellicome, and M. York for helpful discussion and comments on the manuscript, K. Hughes, R. Balzer, C. Faustino, P. Phelps, and J. Rosier for their dedicated field assistance, and the staff of the Sonny Bono Salton Sea National Wildlife Refuge for logistic support. We are grateful to the U.S. Fish and Wildlife Service (Non-game Bird Program), Southern Gas, and Cal Energy for financial support. Publication of this paper was supported, in part, by the Thomas G. Scott Publication Fund. This study was conducted as a part of the Burrowing Owl Research Program, including The Institute for Bird Populations, Oregon Wildlife Institute, Oregon State University, and San Jose State University.

LITERATURE CITED

ARNOLD, T.W. 2011. An experimental study of fledging success in American Coots (*Fulica americana*): effects of brood size, food availability, and hatching asynchrony. *Auk* 128:737–745.

BOTELHO, E.S. 1996. Behavioral ecology and parental care of breeding Western Burrowing Owls (*Speotyto cunicularia hypugaea*) in southern New Mexico. Ph.D. dissertation, New Mexico State University, Las Cruces, NM U.S.A.

BOUTIN, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology* 68:203–220.

BROMMER, J.E., P. KARELL, AND H. PIETIÄINEN. 2004. Supplementary fed Ural Owls increase their reproductive output with a one year time lag. *Oecologia* 139:354–358.

BUKACIŃSKI, D., M. BUKACIŃSKA, AND A.L. SPAANS. 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. AND D.R. ANDERSON. 2002. Model selection and inference: a practical information-theoretic approach, Second Ed. Springer-Verlag, New York, NY U.S.A.

CATLIN, D.H. AND D.K. ROSENBERG. 2008. Breeding dispersal and nesting behavior of Burrowing Owls following experimental nest predation. *American Midland Naturalist* 159:1–7.

CHALFOUN, A.D. AND T.E. MARTIN. 2007. Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. *Animal Behaviour* 73:579–585.

CONWAY, M., C.P. NADEAU, AND C.J. CONWAY. 2012. Intraspecific variation in reproductive traits of Burrowing Owls. *Journal of Ethology* 30:395–402.

COULOMBE, H.N. 1971. Behavior and population ecology of the Burrowing Owl, *Speotyto cunicularia*, in the Imperial Valley of California. *Condor* 73:162–176.

DAWSON, R.D. AND G.R. BORTOLOTTI. 2002. Experimental evidence for food limitation and sex-specific strategies of American Kestrels (*Falco sparverius*) provisioning offspring. *Behavioral Ecology and Sociobiology* 52:43–52.

DEWEY, S.R. AND P.L. KENNEDY. 2001. Effects of supplemental food on parental-care strategies and juvenile survival of Northern Goshawks. *Auk* 118:352–365.

FISHER, R.J., R.G. POULIN, L.D. TODD, AND R.M. BRIGHAM. 2004. Nest stage, wind speed, and air temperature affect the nest defence behaviours of Burrowing Owls. *Canadian Journal of Zoology* 82:707–713.

GARCIA, P.F.J., M.S. MERKLE, AND R.M.R. BARCLAY. 1993. Energy allocation to reproduction and maintenance in Mountain Bluebirds (*Sialia currucoides*): a food supplementation experiment. *Canadian Journal of Zoology* 71:2352–2357.

GERVAIS, J.A. AND R.G. ANTHONY. 2003. Interactions of chronic organochlorine contaminants and environmental variation in the demographics of a population of Burrowing Owls. *Ecological Applications* 13:1250–1262.

———, C.M. HUNTER, AND R.G. ANTHONY. 2006. Interactive effects of prey and p,p′-DDE on Burrowing Owl population dynamics. *Ecological Applications* 16:666–677.

——— AND D.K. ROSENBERG. 1999. Western Burrowing Owls in California produce second broods of chicks. *Wilson Bulletin* 111:569–571.

HALEY, K.L. 2002. The role of food limitation and predation on reproductive success of Burrowing Owls in southern California. M.S. thesis, Oregon State University, Corvallis, OR U.S.A.

HIPKISS, T., B. HÖRNFELDT, U. EKLUND, AND S. BERLIN. 2002. Year-dependent sex-biased mortality in supplementary-fed Tengmalm's Owl nestlings. *Journal of Animal Ecology* 71:693–699.

KONTIAINEN, P., H. PIETIÄINENA, P. KARELL, T. PIHLAJAB, AND J.E. BROMMER. 2010. Hatching asynchrony is an individual property of female Ural Owls which improves nestling survival. *Behavioral Ecology* 21:722–729.

LANDRY, R.E. 1979. Growth and development of the Burrowing Owl, *Athene cunicularia*. M.S. thesis, California State University, Long Beach, CA U.S.A.

MARTIN, T.E. 1987. Food as a limit on breeding birds: a life history perspective. *Annual Review of Ecology and Systematics* 18:453–487.

———. 1992. Interaction of nest predation and food limitation in reproductive strategies. *Current Ornithology* 9:163–197.

MILLSAP, B.A. AND C. BEAR. 1990. Double brooding by Florida Burrowing Owls. *Wilson Bulletin* 102:313–317.

MOCK, D.W. 1994. Brood reduction: narrow sense, broad sense. *Journal of Avian Biology* 25:3–7.

MONAGHAN, P. AND R.G. NAGER. 1997. Why don't birds lay more eggs? *Trends in Ecology and Evolution* 12:270–274.

NEWTON, I. 1998. Population limitation in birds. Academic Press, Inc., San Diego, CA U.S.A.

OLENICK, B.E. 1990. Breeding biology of Burrowing Owls using artificial nest burrows in southeastern Idaho. M.S. thesis, Idaho State University, Boise, ID U.S.A.

PARKER, G.A., D.W. MOCK, AND T.C. LAMEY. 1989. How selfish should stronger sibs be? *American Naturalist* 133:846–868.

POULIN, R.G., L.D. TODD, E.A. HAUG, B.A. MILLSAP, AND M.S. MARTELL. 2011. Burrowing Owl (*Athene cunicularia*). *In* A. Poole [ED.], The birds of North America online, No. 61. Cornell Lab of Ornithology, Ithaca, NY U.S.A. http://bna.birds.cornell.edu/bna/species/061 (last accessed 21 June 2013).

———, T.I. WELLICOME, AND L.D. TODD. 2001. Synchronous and delayed numerical responses of a predatory bird community to a vole outbreak on the Canadian prairies. *Journal of Raptor Research* 35:288–295.

RONAN, N. 2002. Habitat selection, reproductive success, and site fidelity of Burrowing Owls in a grassland ecosystem. M.S. thesis, Oregon State University, Corvallis, OR, U.S.A.

ROSENBERG, D.K. AND K.L. HALEY. 2004. The ecology of Burrowing Owls in the agroecosystem of the Imperial Valley, California. *Studies in Avian Biology* 27:120–135.

SIMONS, L.S. 1988. Experimental studies in the reproductive ecology of Cactus Wrens. Ph.D. dissertation, Arizona State University, Tempe, AZ U.S.A.

——— AND T.E. MARTIN. 1990. Food limitation of avian reproduction: an experiment with the Cactus Wren. *Ecology* 71:869–876.

SKALSKI, J.R. AND R.S. ROBSON. 1992. Techniques for wildlife investigations: design and analysis of capture data. Academic Press, Inc., San Diego, CA U.S.A.

SOLER, M. AND J.J. SOLER. 1996. Effects of experimental food provisioning on reproduction in the Jackdaw, *Corvus monedula*, a semi-colonial species. *Ibis* 138:377–383.

STOLESON, S.H. AND S.R. BEISSINGER. 1997. Hatching asynchrony, brood reduction, and food limitation in a neotropical parrot. *Ecological Monographs* 67:131–154.

TODD, L.D. AND J. SKILNICK. 2002. Large clutch size of a Burrowing Owl, *Athene cunicularia*, found in Saskatchewan. *Canadian Field Naturalist* 116:307–308.

TRULIO, L.A. 1995. Passive relocation: a method to preserve Burrowing Owls on disturbed sites. *Journal of Field Ornithology* 66:99–106.

VERGAUWEN, J., V.C. GOERLICH, T.G. GROOTHUIS, M. EENS, AND W. MÜLLER. 2012. Food conditions affect yolk testosterone deposition but not incubation attendance. *General and Comparative Endocrinology* 176:112–119.

WALSBERG, G.E. 1983. Avian ecological energetics. Pages 161–220 *in* D.S. Farner, J.R. King, and K.C. Parkes [EDS.], Avian biology, Vol. 7, Academic Press, New York, NY U.S.A.

WARD, J.M. AND P.L. KENNEDY. 1996. Effects of supplemental food on size and survival of juvenile Northern Goshawks. *Auk* 113:200–208.

WELLICOME, T.I. 1997. Reproductive performance of Burrowing Owls (*Speotyto cunicularia*): effects of supplemental food. Pages 68–73 *in* J.L. Lincer and K. Steenhof [EDS.]. The Burrowing Owl, its biology and management including the proceedings of the First International Burrowing Owl Symposium. *Raptor Research Report* 9.

———. 2000. Effects of food on reproduction in Burrowing Owls (*Athene cunicularia*) during three stages of the breeding season. Ph.D. dissertation, University of Alberta, Edmonton, Canada.

———. 2005. Hatching asynchrony in Burrowing Owls is influenced by clutch size and hatching success but not by food. *Oecologia* 142:326–334.

WELTY, J.L., J.R. BELTHOFF, J. EGBERT, AND H. SCHWABL. 2012. Relationships between yolk androgens and nest density, laying date, and laying order in Western Burrowing Owls (*Athene cunicularia hypugaea*). *Canadian Journal of Zoology* 90:182–192.

WHITE, G.C. AND K.P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 Supplement:120–138.

WIEBE, K.L. AND G.R. BORTOLOTTI. 1995. Food-dependent benefits of hatching asynchrony in American Kestrels (*Falco sparverius*). *Behavioral Ecology and Sociobiology* 36:49–57.

WIEHN, J. AND E. KORPIMÄKI. 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.

WOODBURN, R.J.W. AND C.M. PERRINS. 1997. Weight change and the body reserves of female Blue Tits, *Parus caeruleus*, during the breeding season. *Journal of Zoology* (London) 243:789–802.

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.

YORK, M., D.K. ROSENBERG, AND K. STURM. 2002. Diet and food-niche breadth of Burrowing Owls (*Athene cunicularia*) in the Imperial Valley, California. *Western North American Naturalist* 62:280–287.

Received 20 November 2012; accepted 13 June 2013
Associate Editor: Joseph B. Buchanan

Appendix. Comparison of model selection criteria of analyses conducted on Burrowing Owl reproductive performance, nest attendance, growth rates, and nestling survival during 1999–2000, Imperial Valley, California. Model comparisons are shown for (1) logistic regression models on reproductive parameters (hatchlings/eggs laid and proportion of nestlings that survived to 28 days), (2) ANOVA models of nest attendance during the incubation and brood-rearing stages, (3) ANOVA models on nestling growth for first- and last-hatched nestlings, and (4) known fate models of nestling survival of first- and last-hatched nestlings. For growth rate models, hatch rank was estimated as hatch order/brood size, and brood size over time was estimated as the rate of nestling loss over time for each nest. For survival models, the age-trend model allowed a linear trend of age and survival, the age-trend + supplementation allowed survival to vary by food supplementation with a common linear age effect, and the age-trend *supplementation allowed a linear effect of age, the slope of which can vary by whether or not the nest received food supplementation. Year was not included in survival models of first-nestlings because all first-nestlings in 2000 survived. The model best supported by the data has the lowest Δ AICc, and the highest Akaike weight (w_i), where K is the number of estimable parameters in the model, and Δ AICc is the difference in AIC from the model with the lowest value. Models are ordered from best to worst.

PARAMETER	MODEL	K	ΔAIC	w_i
Hatchlings/egg laid (n = 28 nests)	Supp	3	0.0	0.38
	Supp + year	4	0.6	0.29
	Null	2	1.4	0.19
	Year	3	2.0	0.14
Prop. nestlings 28 d (n = 24 nests)	Supp + year	4	0.0	0.87
	Supp	3	3.8	0.13
	Year	3	17.8	0.00
	Null	2	21.3	0.00

Appendix. Continued.

PARAMETER	MODEL	K	ΔAIC	w_i
Nest attendance				
Incubation (n = 28 nests)	Supp	3	0.0	0.53
	Null	2	1.5	0.25
	Supp + year	4	2.7	0.14
	Year	3	3.9	0.08
Brood-rearing (n = 27 nests)	Supp	3	0.0	0.59
	Supp + year	4	1.2	0.32
	Null	2	4.6	0.06
	Year	3	5.9	0.03
Growth rate				
First nestling (n = 23 nestlings)	Null	2	0.0	0.47
	Supp	3	1.6	0.22
	Year	3	2.5	0.14
	Supp + hatch rank	4	4.2	0.06
	Supp + year	4	4.2	0.06
	Supp + brood size over time	4	4.4	0.05
Last nestling (n = 18 nestlings)	Supp + year	4	0.0	0.87
	Year	3	4.3	0.10
	Supp	3	8.1	0.01
	Null	2	8.9	0.01
	Supp + brood size over time	4	10.9	0.00
	Supp + hatch rank	4	11.2	0.00
Hatchling survival				
First nestling (n = 8 nestlings)	Null	1	0.0	0.39
	Age	6	1.4	0.19
	Supp	2	1.4	0.19
	Age trend	2	2.0	0.14
	Age trend + supp	3	3.6	0.06
	Age trend * supp	4	5.9	0.02
Last nestling (n = 23 nestlings)	Age trend + supp*year	6	0.0	0.45
	Age trend	2	0.2	0.41
	Age trend*supp*year	10	3.2	0.09
	Age	6	5.3	0.03
	Supp*year	4	8.2	0.00
	Supp	2	11.6	0.00
	Year	2	12.3	0.00
	Null	1	15.0	0.00