

University of Alberta

Effects of Food on Reproduction in Burrowing Owls (*Athene cunicularia*) During Three Stages of the Breeding Season

By

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ABSTRACT

Food availability is an important limiting factor for avian reproduction. In altricial birds, food limitation is assumed to be more severe during the nestling stage than during laying or incubation, but this supposition has not been adequately tested. I determined both the degree and timing of reproductive food limitation for Burrowing Owls (*Athene cunicularia*) nesting in artificial burrows in southern Saskatchewan (1992–1998).

Day of female arrival correlated closely with laying day, which in turn correlated with clutch size. Effects of food and parental age on clutch size were non-significant when the influence of laying day was controlled for statistically. Mean egg size was also unaffected by food or parental age, and showed no seasonal variation. Pairs supplemented with dead laboratory mice, from clutch-initiation through clutch-completion, stored more prey in caches and regurgitated more food-pellets than did controls with similar laying dates. However, this extra food did not increase clutch or egg size, and did not affect the seasonal decline in clutch size. Similarly, natural and experimental variation in food during laying and incubation had no effect on hatching success or hatching asynchrony. In contrast, post-hatch supplemental feeding had positive effects, increasing size and mass of fledglings and allowing supplemented pairs to raise 47% more offspring than controls. This difference in fledging rates resulted from a much higher frequency of starvation within control broods than within food-supplemented broods. Also, pairs supplemented for only the nestling period produced young equal in size, mass, and number to those of pairs supplemented throughout the laying, incubation, and nestling periods.

Overall, reproduction in Burrowing Owls was not food-limited during laying or incubation, but was usually food-limited during the nestling period. Prey-cache sizes showed very low correlation between laying and early brood-rearing. This lack of seasonal predictability might explain why Burrowing Owls did not use early food conditions as a cue for adjusting egg volume, clutch size, or hatching asynchrony to suit food conditions for the nestling period. Instead, Burrowing Owls laid optimistically large clutches, hatched them asynchronously, and lost several

youngest brood members to starvation and sibling-cannibalism when food availability turned out to be inadequate during the nestling period.

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CHAPTER 1

Thesis Introduction

One primary goal of every animal is to convert food into offspring. An individual's success in achieving this goal is ultimately limited by food availability. At the proximate level, many other factors can act to reduce the influence of food, yet several studies have demonstrated direct effects of food on important reproductive parameters (Boutin 1990). In birds, parameters affected by food include laying day, clutch size, egg volume, incubation onset, hatching success, nestling growth, and fledging rate (Martin 1987, Nilsson and Svensson 1993).

Reproductive food limitation occurs whenever energy demands for breeding exceed availability of food. In theory, reproduction could be food-limited during any stage of the breeding season : egg laying, incubation, or nestling-rearing (Fig. 1-1a). For example, if altricial birds time breeding so food availability is highest during nestling rearing, then they must necessarily produce and incubate eggs when food availability is relatively low (Lack 1956, Perrins 1970). Thus, even though eggs require less energy per day than growing nestlings, food limitation may be just as severe early in the breeding cycle as it is later in the cycle. In addition, for birds nesting in regions that experience severe climatic changes within years, the season of favourable weather may be brief in relation to the period required for reproduction (*e.g.*, Price 1985). Birds in such regions may be unable to overlap their most energetically-expensive stage of breeding with the period of peak food availability. Timing of food limitation would then be dictated largely by patterns of food availability within the breeding season (*e.g.*, Korpimaki 1988).

If a reproductive parameter is proximately limited by food, then an increase in food should change that parameter in the direction that increases parental fitness (Martin 1991; Nilsson and Svensson 1993). Thus, if food limits reproduction during the egg-laying stage, clutch size or mean egg volume should increase in good food conditions; if food is limiting during the incubation stage, hatching success should increase; and if food is limiting during the nestling stage, fledgling quality (size, mass, condition) or quantity should increase in good food conditions. However, the reverse may not always be true. That is, if one of the above reproductive parameters changes in response to a food increase, food is not necessarily limiting during the corresponding breeding stage. This is because some birds adaptively modify reproductive effort during one stage to suit the degree of food limitation predicted for a future stage (Fig. 1-1b).

Lack (1947) suggested birds should use food conditions during egg laying to choose a clutch size most appropriate for food levels expected during the nestling period.

However, Lack acknowledged that this anticipatory adjustment of reproductive effort would be impossible in environments where food supply varied unpredictably over the season. When food was unpredictable, he proposed that birds should lay the number of eggs appropriate for very good feeding conditions during brood rearing but allow superfluous offspring to die shortly after hatching if food later proved to be scarce (the brood-reduction strategy; Ricklefs 1965). Lack also felt that birds with this strategy required asynchronous hatching to establish a competitive hierarchy within their broods. The hierarchy would facilitate efficient culling of extra young by focussing the effects of food shortage on last-hatched siblings without placing the entire brood at risk of starvation.

Recently, Wiebe (1995) outlined a potential reproductive adjustment for birds with food supplies that are partially-predictable over the season. When hatching asynchrony has food-dependent benefits during brood-rearing, but also has associated costs, individuals might begin incubation early (resulting in asynchronous hatching) in bad food-years, and begin incubation late in laying (increasing hatching synchrony) in good food-years. This facultative manipulation of hatching asynchrony would allow birds to maximize current reproductive success by minimizing risk to the entire brood when food conditions were poor and by minimizing losses of youngest nestlings when food conditions were favourable.

As indicated above, a bird's choice of reproductive strategies most likely depends on the degree of predictability of its food supply. This means that food predictability may also determine (albeit indirectly) which reproductive parameters are likely to be influenced by variations in food (O'Connor 1978, Wiebe 1995, Soler and Soler 1996). Despite its apparent importance for governing reproductive adjustments, few studies have assessed within-season predictability of food (Wiebe *et al.* 1998).

In addition to food availability, breeding date often explains a considerable amount of intrapopulation variation in reproductive parameters. Perhaps the most well-documented of these seasonal changes is the decrease in clutch size with later laying dates (reviewed in Hochachka 1990). However, several additional components of reproduction show seasonal variation: egg volume (Birkhead and Nettleship 1982; Perrins 1996), onset of incubation and hatching asynchrony (Nilsson and Svensson 1993), hatching success (Burger *et al.* 1996), nestling growth (Ricklefs 1968), and nestling survival (Perrins 1970). It is therefore imperative that experiments control for breeding date when trying to isolate the effects of food on reproductive performance. Nilsson and Svensson (Nilsson 1991, 1993; Nilsson and Svensson 1993) successfully separated the effects of

laying date and food availability on clutch size and hatching asynchrony in two *Parus* species. This was achieved experimentally by starting food-supplementation only after females had laid their first eggs and, thus, already committed to breeding dates similar to those of unsupplemented females. This new experimental technique has been suggested as a promising approach for studies of food limitation in species with large clutches and long laying-periods (Murphy and Haukioja 1986, Stoleson and Beissinger 1995).

In this thesis, I used observational and experimental approaches to investigate the role of food availability in controlling several components of Burrowing Owl (*Athene cunicularia*) reproduction. In Chapter 2, I presented a detailed examination of the effects of annual, seasonal, and inter-individual variation of food on laying date, clutch size, and mean egg volume (1992-1997). I chose two complementary measures of prey intake for individuals: number of prey stored in nests and rate of food-pellet production by pairs. I explored interrelations among arrival dates, laying dates, clutch sizes, and egg volumes, and examined the influence of parental age on these variables. Food-addition experiments (1992, 1993, and 1996; see Appendix 1) allowed me to test if food caused variation in clutch size, mean egg volume, and the seasonal decline in clutch size. By feeding each pair after its laying date had been set (*i.e.*, after clutch-initiation), I avoided the potentially confounding effect of earlier laying that usually results from food supplementation during prelaying (reviewed in Arcese and Smith 1988).

Degree of hatching asynchrony in birds largely reflects the span of time between onset of incubation and clutch completion (Magrath 1992). In Chapter 3, I investigated the effects of food during egg laying on hatching spans of Burrowing Owl pairs. In so doing, I contrasted energy constraint with facultative manipulation of hatching asynchrony. I compared hatching spans among years that varied with respect to feeding conditions (1992, 1993, 1996, and 1997), and compared spans of food-supplemented pairs to those of unsupplemented controls in the same years (1992, 1993, and 1996). Though clutch-size distributions were equivalent for the two experimental groups, I examined how hatching spans varied according to clutch size. In addition, I monitored prey caches to estimate relative changes in food intake within breeding seasons, asking whether food availability at the time of laying could serve as a reliable predictor of food availability during the nestling period.

To determine if food normally limited reproduction during the nestling period, I compared the quality (size, mass, condition) and quantity of fledglings between unsupplemented pairs and pairs provided with extra food from hatching until fledging (1992, 1993, 1996–1998; Chapter 4). In 1993 and 1996, I also tested for any cumulative

effects of extra food by supplementing a third subset of owl pairs from clutch initiation through to fledging (Appendix 1). In these two years, supplemental feeding thus began at different reproductive stages in different treatments – a design not previously employed in any avian experiment. This experimental setup allowed me to measure how fledgling production was influenced by food during three separate nesting stages: egg-laying, incubation, and nestling-rearing. Finally, I explored additional temporal aspects of food limitation in Burrowing Owls by comparing the impact of long-term food shortage, during low food years, and short-term food shortage, during periods of adverse weather conditions (Chapter 4).

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CHAPTER 2

Intraspecific Variation of Egg-production Parameters in Burrowing Owls: Effects of Natural Variations in Food and a Supplementation Experiment

INTRODUCTION

Food supply is a major determinant for allocation of reproductive effort in individuals (Martin 1987). In altricial birds, variation in food supply is correlated with intrapopulation variation in many reproductive parameters (Drent and Daan 1980, Martin 1987); specifically, laying date (Daan *et al.* 1989), laying interval (Lack 1956, Bryant 1975, Newton and Marquiss 1984), clutch size (Klomp 1970, Murphy and Haukioja 1986), inter- and intra-clutch egg volume (Howe 1976, Murphy 1986, Pietiainen *et al.* 1986), sex ratio (Howe 1977, Wiebe and Bortolotti 1992), hatching success (Nilsson and Smith 1988, Korpimaki 1989), hatching asynchrony (Nilsson 1993), nestling survival (Bryant 1975, Bortolotti *et al.* 1991), and nestling growth (Bryant 1975, Quinney *et al.* 1986). Such correlations often are attributed to direct nutritional and energetic constraints (Martin 1987), but there is growing evidence that individual birds manipulate reproductive behaviour, in a facultative manner, to match food conditions in their environment (Hogstedt 1980, Pietiainen *et al.* 1986, Wiebe and Bortolotti 1992, 1994, 1995, Aparicio 1994a, Nilsson 1994, Simmons 1994).

Facultative adjustment of egg production requires individuals to use cues to adjust their reproductive effort, at the time of laying, to levels appropriate for food conditions later in the breeding cycle (Horsfall 1984, Murphy and Haukioja 1986, Pietiainen *et al.* 1986, Nilsson 1991). In support of this idea, egg production sometimes correlates with food supply during prelaying and laying (reviewed in Martin 1987). Such a relationship can be misleading, however, if food supply varies in concert with other environmental variables that have a more direct influence on egg production (*e.g.*, temperature; Perrins 1965, Haftorn 1986, Slagsvold and Lifjeld 1989, Perdeck and Cave 1989). To establish causality, appropriate experimental manipulation of food intake is required (Drent and Daan 1980, Newton 1980, Meijer *et al.* 1988, Ward and Kennedy 1994).

Many studies have examined the proximate control of egg production by providing extra food to birds before egg laying (reviewed in Martin 1987, Arcese and Smith 1988, Boutin 1990). Some species supplemented in this way laid more eggs, and virtually all of them laid earlier in the year (Daan *et al.* 1989, Meijer *et al.* 1990). The latter response makes it difficult to attribute clutch-size variation directly to food because clutch size declines seasonally in almost all single-brooded birds (Klomp 1970, Hochachka 1990). Thus, larger clutches in food-supplemented birds could result either directly, from an

increase in food, or indirectly, from the coincident advancement of laying (Dijkstra *et al.* 1982). A similar problem exists when egg size is investigated, as it sometimes correlates with laying date (Birkhead and Nettleship 1982, Magrath 1992, Perrins 1996). The inability to discriminate between effects of food and of laying date on clutch and egg sizes has been a major shortcoming of previous food-supplementation studies (Hornfeldt and Eklund 1990). Nilsson (1991) and Svensson (Nilsson and Svensson 1993) tested the direct effects of food on clutch size by providing Marsh Tits (*Parus palustris*) and Blue Tits (*P. caeruleus*) with extra food only after laying of the first egg (*i.e.*, after clutch-initiation date had been set). This feeding schedule eliminated the confounding effect of food on laying date, isolating a positive effect of food on clutch size in Marsh Tits (Nilsson 1991). The approach has been suggested as promising for future food-supplementation experiments – especially for study species with large clutches and, hence, long laying-periods (Murphy and Haukioja 1986).

Birds of prey are often presented as species able to adjust egg production to current food supply (Lack 1947, Klomp 1970, Newton 1979). Close correlations between yearly indices of prey abundance and yearly population averages of clutch and egg sizes provide support for this hypothesis (Lack 1947, Southern 1970, Andersson 1981, Lundberg 1981, Smith *et al.* 1981, Pietiainen *et al.* 1986, Korpimaki and Norrdahl 1991, Taylor 1994). Food may also be proximately involved in the seasonal decline of clutch-size in single-brooded birds if late-laying individuals lay smaller clutches in response to lower food intake (Lack 1966, Perrins 1970, Newton 1979, 1986). This explanation is often dismissed for birds of prey because, in temperate species, food generally increases in abundance during the breeding period (reviewed in Daan *et al.* 1989). However, Newton and Marquiss (1984) used indirect evidence to suggest that actual food intake differed among individuals over the season due to various extrinsic and intrinsic factors not related directly to prey abundance (Rotenberry 1980, Bechard 1982, Martin 1986, Boutin 1990). The seasonal decline in clutch size, observed under natural food conditions, was absent in European Kestrel (*Falco tinnunculus*) pairs provisioned with extra food, suggesting the decline is normally a symptom of differential food intake among pairs over the season (Aparicio 1994b). The above studies highlight the need to measure food intake in individuals, rather than general food abundance for a population, as food intake accounts for both extrinsic and intrinsic factors affecting food availability (Martin 1986, Daan *et al.* 1989, Meijer *et al.* 1990). Studies that measure food intake in individuals are surprisingly rare (Daan *et al.* 1989), given that the main tenet of any theory of facultative adjustment to food is that birds react to their individual food circumstances (Hogstedt 1980, Drent and Daan 1980, Boutin 1990).

In this chapter, I present a detailed examination of the effects of annual, seasonal, and inter-individual variation of food on laying date, clutch size, and mean egg volume in the Burrowing Owl (*Athene cunicularia*). I used two complementary measures of prey intake for individuals: number of vertebrate prey stored in nests and rate of food-pellet production by pairs. I explored interrelations among arrival dates, laying dates, clutch sizes, and egg volumes, and examined the influence of parental age on these variables. I also conducted a food-addition experiment to see if food caused changes in clutch size, mean egg volume, and the seasonal decline of clutch size. I began supplementing each pair only after their first egg had been laid, thus eliminating any indirect effect of food on egg production via laying date.

METHODS

Study area and species

I studied Burrowing Owls from 1992 to 1997 in mixed-grass prairie of the Grassland Ecoregion of Saskatchewan (Harris *et al.* 1983) on a 10 000 km² site south of the cities of Moose Jaw and Regina (50° N, 105° W). The northwestern two-thirds of the study area lies on the Regina Plain with the southwestern one-third extending into the Missouri Coteau. The Burrowing Owls in this region are long-distance migrants, arriving unpaired on the breeding grounds between mid-April and late-May each year. They are single-brooded and monogamous (see also Haug *et al.* 1993), nesting in small, heavily-grazed pastures (cattle, horses, or sheep), within a matrix of non-irrigated cereal crops, summer fallow, and a few hayfields. After pairing, the female receives most of her food from her mate, but hunts for herself on occasion in the immediate vicinity of the nest burrow (Plumpton 1992). During prelaying and laying each year, most of the cropland and fallow fields near nests were tilled, and were therefore unfavourable habitat for small mammals that Burrowing Owls relied on for prey (unpubl. data). Owls lay their eggs in underground chambers at the end of 2- to 3-m tunnels originally excavated by Richardson's ground squirrels, *Spermophilus richardsonii*, or badgers, *Taxidea taxus* (Haug *et al.* 1993). Females lay eggs at intervals of approximately 1.5 days (Olenick 1990) and lay between 6 and 12 eggs. Hence, laying lasts between 7.5 and 16.5 days. Clutch mass, as a percentage of female mass, varies from approximately 40 to 75% (Wellcome 1997).

For both males and females, I determined spring arrival dates by making frequent site visits between mid-April and late-May in all years except the first year, 1992. An individual's arrival day was considered to be midway between the last visit preceding

arrival and the first visit subsequent to arrival. When these two visits were more than eight days apart, the individual's arrival day was excluded from analyses. A more stringent criterion of four days between site visits did not change the overall outcome of any analysis, so I present results for only the eight-day cut-off. After pairs began lining burrow entrances with nesting material, I replaced each natural burrow with an artificial nest burrow (Wellicome *et al.* 1997). Pairs started laying eggs in nest chambers of these artificial burrows within a few days to a few weeks of nest-box installation. In addition, some pairs nested in artificial burrows that had been installed in previous years. Nest boxes helped exclude mammalian predators (Wellicome *et al.* 1997), and allowed investigators to monitor contents of burrows during regular checks throughout the season. Day of clutch initiation (hereafter "laying day") was determined either by observing the first egg in the nest or by backdating from a mid-clutch egg count. Clutch size was determined for each nest by counting eggs shortly after clutch completion. In all years except 1994, I used a digital calliper to measure egg dimensions (to the nearest 0.01 mm) during incubation, and calculated egg volumes using Hoyt's (1979) equation: volume (cm^3) = $0.000507 \times \text{maximum length} \times \text{maximum breadth}^2$. To ensure independence of data points, analyses were based on mean egg volume per clutch (sum of volumes of all eggs in nest \times clutch size⁻¹). I included only clutches resulting from a pair's first nesting attempt of the year (*i.e.*, excluded replacement clutches).

Nestlings were banded with one U.S. Fish and Wildlife Service aluminum band, as well as one colour-band indicating the hatching year. Between 1 and 5% of the nestlings from each hatch-year were observed breeding on the study site in subsequent years. The number of returning birds, from clutches laid on known dates between 1992 to 1996, were 2, 3, 5, 11, and 4, respectively. I combined these data for all 5 years to allow a meaningful statistical comparison of return rates for fledglings from clutches laid before median annual laying days (early) and for fledglings from clutches laid after median annual laying days (late).

Neither plumage nor size differs appreciably between sexes in Burrowing Owls (Clayton *et al.* in review; see also Earhart and Johnson 1970, Karalus and Eckert 1987). Sex of adults was therefore determined during prelaying through behavioural observations (Martin 1973), and was later confirmed for a subset of birds examined in-hand for presence of brood patches (Haug *et al.* 1993). I avoided capturing females during egg laying, as this occasionally causes them to replace their clutch (unpubl. data), and instead captured them by hand inside nest boxes late in incubation. I trapped males outside of burrows (as they do not share incubation duties; Haug *et al.* 1993), using noose carpets baited with dead quail (Bloom 1987). I marked each captured adult with a unique

combination of 2 or 3 coloured-plastic leg-bands (5 potential colours) and one U.S. Fish and Wildlife Service aluminum band. For adults not originally banded as nestlings, I used patterns of fault bars on primaries and rectrices to distinguish 1-yr old parents from those greater than 1-yr old (Machmer *et al.* 1992, Pyle 1997). This aging-technique proved reliable when fault bars were present, as it correctly classified all 23 known-age owls (banded birds that were recaptured).

Prey caches and pellets

I counted stored vertebrate prey at least weekly during nest-chamber checks in the 1992 to 1997 breeding seasons. I determined mean cache size for each pair by averaging the number of prey counted in burrows during both the prelaying and laying periods (from time of pairing to laying of the last egg).

Analysis of pellets, containing the indigestible parts of prey, is an excellent technique for studying food habits in medium-sized owls (reviewed in Marti 1987), provided that collections are conducted frequently so decomposition of pellets in the field is minimized (Marti 1974). I collected pellets at nest entrances or on the ground within 10-15 m of nests, usually at 3- to 6-day intervals, throughout the 1992, 1993, 1996, and 1997 breeding periods. Because of a shortage of field staff, less time was available during each nest visit in 1994 and 1995. For this reason, pellets were not collected in those two years. Pellet samples collected after periods of more than 6 days were excluded from analyses. To obtain an index of the rate of food consumption by each pair in both the prelaying and laying periods, I divided the total dry-mass of collected samples by the total time period (hr) covered by collections and multiplied by 24 hours, to yield a pellet-production rate for each nest in grams per day. In several species of owls, dry pellet mass has been shown to correlate with mass of food consumed (review in Wijnandts 1984).

Feeding experiment

The amount of funding for the project varied among years and the number of Burrowing Owl pairs declined between 1992 and 1997. This meant that field staff and sample sizes were adequate to conduct supplemental feeding experiments only in 1992, 1993, and 1996 (see Appendix 1). I conducted supplemental feeding experiments in 1992, 1993, and 1996. Because frequent disturbance inside the nest chamber during early laying was previously thought to increase the probability of nest abandonment (Olenick 1990), I used evidence from above-ground observations to estimate laying days in the first study year, 1992. Laying was considered to commence when a female began

spending most of her time out-of-sight inside the nest burrow. Actual laying days in 1992 were later determined for analyses by backdating from mid-clutch egg counts, and were, on average, 2.7 days later than original estimates for laying days (range: 6 days after to 3 days before). In 1993 and 1996, after each pair had prepared a nest-cup depression in the dirt floor of their nest box, I determined their laying day directly by checking the nest chamber at 2-day intervals. Nests in 1993 and 1996 were thus checked when either the first egg (54 cases) or the second egg (19 cases) had been laid (*cf.* Nilsson 1991). This nest-check schedule caused no renesting or abandonment.

To control for effects of laying day on egg production, pairs were alternately assigned to supplemented and unsupplemented groups according to their estimated laying day in 1992 and their actual laying day in 1996. In 1993, every third pair that laid was assigned to be supplemented, and remaining pairs were not supplemented. Each of the supplemented pairs was provided with dead white laboratory mice at 3-day intervals, beginning on the actual (or estimated) laying day and continuing through the entire egg-laying period. Investigators placed laboratory mice inside the tunnel of each burrow, approximately 60 cm beyond the burrow entrance. This ensured that only intended recipients ate the supplemented food, as Burrowing Owls vigorously exclude other birds from the vicinity of their nests (*pers. observ.*). Pairs were provisioned at a rate of approximately 65 g/nest/d in 1992 and 85 g/nest/d in 1993 and 1996, representing between 2.5 and 3.5 times the amount of food required by an adult Burrowing Owl for daily-existence metabolism in captivity (mean = 26 g; Marti 1973). This level of provisioning ensured that food availability well-exceeded the needs of each female. When counting the number of prey items in prey caches, I included laboratory mice in cache totals if, on a visit at least 3 days later, I found that the owls had piled these mice with other prey in the nest chamber. Unfed pairs were visited every third day and disturbed for the same duration as supplemented pairs.

Because many owls in the experiment were unbandaged, I could not ensure that individuals were represented in analyses for only one breeding year. However, given that annual adult turnover at nests is high, and that nesting locations studied within our area varied considerably among years, a very low proportion of adults were likely represented more than once. Leg bands revealed the identity of the male parent in 55% (54/99), and of the female parent in 74% (73/99), of the supplemented and control breeding events in the experiment. For these known adults, 96% of male breeding events (52 males in 54 cases) and 99% of female breeding events (72 females in 73 cases) involved different individuals, and adults observed breeding in more than one year never paired with the

same mate twice. I therefore considered all 99 breeding events as independent samples for analyses (see also Newton and Marquiss 1981), with year and feeding treatment as factors.

Data analysis

For analysis of parameters measured after the start of laying (*e.g.*, clutch and egg size), I excluded data from fed pairs unless specifically testing the effects of supplemental feeding. Similarly, when relating arrival or laying days to clutch or egg sizes, I used data for unfed pairs only. However, I used data from all pairs when relating arrival day to laying day, as both of these parameters were established before birds were assigned to fed or unfed groups. When comparing prey-cache size and pellet-regurgitation rate among unfed nests, I used data for both the prelaying and laying periods. When comparing these measures of food intake between fed and unfed pairs, I used data for only the laying period (the period in which supplemental food was provided). Probability plots showed that data were normally distributed for all variables except prey-cache size (Wilkinson 1992). I therefore transformed prey-cache sizes by $\log_e(X+1)$ to obtain a normal distribution for parametric testing (Zar 1984). Statistical tests were performed using SYSTAT for Windows (Wilkinson 1992). I used SPSS for Windows to calculate power for tests (using observed effect sizes and variation) when effect sizes were non-trivial yet *P*-values were non-significant. For all statistical tests and power analyses α was set at 0.05. Sample sizes for analyses varied because I was unable to obtain all food intake or breeding measures for every nest.

RESULTS

From 1992 to 1997, clutch-initiation occurred over a 42-day period from 25 April to 6 June, with half of the females beginning to lay between 5 and 17 May (Fig. 2-1). Clutches varied between 6 and 12 eggs (Fig. 2-1; CV = 13.2%), but most pairs (82%) laid 8 to 10 eggs. The largest mean egg volume observed (13.0 cm³) was 1.4 times that of the smallest mean egg volume (9.2 cm³). Egg size was less variable (Fig. 2-1; CV = 7.4%) than clutch size. Mean egg volume and clutch size were not correlated ($P \geq 0.35$ in each of the 5 years that egg volumes were measured; $P = 0.89$, $n = 78$ clutches, all years combined).

Annual variation

Annual means of the mean number of vertebrates cached at each nest during the

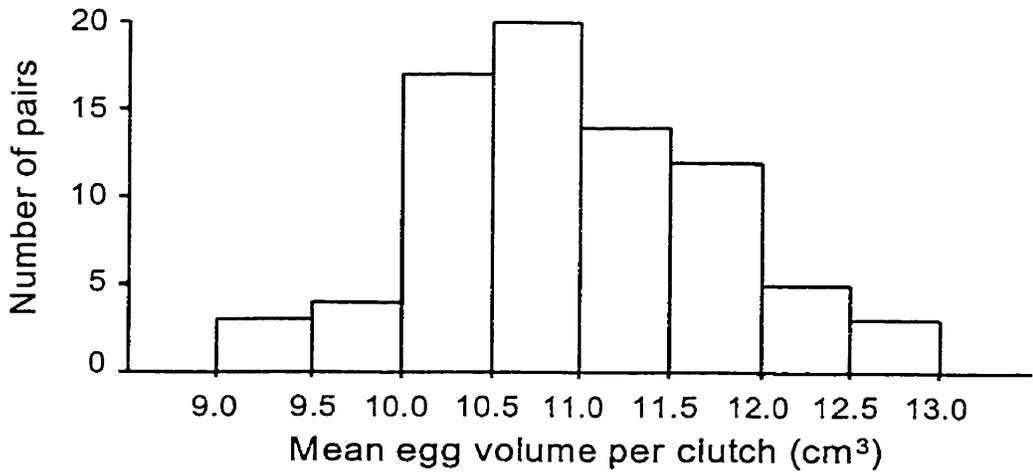
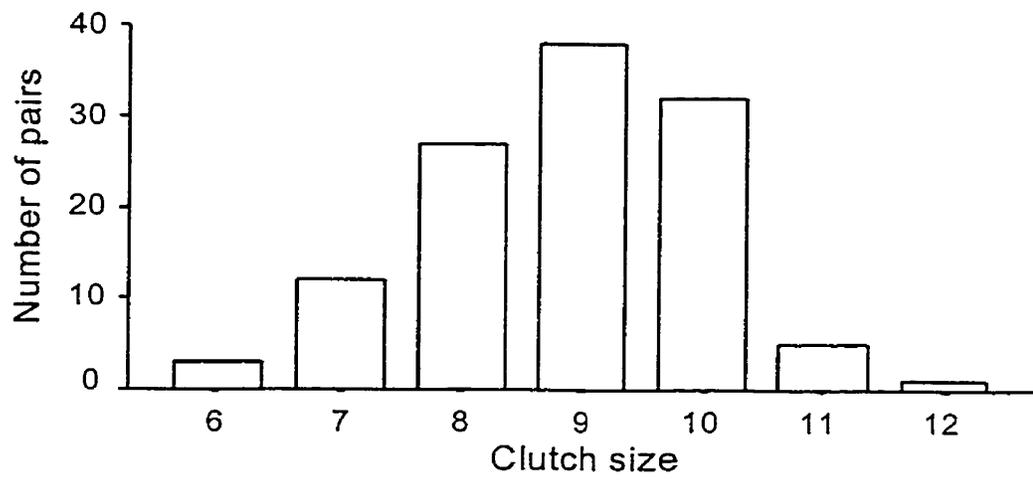
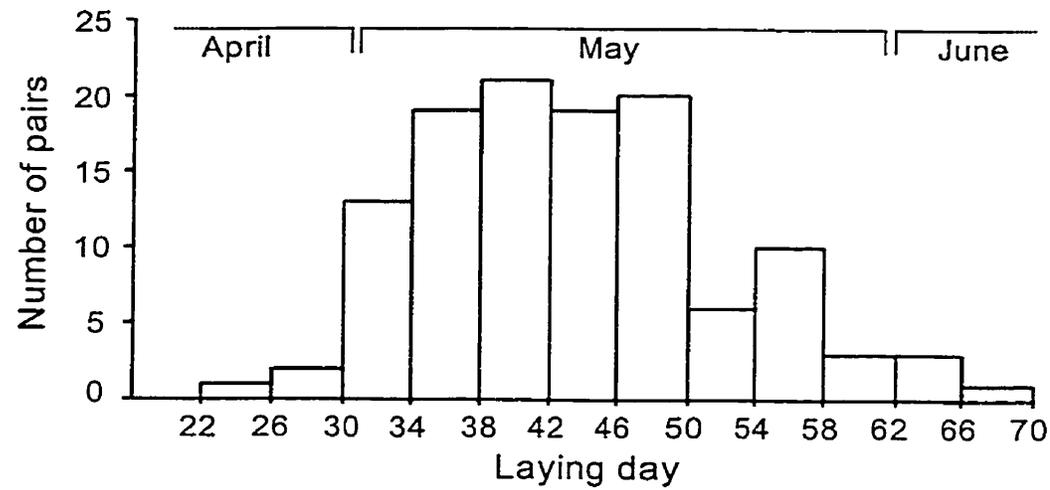


Figure 2-1. Distributions of laying days (day 1 = 1 April), clutch sizes, and mean egg volumes for Burrowing Owls nesting near Regina, Saskatchewan, between 1992 and 1997. Each egg-volume value represents the mean volume of all eggs in a clutch. Data are for first-nesting attempts of unsupplemented pairs.

prelaying and laying periods varied substantially among years (Fig. 2-2; ANOVA, $F = 10.16$, $P < 0.001$). Prey caches in 1997 were significantly larger than in any of the other 5 years (Tukey test; $P \leq 0.035$ for all comparisons). Caches were also larger in 1995 than in either 1992 or 1996 (Tukey tests; $P = 0.018$ and $P = 0.014$, respectively). Prey caches in 1997 were 16 times larger on average than in the year with the smallest prey caches, 1996, and 3.4 times larger than in the year with the second largest prey caches, 1995. Almost all vertebrate prey were either deer mice (*Peromyscus maniculatus*) or meadow voles (*Microtus pennsylvanicus*; Fig. 2-2). Other vertebrate prey included sagebrush voles (*Lagurus curtatus*), prairie voles (*Microtus ochrogaster*), house mice (*Mus musculus*), shrews (*Sorex* spp.), passerines, and tiger salamanders (*Abystoma tigrinum*). The large overall caches in 1997 were comprised predominantly of meadow voles, confirming reports from many local farmers, who all agreed they had seen more voles during seeding in 1997 than they had since the last vole “outbreak” in 1969 (Houston 1997).

A significant among-year difference in pellet-regurgitation rates during the prelaying and laying periods (ANOVA, $F = 9.99$, $P < 0.001$; Fig. 2-3) provides further evidence that 1997 was a year of superabundant prey. Although pellet-regurgitation rates did not differ in 1992, 1993, and 1996 (Tukey test; $P \geq 0.26$ for the three pair-wise comparisons), Burrowing Owls produced a significantly greater total mass of pellets per day in 1997 than they did in any of the other three years in which pellets were collected ($P \leq 0.001$ for the three pairwise comparisons).

Mean arrival days of males varied annually by as much as 12 days (Table 2-1; ANOVA, $F = 10.49$, $P < 0.001$), and those of females varied by as much as 14 days (Table 2-1; ANOVA, $F = 12.21$, $P < 0.001$). Arrival days for both sexes tended to be later in 1995 than in any other year (Tukey tests; $P \leq 0.07$ for all pair-wise comparisons), and were also later in 1996 than in 1993 ($P \leq 0.02$, both sexes). Mean annual laying day varied by as much as 9.4 days (Table 2-1; ANOVA, $F = 4.70$, $P = 0.001$). Laying days were significantly later in 1995 than in 1992, 1993, or 1994 (Tukey test, $P = 0.032$, 0.009, and 0.004, respectively), and were marginally later in 1995 than in 1997 ($P = 0.06$). The smallest mean annual clutch size was in 1995 and the largest in 1997. The maximum difference was thus 0.9 eggs, but among-year effects were not significant (Table 2-1; $F = 1.56$, $P = 0.18$, $POWER = 0.53$). Annual variation in mean egg volume approached significance (Table 2-1; $F = 2.39$, $P = 0.06$, $POWER = 0.66$) because of a marginal difference between 1993 and 1996 (Tukey test, $P = 0.08$).

Arrival, laying day, and egg production

In each of the 5 years that arrival days were measured, female arrival days were

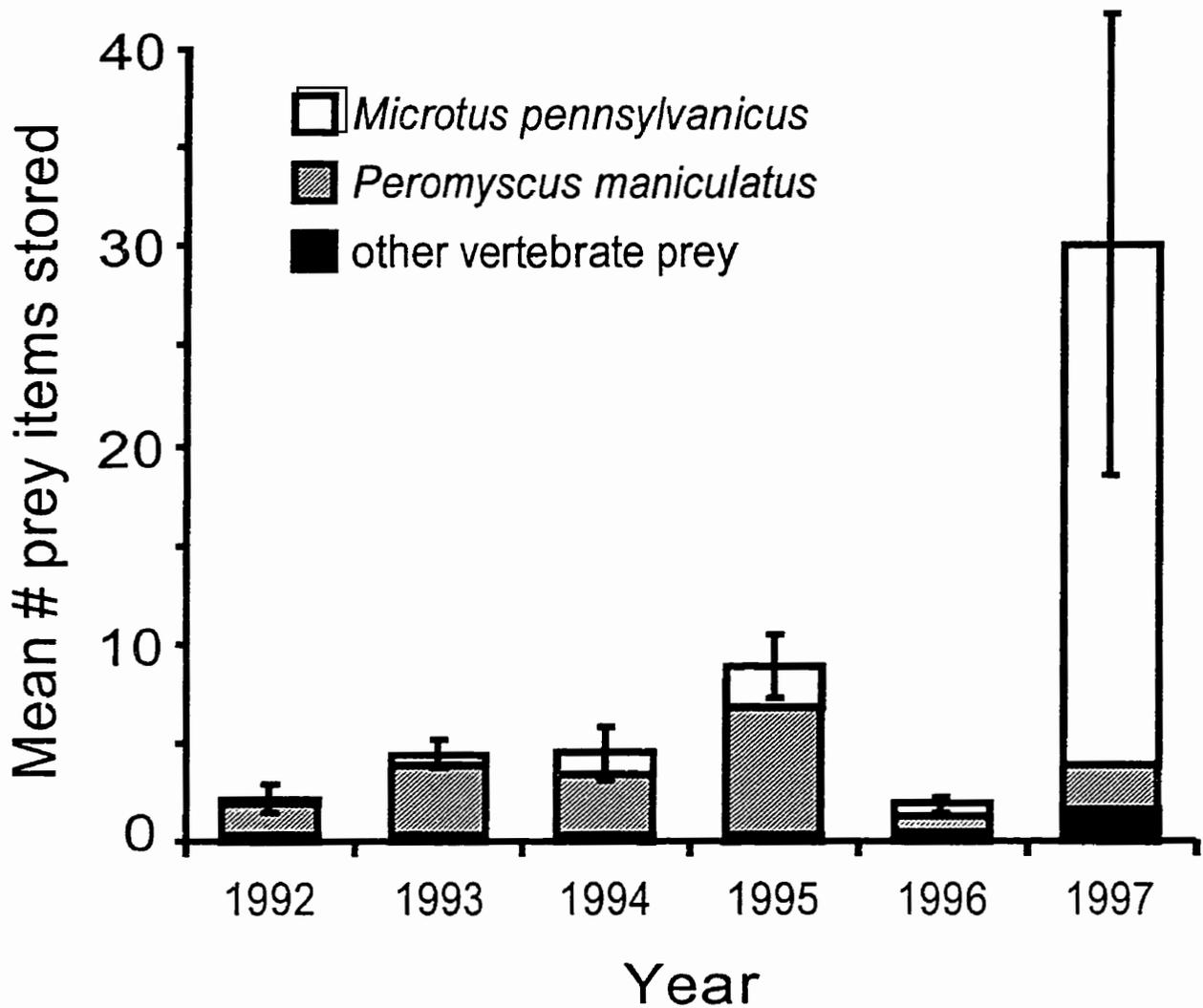


Figure 2-2. Mean numbers of vertebrates cached by Burrowing Owl pairs in each of six years. Values were calculated for each pair by averaging the number of prey counted in nest stores during checks in both the prelaying and laying periods. Bars indicate annual means of all vertebrate prey cached and error bars show standard errors. Shading within each bar shows the breakdown of prey species. ‘Other vertebrate prey’ included sagebrush voles, prairie voles, house mice, shrews, passerines, and tiger salamanders. Prey-cache data were collected from 13, 24, 16, 26, 17, and 18 unsupplemented pairs in 1992-1997, respectively. Average cache size for each pair was transformed by $\log_e(X+1)$ for statistical testing.

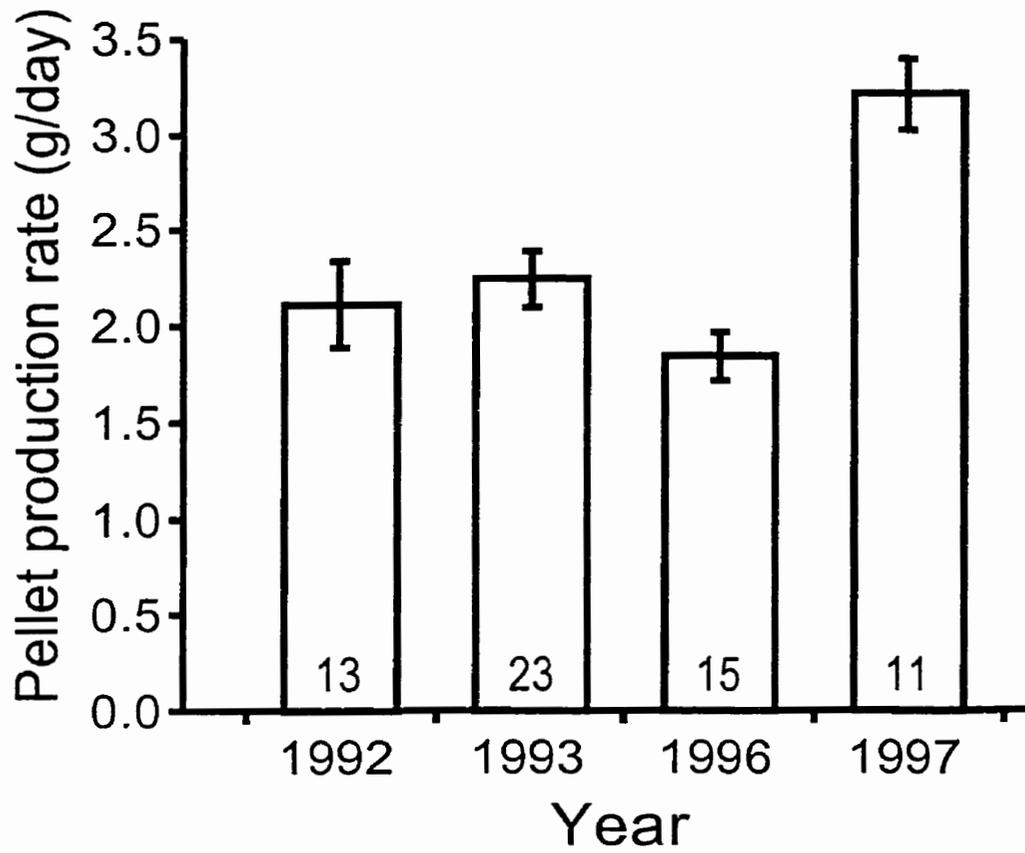


Figure 2-3. Annual means (± 1 SE) of pellet-regurgitation rates (prelaying and laying) for unsupplemented Burrowing Owl pairs in the four years pellets were collected. Values at the base of each bar indicate the number of pairs for which information was obtained.

Table 2-1. Annual means \pm 1 SE for male and female arrival day, laying day, clutch size, and mean egg volume for Burrowing Owls nesting in 1992–1997. Values in parentheses indicate number of owl pairs for which information was collected. Egg volumes were not measured in 1995. Arrival days were not recorded in 1992, but were obtained for most breeding individuals in other years. Arrival days were averaged for all adults, whether they were subsequently supplemented or unsupplemented during laying; however, laying day, clutch size, and mean egg volume are given for unsupplemented pairs only. Day 1 = 1 April, day 31 = 1 May.

Year	Male arrival day	Female arrival day	Laying day	Clutch size	Mean egg volume
1992	--	--	39.5 \pm 1.1 (13)	9.00 \pm 0.23 (14)	10.89 \pm 0.11 (13)
1993	22.6 \pm 1.1 (31)	26.2 \pm 0.9 (35)	39.9 \pm 1.2 (24)	8.96 \pm 0.20 (24)	11.34 \pm 0.18 (24)
1994	22.7 \pm 2.8 (10)	27.1 \pm 3.1 (12)	38.5 \pm 2.0 (17)	8.94 \pm 0.26 (17)	10.60 \pm 0.40 (5)
1995	34.6 \pm 1.6 (18)	40.2 \pm 2.0 (22)	47.9 \pm 2.1 (26)	8.50 \pm 0.26 (26)	--
1996	28.9 \pm 1.2 (21)	32.7 \pm 1.5 (25)	45.8 \pm 1.9 (17)	8.71 \pm 0.28 (17)	10.69 \pm 0.17 (17)
1997	27.8 \pm 2.4 (12)	30.6 \pm 1.8 (15)	41.1 \pm 1.8 (20)	9.40 \pm 0.28 (20)	10.79 \pm 0.21 (18)

positively associated with those of their mates (Table 2-2). Arrival day, for both males and females, was positively associated with laying day in all years, but female arrival explained more variation in laying day than did male arrival (Table 2-2). If food intake affected the relationship between female arrival and laying day, this relationship would have been different in years of low prey availability than it was in 1997, when females had access to large food caches. However, the observed relationship between female arrival and laying day was consistent among years (Fig. 2-4); *i.e.*, regressions did not differ annually with respect to slope (ANCOVA, covariate = day of female arrival; $F = 0.97$, $P = 0.43$) or Y -intercept ($F = 1.19$, $P = 0.32$). When a single regression line was fit for all years combined, female arrival day explained 91% of the total variation in laying day, with an average 12-d lag between arrival and laying. Clutch size was not closely related to male arrival in any year (Table 2-2). Clutch size was, however, closely associated with female arrival in most years, with an average of 34% of within-year variation in clutch size being explained by female arrival date (Table 2-2).

Mean egg volume was not related to laying day in any of the five years I measured eggs (Table 2-2). In contrast, clutch size declined significantly as the season progressed in each of the six study years (Table 2-2). Regressions of clutch size on laying day did not differ among years with respect to slopes (Fig. 2-5; ANCOVA, covariate = laying day; $F = 0.13$, $P = 0.99$) or intercepts ($F = 1.40$, $P = 0.23$), suggesting clutch size was determined each year largely by calendar date. For all years combined, date explained 41% of the total variation in clutch size (Table 2-2), and clutch size declined an average 0.63 eggs/week.

If initiating a clutch early rather than late in the season increases the probability of fledged young surviving, one might expect that, of the young returning to breed in the study area, a higher proportion would have originated from early nests than from late nests (*e.g.*, Perrins 1966, Newton and Marquiss 1984, Hochachka 1990). Accordingly, of 25 owls that fledged between 1992 and 1996 and returned to breed within the study area, 19 were fledged by pairs with laying days earlier than the population's median laying day for the given year, and only 6 came from pairs with laying days later than the yearly median (one-sample $\chi^2 = 6.76$, $P < 0.01$).

Measures of Burrowing Owl food intake did not vary significantly over the breeding season. The slope of the regression line of mean prey-cache size, during prelaying and laying, against laying day was not significantly different from zero ($P = 0.12$, $n = 114$, 6 years combined) and explained a very low proportion of the variation in laying day ($r^2 = 0.02$). In years that pellets were collected, the pellet-regurgitation rate of pairs during prelaying and laying was unrelated to their laying day ($P = 0.35$, $n = 60$, 4 years

Table 2-2. Within-year covariation in female and male arrival day, laying day and male arrival day, laying day and female arrival day, clutch size and male arrival day, clutch size and female arrival day, mean egg volume and laying day, and clutch size and laying day. *Y*-intercepts, slopes, coefficients of determination (r^2), and significance levels (*P*) shown for least-squares linear regressions. *n* = number of nests at which information was collected. Day 1 = 1 April. Regressions involving clutch or egg size included unfed birds only; whereas, regressions involving only laying day or arrival day included individuals that subsequently became either fed or unfed. Arrival dates were not recorded in 1992 and egg volumes were not measured in 1995.

Year	<i>n</i>	<i>Y</i> -intercept	Slope	r^2	<i>P</i>
Female arrival day vs. Male arrival day					
1993	31	11.21	0.67	0.51	< .001
1994	10	-0.06	1.24	0.92	< .001
1995	18	5.85	1.01	0.56	< .001
1996	21	5.68	0.92	0.75	< .001
1997	11	12.68	0.70	0.86	< .001
All years	91	5.25	0.97	0.75	< .001
Laying day vs. Male arrival day					
1993	31	26.50	0.52	0.28	0.002
1994	10	15.39	1.06	0.90	< .001
1995	18	14.93	1.05	0.66	< .001
1996	21	20.41	0.85	0.67	< .001
1997	12	25.66	0.70	0.64	0.002
All years	92	19.29	0.89	0.69	< .001
Laying day vs. Female arrival day					
1993	35	14.18	0.92	0.74	< .001
1994	12	15.95	0.84	0.94	< .001
1995	22	12.05	0.97	0.93	< .001
1996	25	17.01	0.88	0.90	< .001
1997	15	10.46	1.06	0.91	< .001
All years	109	14.36	0.92	0.91	< .001
Clutch size vs. Male arrival day					
1993	18	9.30	-0.02	0.02	0.630
1994	10	9.86	-0.06	0.24	0.152
1995	18	10.38	-0.06	0.15	0.117
1996	11	9.51	-0.01	.004	0.860
1997	11	9.55	-0.03	0.08	0.412
All years	67	9.90	-0.04	0.12	0.004

Table 2-2 (continued)

Year	<i>n</i>	<i>Y</i> -intercept	Slope	<i>r</i> ²	<i>P</i>
Clutch size vs. Female arrival day					
1993	19	10.13	-0.04	0.04	0.393
1994	11	10.13	-0.05	0.29	0.088
1995	22	11.63	-0.09	0.43	0.001
1996	14	11.43	-0.08	0.35	0.027
1997	14	11.70	-0.08	0.27	0.060
All years	80	11.09	-0.07	0.34	<.001
Mean egg volume vs. Laying day					
1992	13	10.10	0.02	0.11	0.262
1993	24	12.25	-0.02	0.03	0.462
1994	5	12.25	-0.04	0.45	0.214
1996	17	10.96	-0.01	0.004	0.803
1997	18	10.74	0.001	<.001	0.967
All years	79	11.45	-0.01	0.02	0.291
Clutch size vs. Laying day					
1992	13	12.79	-0.09	0.29	0.053
1993	24	11.84	-0.07	0.19	0.011
1994	17	12.06	-0.08	0.40	0.007
1995	26	12.93	-0.09	0.60	<.001
1996	17	12.81	-0.09	0.37	0.010
1997	20	13.56	-0.10	0.42	0.002
All years	117	12.51	-0.09	0.41	<.001

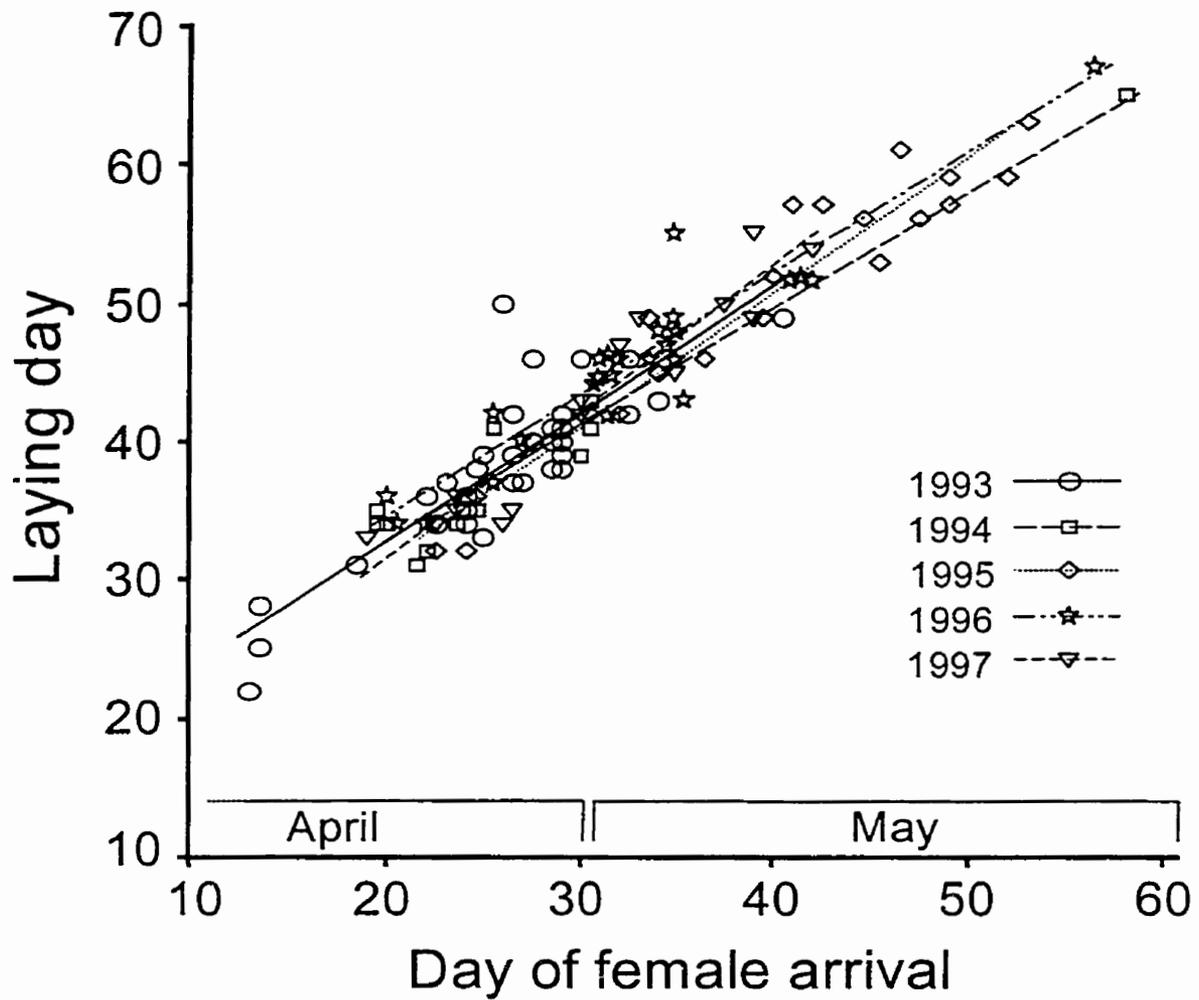


Figure 2-4. Days of arrival and of laying for females in five different years (day 1 = 1 April). Symbols indicate days for individual females, which were later either fed or unfed. Slopes of least-squares regressions were significantly different from zero in all years (Table 2-2). Neither slopes nor Y -intercepts differed among years, despite substantial annual variation in food intake (Figs. 2-2 and 2-3).

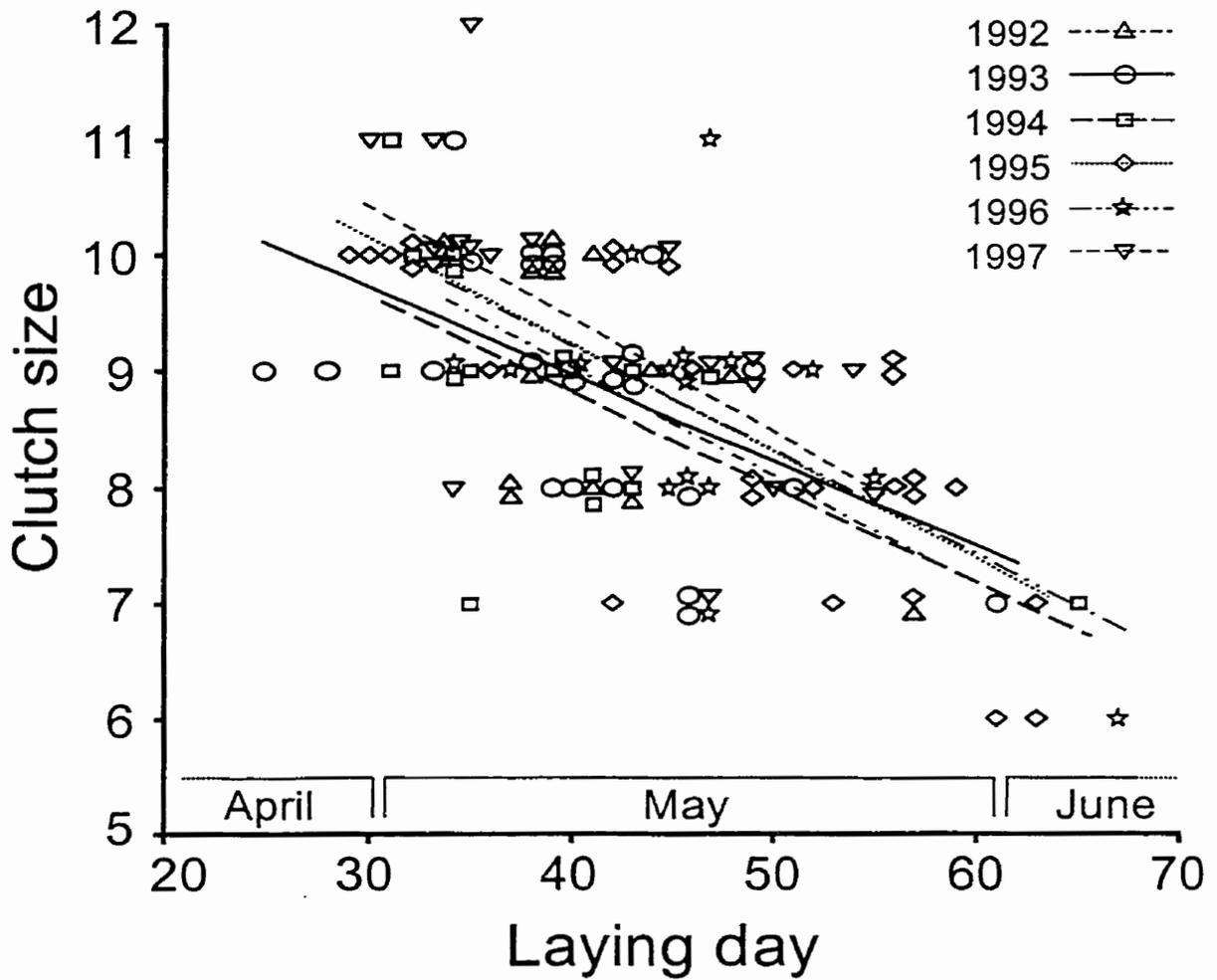


Figure 2-5. Seasonal decline in Burrowing Owl clutch size for pairs in each of six years (day 1 = 1 April). Each symbol indicates a value for one unsupplemented pair. Lines show least-squares linear regressions. Slopes were significantly different from zero in all years (Table 2-2), and neither slopes nor Y-intercepts differed among years.

combined).

Variation among individuals

Food intake. – If food affects egg production, one would expect positive relationships between measures of a pair's food intake and their reproductive performance in a given year. However, slopes of regression lines of clutch size on mean prey-cache size (during prelaying and laying) did not differ significantly from zero in any year ($P \geq 0.38$ in each of 6 years; see Fig. 2-2 for sample sizes), or for all years combined ($P = 0.65$). Nor were the slopes of regressions of mean egg volume on mean prey-cache size significantly different from zero in any year (1992, $P = 0.35$, $n = 13$; 1993, $P = 0.71$, $n = 24$; 1996, $P = 0.63$, $n = 17$; 1997, $P = 0.50$, $n = 16$; all years combined, $P = 0.27$). Similarly, regressions of clutch size on pellet-regurgitation rate (during prelaying and laying) were non-significant ($P \geq 0.43$ in each of the 4 years, see Fig. 2-3 for sample sizes; $P = 0.31$, all years combined), as were regressions of mean egg volume on pellet-regurgitation rate ($P \geq 0.24$ in each of the 4 years; $P = 0.22$, all years combined). As might be expected, mean prey-cache size and pellet-regurgitation rate were positively correlated for pairs ($r = 0.54$, $P < 0.001$, $n = 59$, 4 years combined).

Age effects. – I was able to determine arrival day and age for 35 males and 48 females between 1993 and 1997. In both sexes, arrival days were later for yearlings than for older birds (Table 2-3). Regressions of laying day on male arrival day were significant in both age-categories (1-yr old: $r = 0.82$, $P = 0.001$; >1-yr old: $r = 0.79$, $P < 0.001$), but neither slopes (ANCOVA, covariate = male arrival day; $F = 0.93$, $P = 0.34$) nor intercepts ($F = 0.38$, $P = 0.54$) differed with male age. Regressions of laying day on female arrival day were also significant in both age categories (1-yr old: $r = 0.93$, $P < 0.001$; >1-yr old: $r = 0.93$, $P < 0.001$), and age had no influence on slopes (ANCOVA, covariate = female arrival day; $F = 1.41$, $P = 0.24$) or intercepts ($F = 0.02$, $P = 0.88$). Thus, for a given arrival day, laying days were similar in both yearling and older parents.

Of 118 males and 118 females for which I collected information on egg production (unsupplemented birds only; 1992-1997), I was able to determine the age of 43 males (36.4%) and 51 females (43.2%). For this subset of birds, age of parent had no influence on mean egg volumes (Table 2-3). Likewise, male age did not affect mean prey-cache size ($t = 0.56$, $n = 39$, $P = 0.58$) or pellet-regurgitation rate ($t = 0.98$, $n = 18$, $P = 0.35$). Nor did female age affect these measures of food intake (caches: $t = 0.33$, $n = 48$, $P = 0.74$; pellet rate: $t = 0.01$, $n = 30$, $P = 0.99$). However, laying day was later for yearling parents than for older parents by more than 1 week on average (Table 2-3). Clutch sizes were smaller by approximately 1 egg for yearling males than for older males (Table 2-3).

Table 2-3. Arrival day, laying day, clutch size, and mean egg volume of Burrowing Owls in relation to sex and age of parent. Values in parentheses indicate numbers of known-age owls. See Table 2-1 caption for description of data collection. Significance levels (*P*) and *t*-values are from Student's *t*-tests. All years combined for analyses. Day 1 = 1 April, day 31 = 1 May.

Sex	1-yr old parent	>1-yr old parent	<i>t</i>	<i>P</i>
Arrival day				
Male	32.3 ± 2.1 (12)	26.7 ± 1.4 (23)	2.29	0.03
Female	38.4 ± 2.4 (14)	30.3 ± 1.4 (34)	3.03	<0.01
Laying day				
Male	48.1 ± 3.5 (10)	40.6 ± 1.5 (33)	2.24	0.03
Female	49.1 ± 2.0 (18)	41.2 ± 1.5 (33)	3.20	<0.01
Clutch size				
Male	8.20 ± 0.33 (10)	9.18 ± 0.21 (33)	-2.36	0.02
Female	8.44 ± 0.25 (18)	8.91 ± 0.22 (33)	-1.34	0.19
Mean egg volume				
Male	10.66 ± 0.25 (7)	10.91 ± 0.18 (20)	-0.83	0.42
Female	10.75 ± 0.19 (16)	11.02 ± 0.19 (22)	-1.00	0.33

Clutches were almost 0.5 eggs smaller on average for yearling females than for older females, but statistical power was low (0.26) and the difference was not significant (Table 2-3). Clutch size declined seasonally in both age groups of males (1-yr old: $r = -0.63$, $P = 0.05$; >1-yr old: $r = -0.74$, $P < 0.001$) and of females (1-yr old: $r = -0.74$, $P < 0.001$; >1-yr old: $r = -0.78$, $P < 0.001$). For both males (ANCOVA, covariate = laying day; $F = 1.98$, $P = 0.17$, $n = 43$) and females ($F = 0.91$, $P = 0.34$, $n = 51$), there was no interaction of laying-day and clutch-size effects between yearling parents and older parents; *i.e.*, rates of seasonal declines in clutch size did not differ between the two age categories. Nor did intercepts of the regressions of clutch size on laying day differ between ages of males (ANCOVA; $F = 1.05$, $P = 0.31$) or of females ($F = 2.34$, $P = 0.13$). It appears, therefore, that overall differences in clutch size between yearling and older parents can be attributed mainly to the coincident difference in their laying days. For both sexes, the disparity in laying days between age categories may be explained by the concordant disparity in arrival days.

Feeding experiment

To confirm that provisioning of extra food during egg laying increased Burrowing Owl food intake during that period, I performed two-way ANOVAs. There were significant effects of both year ($F = 5.02$, $P = 0.009$; Fig. 2-6a) and feeding treatment ($F = 8.41$, $P = 0.005$) on prey-cache size, but no year-by-treatment interaction ($F = 1.09$, $P = 0.34$). Caches were larger in 1993 than in either 1992 (Tukey test; $P = 0.01$) or 1996 ($P = 0.05$) and were larger for fed pairs than for unfed pairs. Pellet-regurgitation rates showed trends similar to those for prey caches, in that rates during laying were higher for supplemented pairs than for unsupplemented pairs (Fig. 2-6b; $F = 5.16$, $P = 0.03$), and there was no year-by-treatment interaction ($F = 0.22$, $P = 0.80$); however, year had no influence on regurgitation rate ($F = 0.93$, $P = 0.40$).

The use of laying day to alternately assign pairs to supplemented and unsupplemented groups successfully controlled for the effects of laying day on egg production. The resulting distributions of laying days did not differ between experimental and control pairs in any year (mean day \pm 1 SE for fed vs. unfed, respectively: 1992, 37.4 ± 0.9 vs. 39.5 ± 1.1 , $P = 0.34$; 1993, 39.9 ± 1.8 vs. 39.9 ± 1.2 , $P = 0.84$; 1996, 46.3 ± 1.7 vs. 45.8 ± 1.9 , $P = 0.99$; Kolmogorov-Smirnov two-sample tests; see Fig. 2-7a for sample sizes).

Providing extra food to pairs during egg laying had no obvious effects on egg production parameters. In two of three experimental years, average clutch size was 0.3 eggs (3.3%) larger for fed pairs than for control pairs; however, a two-way ANOVA showed no significant effect of treatment ($F = 1.41$, $P = 0.24$, $POWER = 0.22$) or of year (F

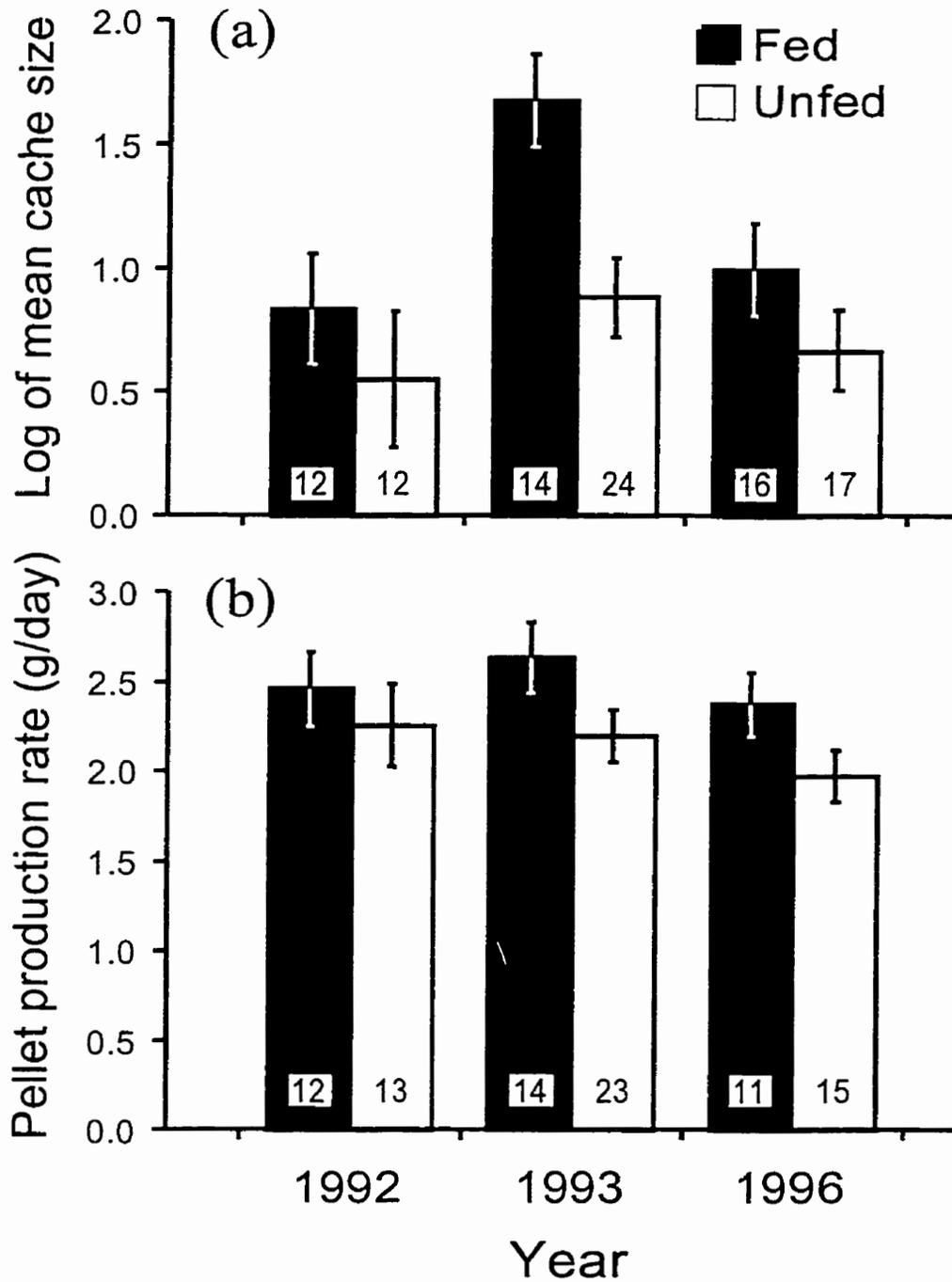


Figure 2-6. Annual means and SE's of (a) mean prey-cache sizes and (b) pellet-regurgitation rates for supplemented (Fed) and unsupplemented (Unfed) pairs in each of three years. Prey-cache values were calculated for each pair by averaging numbers of vertebrate prey counted during nest-checks in only the laying period, and were then transformed by $\log_e(X+1)$ to ensure a normal distribution for testing. Pellet production rate was calculated by dividing the total dry-mass of pellets collected during laying by the total hours represented in collection periods, and then multiplying by 24 hours.

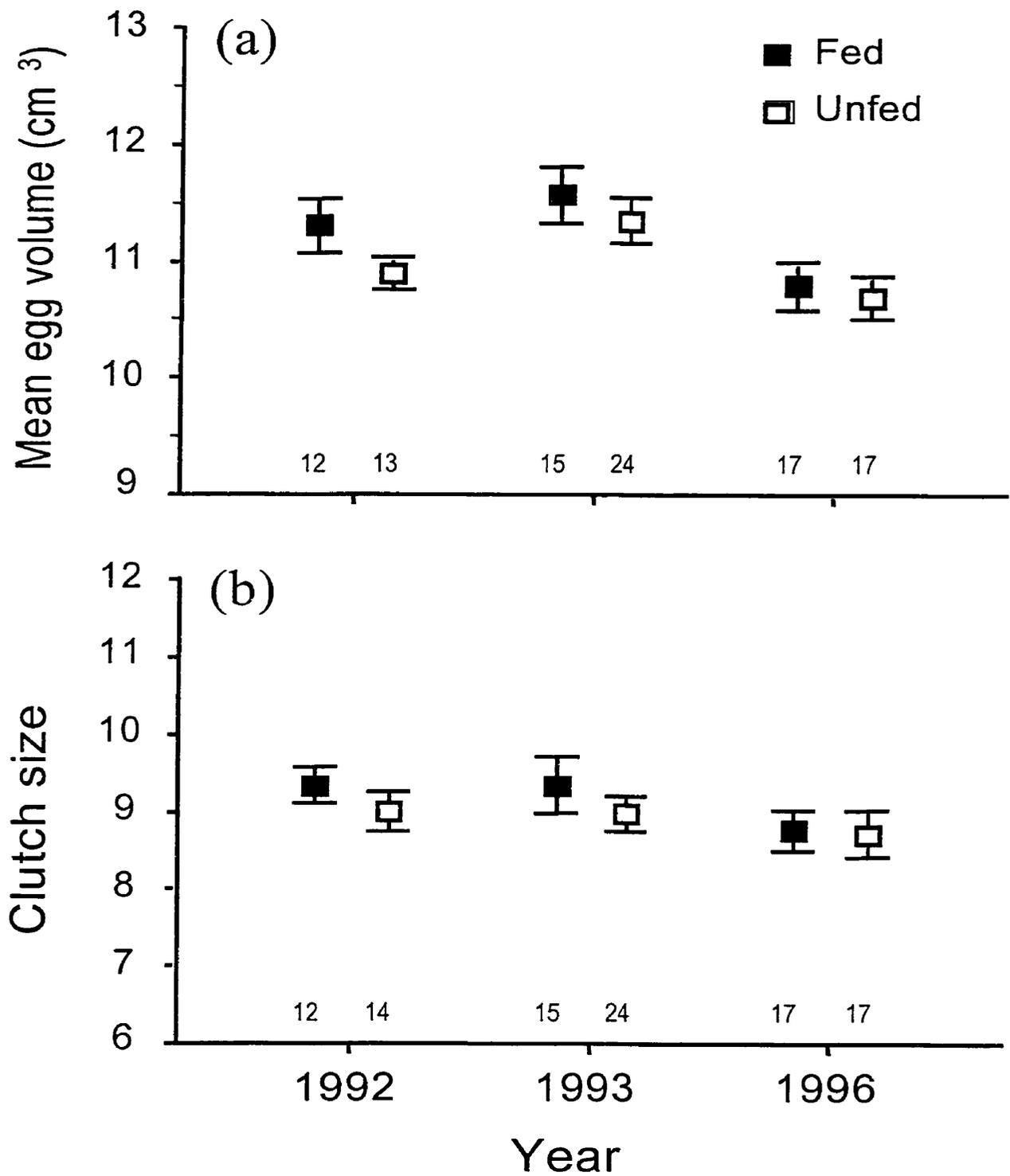


Figure 2-7. Annual means and SE's of (a) mean egg volume and (b) clutch size for supplemented pairs (Fed) and for controls (Unfed) in each of three years. Values at the base of each graph indicate number of pairs. Y-axes are scaled to observed range for each egg-production variable.

= 1.70, $P = 0.18$) on clutch size ($n = 99$; Fig. 2-7b). Had the clutch-size effect been of a more biologically-meaningful magnitude – say 10% (0.9 eggs) – power would have been 0.99. A two-way ANOVA on mean egg volume showed a significant effect of year ($F = 7.74$, $P = 0.001$); mean egg volume was higher in 1993 than it was in 1996 (Tukey test, $P < 0.001$). Mean egg volume for fed pairs was larger than for unfed pairs by 0.4 cm^3 (3.7%) in 1992; whereas, effect-sizes in the other two years were minute. Thus, supplemental feeding showed no statistically significant effect on mean egg volume per clutch ($F = 2.18$, $P = 0.14$, $n = 98$, $POWER = 0.31$; Fig. 2-7a). If there had been a 10% effect-size (1.1 cm^3), statistical power would have been 1.0.

To look for an effect of supplemental feeding on the seasonal clutch-size decline, I performed an ANCOVA, with clutch size as the response variable, laying day as the covariate, and treatment as the grouping variable. There was no interaction between treatment and laying day (ANCOVA, $F = 0.62$, $P = 0.44$, $n = 98$; data for 1992, 1993, and 1996 combined), indicating the slopes of the seasonal clutch declines did not differ between fed and unfed groups (Fig. 2-8). Nor did the intercepts of the regressions of clutch size on laying day differ between fed and unfed pairs ($F = 1.33$, $P = 0.25$, $n = 98$). Clutch size thus declined in a similar way for both fed and unfed experimental groups, showing that seasonal declines do not result from late pairs having less food than early pairs.

DISCUSSION

Laying day

Variation in the timing of avian breeding often correlates with variation in food availability during prelaying (Martin 1987). In 16 of 24 studies that provided extra food well before laying, birds responded by producing eggs significantly earlier in the season (reviewed in Meijer *et al.* 1990). Similarly, most populations laid eggs earlier in years of high food abundance than in years of low food abundance (Martin 1987). Such correlations could result either because food availability acts as a direct constraint on laying females (Perrins 1965) or because early food-levels provide a proximate cue for the timing of peak food levels later in the season (Daan *et al.* 1989). In the present study, providing extra food only after clutch-initiation had already occurred precluded any effect of supplementation on laying day (*cf.* Nilsson 1991, Nilsson and Svensson 1993). However, annual differences in mean laying days appeared to be unrelated to annual differences in measures of food intake, as laying day was not earlier in the year of superabundant food (1997) than it was in other years. Owls must not have adjusted their

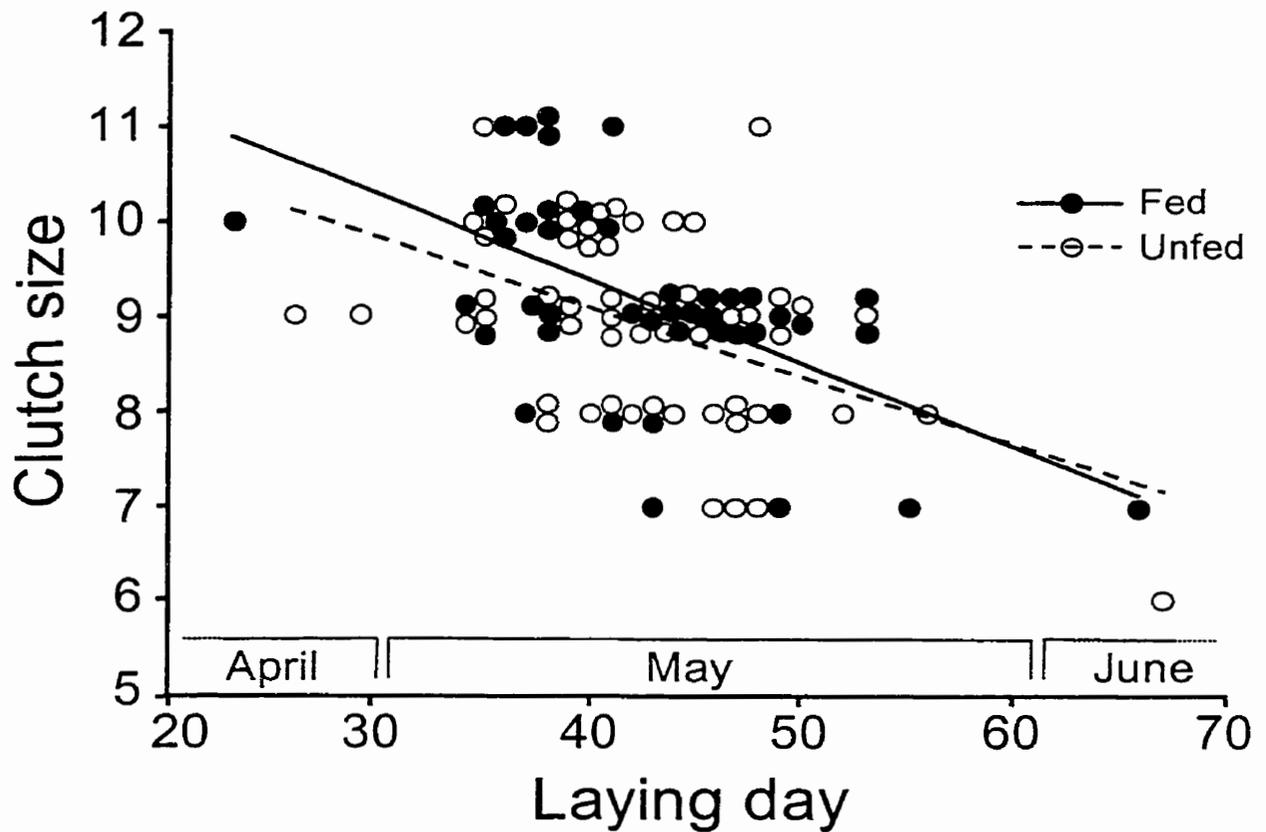


Figure 2-8. Seasonal decline in clutch size for food-supplemented (Fed) and control (Unfed) pairs. Symbols show individual values for pairs and lines indicate least-squares linear regressions. Data are combined from feeding experiments in 1992, 1993, and 1996. Neither slopes nor Y -intercepts differed between Fed and Unfed groups. Equations for the lines: Fed, $Y = 11.22 - 0.09X$; Unfed, $Y = 10.54 - 0.07X$. Day 1 = 1 April.

laying day according to their intake of prey during prelaying, nor could they have been energetically constrained by food availability, or females would have laid earlier when food intake was higher.

In contrast, arrival day had an obvious positive association with laying day. Female arrival, in particular, explained 91% of the total within-year variation in laying day (Table 2-2). Male arrival was also related significantly to laying day, but this relationship may simply have reflected the close correlation between male and female arrival days. Females arrived at nests shortly after their mates (mean difference of 4 days), and laying followed female arrival by only 12 days on average (Table 2-1). Thus, prelaying activities, such as nest preparation, copulation, brood patch formation, and follicular development, all happened within a relatively narrow window of time. It is, therefore, conceivable that females laid eggs as soon as possible after arrival, with other factors having little influence. For example, after taking the effect of arrival time into account, annual differences in food supply during prelaying did not lead to annual differences in the time between female arrival and laying, or intercepts of regression lines would have differed among years (Fig. 2-4). If arrival day commonly constrains laying day, it is not surprising that food-supplementation of migrant species in temperate regions has caused, at most, restricted advances in initiation date (Crick *et al.* 1993, Meijer *et al.* 1990, Wiebe and Bortolotti 1994, Svensson and Nilsson 1995, Kelly and Van Horne 1997).

As has been found in many other species (reviewed in Perdeck and Cave 1992), laying day in Burrowing Owls differed according to the age of the male and of the female. This difference did not, however, appear to be caused by lower food intake for yearlings than for older birds, as prey caches and pellet-regurgitation rates did not differ with age of parent. Rather, age appeared to affect laying day indirectly by affecting arrival day. Average arrival and laying days differed between age categories in each sex by approximately 1 week, but individuals of different ages that arrived on similar days initiated laying at the same time. Perhaps younger birds leave wintering grounds later (*e.g.*, Marra *et al.* 1998), or take longer on average than older birds to reach the breeding grounds and find a suitable nest burrow. This later arrival at nests then results in later laying. Experimentation would be necessary, however, to confirm such a cause-and-effect relationship between arrival day and laying day (*e.g.*, Cristol 1995).

Mean egg volume

Because larger eggs produce larger hatchlings with a better chance of surviving (Parsons 1970, O'Connor 1975, Amundsen and Stokland 1990, Magrath 1991), individuals in some species channel extra energy into increased egg size rather than egg

number (Murphy 1986, Hill 1988, Wiebe and Bortolotti 1995). In the present study, none of the evidence suggested egg size was appreciably larger when food intake was higher. In fact, mean egg volume was greatest for the population in 1993, when food supply was merely average. Egg size in birds often varies with female age (Davis 1975, Potti 1993), but both yearling owls and older owls produced eggs of similar size (~2.5% difference in mean egg volumes).

Clutch size

Number of eggs laid varied more than egg size among individuals in the Burrowing Owl population. However, clutch size varied little among years, showed no correlation with measures of food intake for individuals, and was not noticeably affected by supplemental feeding during egg laying (largest effect-size was 3.3%). This lack of an influence of food cannot be explained by reduced foraging in males when food was high (e.g., Poole 1985) because prey caches and pellet-regurgitation rates were significantly higher for supplemented pairs than for control pairs, and were much higher in 1997 than in other years. Although my findings differ from those in some avian studies, where clutch size showed an obvious response to natural variations in food supply (even when laying day was accounted for; Korpimaki and Hakkarainen 1991) and to supplemental feeding (Newton and Marquiss 1981, Pietiainen *et al.* 1986, Hornfeldt and Eklund 1990, Nilsson 1991, Aparicio 1994b), my results agree with most studies, in which clutch size was unaffected, or affected only slightly, by natural food-variations (Murphy 1986, Poole 1985) and by food supplementation (reviewed in Arcese and Smith 1988; see also Meijer *et al.* 1988, Arnold 1992, 1994, Wiebe and Bortolotti 1995).

A variety of factors can cause intrapopulation clutch-size variation in birds. For example, younger birds often lay fewer eggs than older birds (reviewed in Lack 1947, Klomp 1970, and Perrins 1979). In predatory birds, male age often has more influence on reproduction than does female age (Newton *et al.* 1981, Village 1986, Korpimaki 1988), likely because males hunt for the pair while females are laying or incubating eggs. In the present study, clutch-size differences between yearlings and older birds were more pronounced in males than in females. Differences were explained largely by later laying in yearlings; once laying day was accounted for statistically, there was no additional effect of age of parent. Later laying by young birds may also explain clutch-size effects reported in previous studies that did not include laying day as a covariate (examples in Klomp 1970).

Density of breeding pairs also influences clutch size in some birds (Lack 1954, Perrins 1979, Arcese and Smith 1988). My study population, and the provincial population,

declined by approximately 20% per year without a concomitant loss of habitat (unpubl. data; Wellicome and Haug 1995), making the density of owls in 1997 about one-third of that in 1992. Given that density decreased consistently with each year of the study yet clutch size did not, density appears to be unimportant for clutch-size determination in Burrowing Owls.

Overall, my results concur with those of a number of authors, who found that most intrapopulation variation in clutch size was explained by laying day (Murphy 1986, Pietiainen *et al.* 1986, Meijer *et al.* 1988, Nilsson 1991, Arnold 1994). Clutch size may therefore be affected most by factors that affect laying day – factors seemingly independent of food intake in Burrowing Owl pairs. Female arrival explained most of the variation in laying day, and accordingly, explained a considerable amount of variation in clutch size (34%). To my knowledge, few studies of migratory birds have examined interrelations among arrival days, laying days, and clutch sizes (but see Hogstedt 1974). The importance of arrival day for reproduction in Burrowing Owls suggests that these interrelations should perhaps be explored further in other species of birds.

Seasonal clutch-size decline

Seasonal declines in clutch size are very common in single-brooded bird species (Klomp 1970, Hochachka 1990, Meijer *et al.* 1990). Although many hypotheses for the decline invoke no proximate role for food resources (reviewed in Murphy 1986), those that do, propose that lower food intake for late breeders causes smaller clutches and the result is a seasonal decline in clutch size (Newton 1979, 1986, Dijkstra *et al.* 1988). This situation could arise if (1) prey abundance declines over the season, (2) prey availability declines over the season (*e.g.*, vegetative cover increases, making prey less accessible), (3) pairs who are poor foragers breed later than pairs who are good foragers, or (4) pairs in territories with low food availability breed later than pairs in territories with high food availability. These hypotheses do not necessarily require food limitation during egg laying; birds could, instead, use food supply during laying as a cue to predict food limitation at some later breeding stage. Regardless, if food intake is no lower for those individuals breeding late in the season than for those breeding early in the season, all four hypotheses are refuted.

Burrowing Owl clutch size declined significantly over the season in all six study years, and was remarkably consistent among years despite obvious annual fluctuations in prey supply, measures of food intake, and weather (Chapter 4). Though yearling parents sometimes have inferior foraging abilities in birds (*e.g.*, Marchetti and Price 1989), the regressions of clutch size on laying day were similar between yearling and older owls.

Moreover, neither the number of prey stored in nests nor the pellet-regurgitation rate of pairs correlated with laying day. Finally, when food intake in some pairs was artificially increased by supplemental feeding during laying, the seasonal clutch decline did not differ between the fed group and a control group with the same distribution of laying days. The latter finding is at odds with that of Aparicio (1994b) and Soler and Soler (1996), but supports those of Meijer *et al.* (1988), Nilsson (1991), and Arnold (1994), indicating seasonal clutch-size decline in Burrowing Owls does not result from differential food intake of pairs laying on different days.

Date itself appears to be the most important variable affecting clutch size in many species (Perrins 1979, Murphy 1986, Arnold 1994). How might birds modify their clutch size to match laying day? For Burrowing Owls, the consistency of the laying day/clutch size relationship among years suggests that photoperiod, a reliable indicator of date in temperate regions, is the proximate cue used to adjust clutch size to time-of-year. Indeed, this ability seems common in birds; photoperiod manipulation in captivity has altered breeding date for over 60 species (Newton 1979). Although my study was not designed to examine ultimate causes of the clutch-size decline, many current theories link the decline to a decreasing probability of juvenile recruitment with progressive laying day (Daan *et al.* 1989, Nilsson 1991). Consistent with these ideas, most offspring returning to my study area came from clutches laid early in the year.

Reproductive strategy

None of the parameters associated with egg production in this study were significantly affected by variations in the owls' intake of natural or artificial food. I conclude, therefore, that food limitation for Burrowing Owls during the prelaying and laying periods was negligible. Food limitation during the nestling period, on the other hand, was obvious and common in the owl population (Chapter 4). In all years except 1997, virtually every nest lost at least one nestling (and sometimes many nestlings) to starvation. Exceptional years like 1997, when voles are superabundant, appear to be very rare in southern Saskatchewan; records from 1952 to 1996 show only two previous 'outbreak' years (1960 and 1969; Houston 1997). This raises the question of why Burrowing Owls lay large clutches in every year, regardless of food conditions during laying, when they are seldom able to adequately nourish the large broods that result?

This apparent inconsistency is perhaps best understood in the context of a brood-reduction strategy (Lack 1947, 1954; Ricklefs 1965). Brood reduction can be thought of as an alternative to clutch adjustment (O'Connor 1978, Shaw 1985): birds that are unable to tailor clutch size, by predicting post-hatch food supplies at the time of laying, produce

an 'optimistic clutch', which corresponds to the maximal brood size that could be raised in the very best food year (Mock and Forbes 1995). If need be, family size is subsequently trimmed, through death of one or more of the young, to match food conditions during brood-rearing (Chapter 4). 'Clutch adjusters' are expected to react to food variations at the time of egg laying; whereas, 'brood reducers' should react to food supply during the nestling period. This dichotomy has recently been used to explain positive responses of brood-reducing species to supplemental feeding during the nestling stage (Soler and Soler 1996), and seems also to be consistent with the Burrowing Owl's lack of adjustment to food during egg production.

The Burrowing Owl population shares many characteristics with other brood-reducing species: asynchronous hatching of chicks (1-7 d span; Chapter 3), low year-to-year variation in clutch size but high variation in nestling mortality due to starvation (particularly for last-hatched young), dependence on an unpredictable (Chapter 3) or variable food supply (Chapter 4), and low costs in egg production (Shaw 1985, O'Connor 1978). The mass of a single egg as a percentage of female mass in the Burrowing Owl is approximately 6%, which is much lower than in any of the other 17 owl species presented by Lack (1968).

In all but one year, deer mice were the dominant prey of the owls (Fig. 2-2). Although populations of deer mice do not exhibit radical year-to-year changes, they do undergo stochastic seasonal variations such that spring densities are poorly correlated with fall densities (Terman 1968). In addition, *availability* of deer mice for owls can vary substantially over a short period, as factors such as moonlight intensity, wind speeds, and amount of rainfall (Chapter 4) can affect both the activity levels of prey (Falls 1968, Baumler 1975, Lehmann and Sommersberg 1980) and the ability of owls to hunt effectively (Dice 1945, Hirons 1982, Wijnandts 1984). Though insects were much less important than small mammals as prey during this investigation (Appendix 2), in years of dramatic grasshopper "outbreaks", Burrowing Owls in and near my study area ate large numbers of grasshoppers in mid- to late-summer (Haug 1985, James and Fox 1987, Schmutz *et al.* 1991). Such unpredictable 'windfalls' may sometimes enable the survival of the normally expendable last-hatched young.

Murphy and Haukioja (1986) suggested that predictability of food is probably low for most bird species, particularly for those with prolonged breeding cycles and those that rely on different prey taxa at different phases of the reproductive attempt. The combined effects of the random seasonal fluctuations in small-mammal availability, the consumption of different prey species in different years or times of season, and the prevailing influence of weather in the northern prairie environment probably limit any

opportunity for Burrowing Owls to adjust egg production to suit conditions later in the breeding season.

The consistency of the seasonal decline in clutch size among years also may be explained by lack of predictability. Birds cannot react to a factor causing seasonally decreasing prospects for juvenile recruitment – be it food supply or any other factor – if it operates at a subsequent stage and cannot be forecasted at the time of laying (Hirschfield and Tinkle 1975, Goodman 1979). Arnold (1994) showed that rate of seasonal clutch-size decline in American Coots (*Fulica americana*) varied with pond depth in May. He suggested coots were using pond depth to predict future seasonal patterns of nesting success. Food supply during laying was not an important cue for coots, as seasonal clutch declines did not differ between fed and unfed groups. In contrast, feeding experiments with the European Kestrel in Spain, showed that clutches of pairs in an unfed group declined over the season but clutches of pairs in a fed group did not (Aparicio 1994b). It appears, therefore, that European Kestrels used food supply during laying as a reliable cue for whichever factor caused the seasonal decline in juvenile survival (*cf.* Korpimaki and Hakkarainen 1991). Because the seasonal decline in Burrowing Owl clutches did not vary with food during egg laying, either the prospects for juvenile survival declined in the same way each year (*cf.* Daan and Dijkstra 1988 in Korpimaki and Hakkarainen 1991) or they were unpredictable at the time of egg laying.

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CHAPTER 3

Effects of Food and Clutch Size on Intrapopulation Variation in Hatching Spans of Burrowing Owls

INTRODUCTION

Age differences within avian broods frequently lead to the death of youngest members from starvation, trampling, eviction, or even bludgeoning by their older siblings (Howe 1978, Mock 1984). Curiously, it is the parents that set the stage for the demise of their youngest by starting to incubate before clutch completion, thus inducing an age- and size-disadvantage for hatchlings from last-laid eggs (Magrath 1992). This 'paradox of hatching asynchrony', has puzzled ornithologists for almost a century (Salter 1904 and Dunlop 1910, in Magrath 1990), inspiring hundreds of studies and a profusion of hypotheses (Stoleson and Beissinger 1995).

Three recent reviews (Magrath 1990, Stoleson and Beissinger 1995, Stenning 1996) revealed more contradiction than congruency in the literature on hatching asynchrony, and failed to provide a general explanation for the phenomenon. The reviews did, however, establish a conceptual framework for the array of hypotheses (which now number close to twenty), separating proposed functions of early incubation-onset into two major categories: saving time for parents or for offspring from early-laid eggs (time-savings hypotheses), and inducing an age/size hierarchy to help cope with food limitation during the nestling period (nestling food-limitation hypotheses; Table 3-1).

Numerous experiments have manipulated age-hierarchies within broods, focussing on the consequences of hatching asynchrony during the nestling period (reviews in Amundsen and Slagsvold 1991, Stoleson and Beissinger 1995). In comparison, the proximate determination of natural intrapopulation variation in hatching asynchrony has been largely ignored (Slagsvold and Lifjeld 1989). Given this bias in experimental focus, the two most recent reviews (Stoleson and Beissinger 1995, Stenning 1996) each concluded with a plea for increased concentration on factors that might be influential during the laying period, when hatching asynchrony is actually determined through onset of incubation.

Numerous observational studies have recorded intrapopulation variation in hatching asynchrony. For instance, levels of hatching asynchrony for birds often increase with increases in clutch size (Howe 1978, Slagsvold 1986, Smith 1988, Hebert and Sealy 1992, Magrath 1992, Wiebe and Bortolotti 1994, Wiebe *et al.* 1998). Also, despite typical seasonal declines in clutch size (Hochacka 1990), hatching asynchrony sometimes increases seasonally (Gibb 1950, Nisbet and Cohen 1975, Mead and Morton 1985,

Table 3-1. Hypotheses to explain the function of early onset of incubation and hatching asynchrony. Hypotheses are presented under two main headings. Additional hypotheses that do not fit into either of these categories are not presented here.

Hypothesis	Explanation	Reference
<i>Nestling food-limitation</i>		
Brood reduction	If food becomes short, smallest chicks are easily sacrificed to benefit others	Lack 1947, 1954 Ricklefs 1965
Offspring quality assurance	Ensures optimal growth, and thus high quality, of older young	Slagsvold <i>et al.</i> 1995
Sibling rivalry	Saves energy by minimizing disputes because older nestlings easily dominate younger siblings	Hahn 1981
Peak-load reduction	Each nestling reaches its maximum energy demand at a different time during brood-rearing	Ingram 1959 Hussell 1972
Sexual conflict	Female spends longer period incubating eggs and brooding young, thus getting more care from male	Slagsvold & Lifjeld 1989
Ice-box hypothesis	In cannibalistic species, younger chicks provide easy meals for older siblings during food crunch	Alexander 1974
<i>Time-savings</i>		
Nest failure	Hatching asynchrony set to minimize daily risk of failure, depending on usual timing of predation	Hussell 1972 Clark & Wilson 1981
Adult predation	Hatching asynchrony set to minimize risk of death for incubating parents, depending on timing of predation	Hussell 1972 Magrath 1988
Hurry-up	Early incubation ensures first eggs hatch and fledge sooner. This is useful if nestling or post-fledging survival or quality declines seasonally	Hussell 1972 Clark & Wilson 1981 Nilsson 1993
Egg viability	Early incubation increases hatching success by ensuring 1st-laid eggs do not sit cold for too long	Arnold <i>et al.</i> 1987
Limited breeding opportunities	Birds begin incubation as soon as possible so nest cavity is occupied early	Beissinger & Waltman 1991

Slagsvold 1986, Veiga and Viñuela 1993). Lack (1966), for one, interpreted the seasonal increase in hatching asynchrony as an adaptation to a seasonal reduction in food availability. He felt that late-laying females hatched their eggs asynchronously because they were more likely than early-laying females to experience food shortage for nestlings. Conversely, Slagsvold (1986) suggested that seasonal increases in hatching asynchrony resulted from seasonal increases in food availability. He assumed asynchronous hatching was optimal, but suggested that proximate food limitation forced some females (in this case, early-laying females) to delay incubation and thus hatch their broods over a shorter span of time (energy constraint hypothesis, Slagsvold and Lifjeld 1989).

Nilsson (1993) and Nilsson and Svensson (1993) were the first to experimentally manipulate a potential source of variation in hatching asynchrony, by providing female Marsh Tits and Blue Tits, respectively, with supplementary food during egg laying. Supplemented females began incubating 1–2 days before their final egg; whereas, unsupplemented tits delayed incubation until clutch completion. In these studies, extra food seemed to help pairs overcome food limitation during laying, lending support to the energy constraint hypothesis. Stoleson and Beissinger (1995) suggested that species in which males provide all the food requirements of incubating females should be free of constraints during laying because females have no time-conflict between foraging and incubating. However, energetic constraint cannot be completely dismissed for such species, as simultaneously incubating and producing eggs is more energetically expensive on a daily basis than simply resting during laying and postponing incubation until clutch completion (Ricklefs 1974).

Two food-supplementation experiments – both with diurnal raptors – have yielded results opposite to those predicted by the energy constraint hypothesis. When given extra food prior to laying, American Kestrel (*Falco sparverius*; Wiebe and Bortolotti 1994) and Osprey (*Pandion haliaetus*; Green and Krebs 1995) pairs decreased their hatching asynchrony relative to that of control pairs. The birds were not food-constrained early in the season, but instead used food intake at the time of laying to facultatively manipulate hatching asynchrony to suit anticipated food-conditions later in the season. With this strategy, individuals maximise their lifetime reproductive success by hatching broods asynchronously when food is in short supply, and synchronously when food is abundant (Wiebe and Bortolotti 1994). Such facultative manipulation of hatching patterns is plausible only when (1) asynchrony has food-dependent benefits during brood rearing but also has associated costs, and (2) food supply at the time of laying is correlated with food supply during brooding so that future conditions are at least partially predictable at the onset of incubation. Wiebe (1995) suggested these criteria are especially likely to be met

for hawks (Falconiformes) and owls (Strigiformes) that rely on small mammals as their main prey.

Here, I examine the proximate effects of food during egg laying on hatching spans within a population of Burrowing Owls (*Athene cunicularia*), and in so doing, test the energy constraint and facultative manipulation hypotheses. I compared hatching spans among years that varied with respect to feeding conditions, and compared spans of food-supplemented birds to those of unsupplemented controls in the same years. By feeding each pair after its laying date was already set (*i.e.*, after clutch-initiation), I avoided the potentially confounding effect of earlier laying that often results from food supplementation (reviewed in Arcese and Smith 1988). Owls in this study population did not modify their clutch size in response to supplemental feeding (Chapter 2), so clutch size distributions were equivalent for the two experimental groups. Because pairs cached food in their nests, I was able to estimate relative changes in food intake within breeding seasons to see if food availability at the time of laying was a reliable predictor of food availability during the nestling period.

METHODS

Study species

For many reasons, Burrowing Owls make good subjects for a study on hatching asynchrony. Burrowing Owls show marked asynchrony and considerable natural variation in hatching spans among broods (Landry 1979, Olenick 1990). They are monogamous, single-brooded, and short-lived, so most individuals breed only once or twice in their lifetime (Haug *et al.* 1993, Wellicome 1997). They are small owls (~160 g) with large clutches of 6 to 12 eggs laid over approximately 8 to 17 days. The female alone incubates eggs and broods hatchlings, and males accommodate almost all of the females' food requirements from prelaying until the end of brooding, after which time females help capture prey for growing nestlings (Haug *et al.* 1993). Virtually all partial-brood loss in this study population (near Regina, Saskatchewan) results from starvation of youngest chicks when food is short (Chapter 4). The majority of the populations' dietary biomass, throughout the nesting period, is comprised by deer mice (*Peromyscus maniculatus*) and meadow voles (*Microtus pennsylvanicus*; Fig. 2-2, Appendix 2). For additional information on the study area and study population, see Chapter 2.

Monitoring reproduction

All Burrowing Owl pairs in this study bred in artificial burrows, permitting easy access to nesting chambers throughout the breeding season (Wellicome *et al.* 1997).

Reproduction was monitored in 1992, 1993, 1996, and 1997. Laying date (*i.e.*, day first egg was laid) was determined for each pair either by observing the first egg in the nest or by backdating from a mid-clutch egg count. Nest-checks that were conducted at intervals of two or more days invariably revealed a laying rate of 1 egg per 1.5 days. When eggs were first observed in nests, they were numbered on both ends with indelible ink. Exact laying order could not be ascertained for eggs when nest-checks were separated by more than two days. Clutch size was determined by counting eggs within a few days of clutch completion. Hatching success was calculated for each pair by dividing the number of eggs hatched by the number of eggs laid. Although nest predators in the study area sometimes caused the loss of whole clutches (Wellicome *et al.* 1997), they were never responsible for the loss of only one or a few eggs within a clutch. Partial hatching failure resulted from infertility of individual eggs, from death of embryos during development or hatching, and, occasionally, from damage to eggshells caused by incubating females.

Measuring hatching asynchrony

Each clutch was checked for signs of hatching 27 days after the first egg was laid (mean laying date = 12 May). The clutch was then rechecked at 2- or 3-day intervals, depending on the conditions of egg surfaces (see below), until all viable eggs had hatched. A chick was considered to have hatched once it became free of its eggshell. At the start of the hatching process, each chick pecked tiny, star-shaped cracks that eventually formed a ring around the small axis of its egg. During nest-checks in the hatching period, I assessed the extent of cracking on each egg. An egg with a line of star-cracks extending more than halfway around was recorded as hatching later that day. If the line extended between one-half and one-eighth of the way around the egg, hatching was considered to occur the following day. Wet down on a chick indicated it had hatched earlier that day. When each chick was first observed after hatching, the insides of its legs were marked with two, of a possible four, felt-pen colours to distinguish it from its nest-mates.

Hatching span was defined as the number of days separating first- and last-hatched nestlings within a brood (*i.e.*, the maximum nestling age-disparity). I was able to determine hatching span for 108 of the 112 pairs for which hatching success was measured in the four study years. Two of the four broods for which hatching span could not be accurately determined were from 1992 (one supplemented, one unsupplemented). In each of these two nests, most but not all eggs had hatched before my last visit prior to the nests being depredated. During these last visits, I removed eggshell halves left by hatched chicks. I knew the final eggs would soon hatch because chicks made audible

peeping sounds from inside the eggs and some of them had started to pip. All hatchlings disappeared in the predation events, but numbered eggshell halves remained with cracking patterns indicating they had hatched. At a third nest (in 1996) three eggs were accidentally cracked during a nest check immediately prior to hatching. All three chicks inside these eggs were healthy at the time, but soon died. For the analysis of hatching success, I considered the three chicks to have hatched. Hatching span was also not measured at a fourth study nest (1997) because the nest was inadvertently checked late, after all chicks had already hatched and dried.

Prey caches

I monitored the number of vertebrate prey stored by pairs in the 1992, 1993, 1996, and 1997 breeding seasons. In addition, I monitored prey caches for pairs in 1998, though hatching spans were not measured in that year. Because I am interested in natural variation in the owls' food intake, I present caches only for pairs that remained unsupplemented in both pre- and post-hatch feeding experiments (see Chapter 4 for post-hatch experiments). Virtually all prey stored in nest chambers were either deer mice or meadow voles, but other vertebrate prey were occasionally found in caches (see Chapter 2 for list of rare prey).

I examined the seasonal predictability of food stores by relating mean prey-cache size during the prelaying/laying period to mean prey-cache size during the brooding period. Within these two periods, mean cache size was calculated for each pair by averaging the number of prey counted at 2- to 6-day intervals during nest checks. The pre-laying/laying period lasted from the day the female arrived in spring (see Chapter 2) until the day she completed her clutch, for a duration of ~25 days. The brooding period lasted from the day the first nestling hatched until all nestlings in the brood reached the age at which owlets are typically able to thermoregulate and tear up food on their own (~17-day period; Landry 1979, Haug *et al.* 1993).

Food supplementation

I provided extra food to some of the breeding pairs in each of the 1992, 1993, and 1996 seasons. Each supplemented pair was provided with 195–255 g of dead laboratory mice every third day, at a rate of 65g/day in 1992, and 85g/day in 1993 and 1996. This extra food represented 2.5 to 3.5 times the amount required by an adult Burrowing Owl for daily-existence metabolism in captivity (mean = 26 g; Marti 1973). To avoid affecting laying date, I started provisioning after females had initiated their clutches (see Chapter 2 for details). In 1992, I stopped supplementing shortly after laying was complete, but in

1993 and 1996, I continued supplementing through the incubation stage. Clutch and egg sizes did not differ between supplemented and unsupplemented pairs, and mean clutch size did not vary among the four years of the study (Chapter 2).

Statistical analyses

All statistical tests were performed with SPSS for Windows (SPSS 1996). Proportions of eggs hatched were arcsine transformed, and prey-cache sizes were transformed by $\log_e(X+1)$, before parametric tests were applied. Annual variation in hatching success, hatching-span deviation (see Results for definition), and mean prey-caches during laying was assessed for unsupplemented pairs with one-way ANOVAs. To test for effects of supplemental feeding on hatching-span deviation and hatching success, I performed two-way ANOVAs, with year and feeding treatment as factors. Interaction terms were initially included, but were subsequently excluded if non-significant, in which case probability values for predictors were recalculated.

RESULTS

Hatching success

Burrowing Owl pairs often experienced partial hatching failure, where most but not all eggs in a clutch hatch. In nests that successfully hatched at least one young ($n = 112$), the number of failed eggs varied between 0 and 4, and the percentage of hatched eggs varied between 50 and 100%. Hatching success showed no association with clutch size, whether data were examined for each year separately (unsupplemented pairs only; 1992, $r = 0.49$, $P = 0.89$, $n = 11$; 1993, $r = -0.01$, $P = 0.95$, $n = 23$; 1996, $r = -0.34$, $P = 0.20$, $n = 16$; 1997, $r = -0.30$, $P = 0.20$, $n = 20$) or for all years combined ($r = -0.15$, $P = 0.21$, $n = 70$).

Though mean prey-cache size during prelaying/laying (an index of food intake) varied substantially among the 4 study years (Fig. 3-1; ANOVA, $F = 6.073$, $P = 0.001$), the mean percentage of eggs hatched by unsupplemented pairs did not vary significantly among years (Table 3-2; ANOVA, $F = 0.46$, $P = 0.71$). Nor did year influence mean hatching success of owls when supplemented and control pairs from 1992, 1993, and 1996 were included in a 2-way ANOVA ($F = 0.77$, $P = 0.47$). Hatching success was also unaltered by supplemental feeding (Table 3-2; 2-way ANOVA, $F = 0.08$, $P = 0.77$). The fact that supplementation ceased after clutch completion in 1992, but continued through incubation in 1993 and 1996 (see *Methods*), made no difference to hatching success, as mean percentages for supplemented pairs were virtually identical among the three years of experiments. There was also no interaction between treatment and year ($F = 0.12$, $P = 0.89$).

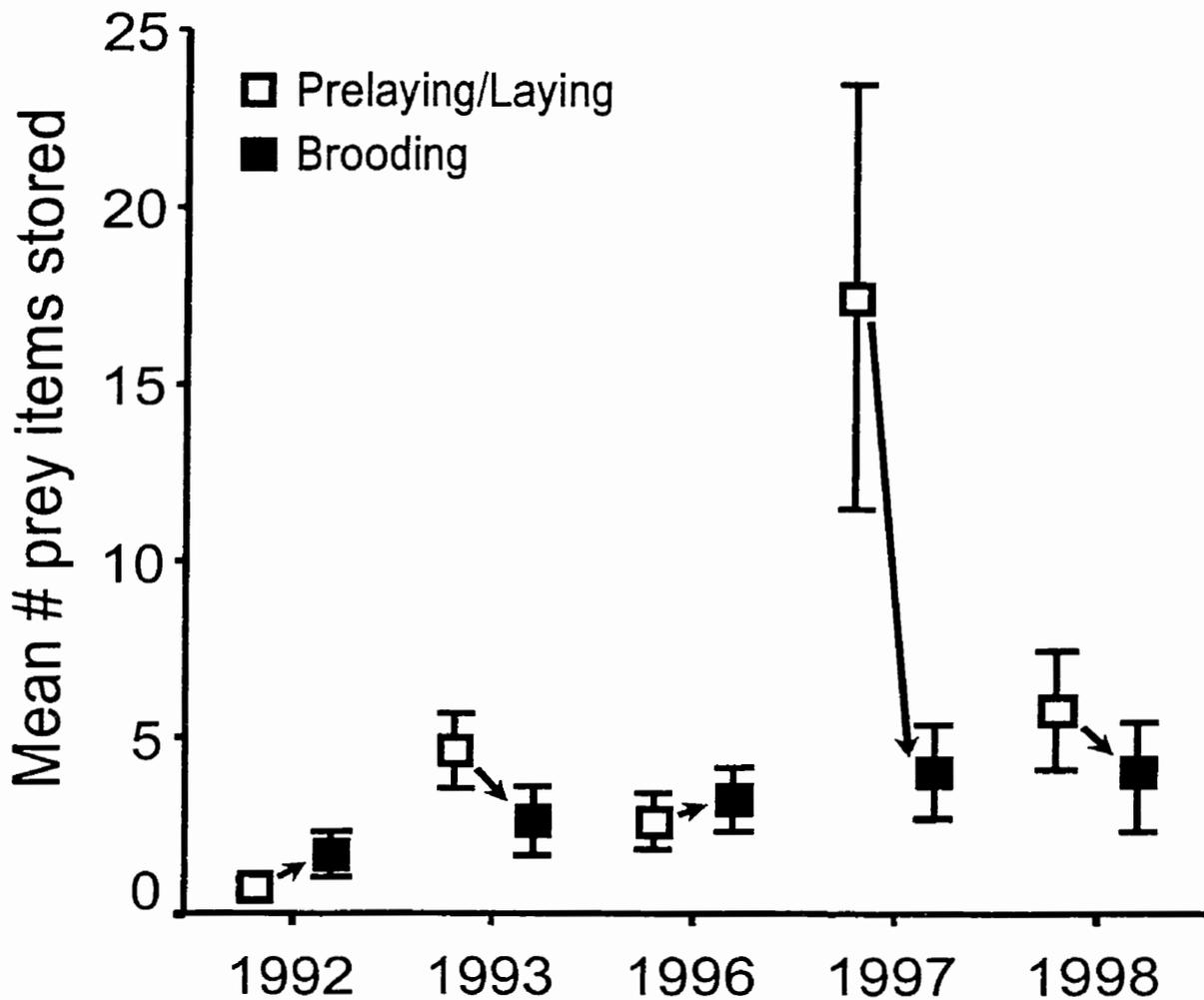


Figure 3-1. Mean (\pm SE) number of vertebrate prey items cached (an index of food intake) in nests of Burrowing Owl pairs at the time of egg production (prelaying plus laying) and during brooding in each of five years. Arrows connect the two mean prey-cache values within each year. Data are presented only for owls that remained unsupplemented both pre- and post-hatching. Number of pairs: 1992, $n = 5$; 1993, $n = 13$; 1996, $n = 6$; 1997, $n = 5$; 1998, $n = 5$.

Table 3-2. Hatching success (% eggs hatched per clutch, excluding nesting failures) for Burrowing Owls in relation to year and feeding treatment. No pairs were supplemented in 1997. *n* = number of pairs in each treatment.

Year	Supplemented			Unsupplemented		
	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>
1992	90.2	2.8	11	83.8	5.6	11
1993	90.8	2.8	14	91.2	2.4	23
1996	90.6	3.8	17	91.1	2.4	16
1997	--	--	0	90.8	2.8	20

Hatching asynchrony

Hatching asynchrony varied considerably among Burrowing Owl broods ($n = 108$). Generally, more than half of the eggs in a clutch hatched on the first day, with the remaining eggs hatching at one- or two-day intervals thereafter. Hatching span ranged between 1 and 7 days, with a mode and median of 4 days, and a mean of 3.8 days.

Clutch size explained a significant proportion (11%) of variation in hatching span when unsupplemented pairs from all years were analysed (Table 3-3), and the same was true when both supplemented and unsupplemented pairs were examined together (14% of variation). Because span relies on the day of hatch of first and last hatchlings, one would expect this measure to sometimes be sensitive to hatching failures: as the number of egg failures increases, so too should the probability that one of the failed eggs would have been either the first or the last egg to hatch. Regressions of hatching span on clutch size, when run separately for each 'number of eggs unhatched' category, were significant for 0, 1, and 2 unhatched eggs per clutch, but were non-significant for 3 and 4 unhatched eggs (Table 3-3). This pattern of significance resulted whether all pairs, or only unsupplemented pairs, were included in regressions. Exclusion of the 13 (12% of 108) nests with either 3 or 4 unhatched eggs, increased the percentage of hatching-span variation explained by clutch size to 16% for unsupplemented pairs alone ($P = 0.002$, $n = 58$) and to 17% for supplemented and unsupplemented pairs combined ($P < 0.001$, $n = 95$).

Presumably, hatching pattern in Burrowing Owls, as in other altricial species (Magrath 1990), results largely from the timing of incubation onset during laying (Magrath 1992). Assuming that the owls use simple rules for deciding when to begin incubation, one can predict how hatching spans should vary with changes in clutch size. For example, if a female began incubation on the penultimate egg, hatching span would be about 1.5 days (the average laying interval for one egg), regardless of clutch size. If she began incubating on the third-to-last egg, hatching span would be 3 days; if onset was on the fourth-to-last egg, span would be 4.5 days; and so on. Alternatively, if owls began incubation after a set number of eggs had been laid, hatching span would increase consistently with increases in clutch size. Although observed hatching spans for the owls in this study increased with clutch size, incubation did not appear to begin after a set number of eggs had been laid (Fig. 3-2). When clutch size was ≤ 8 eggs, incubation seemed to begin before the 5th or 6th egg; whereas, when clutch size was ≥ 9 eggs, incubation began sometime after the 6th or 7th egg had been laid.

To explore the influence of food on hatching span without the confounding effects of clutch size and number of unhatched eggs, residuals from the separate regressions of

Table 3-3. Covariation of hatching span and clutch size for Burrowing Owl pairs in relation to number of eggs failing to hatch per clutch. Data are combined for all years (1992, 1993, 1996, 1997).

# Eggs unhatched	Pairs included ^a	# Nests	% Nests	Regression of hatching span on clutch size			
				Y-intercept	Slope	r ²	P
0	Unfed only	31	46	0.28	0.43	0.12	0.059
0	Fed & Unfed	50	46	-0.12	0.47	0.13	0.010
1	Unfed only	19	28	-3.34	0.80	0.24	0.032
1	Fed & Unfed	34	32	-1.96	0.64	0.25	0.002
2	Unfed only	8	12	-5.20	0.90	0.88	0.001
2	Fed & Unfed	11	10	-3.02	0.68	0.55	0.009
3	Unfed only	6	9	1.00	0.25	0.02	0.783
3	Fed & Unfed	8	7	2.34	0.13	0.01	0.845
4	Unfed only	3	5	—	—	—	—
4	Fed & Unfed	5	5	3.88	-0.13	0.06	0.685
Pooled	Unfed only	67	100	-0.08	0.43	0.11	0.007
Pooled	Fed & Unfed	108	100	-0.33	0.46	0.14	<.001

^a 'Unfed only' means only pairs not supplemented with food at the time of egg laying were included in the analysis; 'Fed & Unfed' indicates that both supplemented and unsupplemented pairs were included.

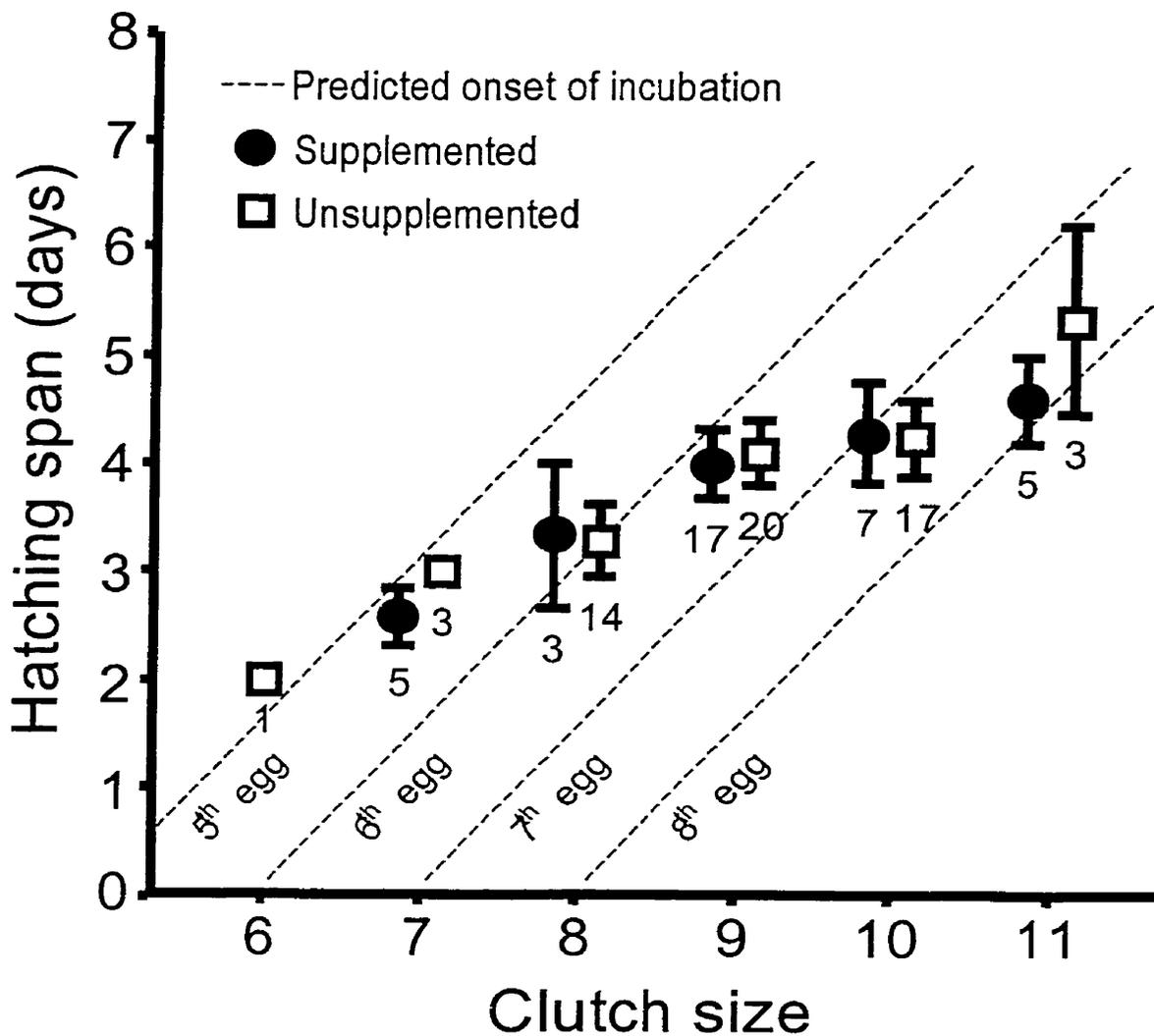


Figure 3-2. Mean (\pm SE) hatching spans for food-supplemented and control pairs (1992, 1993, 1996, 1997) in relation to clutch size. Only nests with fewer than three unhatched eggs were included (twelve nests excluded). Numbers of pairs are shown below each mean. Reference lines indicate hypothetical relationships between hatching span and clutch size if pairs had all started to incubate after the same egg number (after the 5th egg, or after the 6th egg, *etc.*). Alternatively, hatching span would have been invariant with respect to clutch size if incubation had begun consistently after the ultimate egg (hatching span = 0 days), the penultimate egg (1.5 days), the antepenultimate egg (3 days), *etc.*

hatching span on clutch size (Table 3-3, 'Fed & Unfed', number of eggs unhatched = 0, 1, and 2) were used in place of hatching span for all further analyses (the 13 nests with 3 or 4 unhatched eggs were excluded). For each nest, these residuals (hereafter, hatching-span deviations) provided a measure of the deviation of observed from expected hatching span, given the pair's clutch size and number of failed eggs.

If pairs began incubation early (causing hatching span to be large) when food intake was high, one would expect a negative relationship between hatching-span deviation and prey-cache size during laying. However, hatching-span deviation was unrelated to prey-cache size for unsupplemented pairs within each year (1992, $r = -0.01$, $P = 0.99$, $n = 7$; 1993, $r = -0.20$, $P = 0.38$, $n = 22$; 1996, $r = 0.47$, $P = 0.09$, $n = 14$; 1997, $r = 0.001$, $P = 1.00$, $n = 13$) or for all years combined ($r = 0.10$, $P = 0.47$, $n = 56$; Fig. 3-3).

Mean deviation of hatching span in unsupplemented pairs did not vary among the four study years (ANOVA, $F = 0.64$, $P = 0.59$; Fig. 3-4). Furthermore, there was no influence of supplemental feeding on hatching-span deviation (2-way ANOVA, $F = 0.09$, $P = 0.76$; Fig. 3-4, 1997 excluded), no effect of year-of-experiment ($F = 0.46$, $P = 0.64$), and no year-by-treatment interaction ($F = 1.7$, $P = 0.19$).

The use of laying date to alternately assign pairs to either supplemented or control groups ensured that laying dates were distributed similarly for the two groups. Therefore, both supplemented and control pairs were combined when testing for seasonal variation in hatching span. Laying date and hatching span were unrelated within years (1992, $r = 0.03$, $P = 0.89$, $n = 20$; 1993, $r = -0.18$, $P = 0.29$, $n = 37$; 1996, $r = -0.26$, $P = 0.14$, $n = 32$; 1997, $r = -0.03$, $P = 0.89$, $n = 19$), but showed a significant negative relationship when breeding events from all years were considered together ($r = -0.20$, $P = 0.04$, $n = 108$). However, laying date was unrelated to hatching-span deviation, whether years were analysed separately (1992, $r = 0.29$, $P = 0.28$, $n = 16$; 1993, $r = 0.02$, $P = 0.90$, $n = 35$; 1996, $r = -0.06$, $P = 0.75$, $n = 29$; 1997, $r = 0.34$, $P = 0.22$, $n = 15$) or together ($r = 0.02$, $P = 0.84$, $n = 95$). Thus, the association between laying date and hatching span disappeared once the influence of clutch size on hatching span was removed.

Predictability of food

If seasonal changes in food availability were fairly consistent among years, pairs could potentially use their rate of food intake during egg formation to forecast their food intake during the nestling period. In contrast to this scenario, the direction of change for mean prey-cache size between the laying period and the early-nestling period varied for the owl population among years (Fig. 3-1). In 1992 and 1996, mean prey-cache size appeared to increase slightly between laying and hatching; in 1993 and 1998, mean prey-cache size

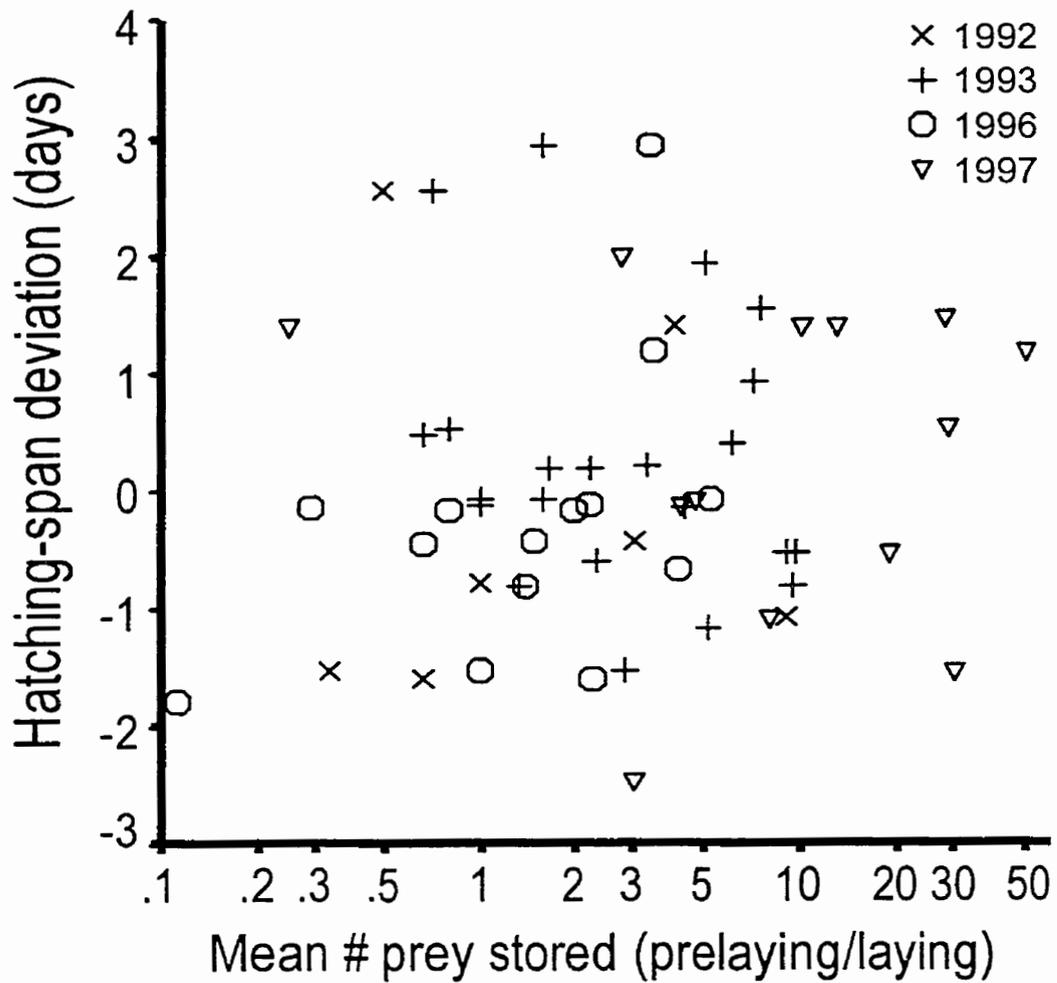


Figure 3-3. Relationship between hatching-span deviation (hatching span after accounting for effects of clutch size and number of unhatched eggs) and amount of prey cached by each pair around the time of egg production. Each symbol indicates a single breeding event that is coded by year. The X-axis is on a log scale.

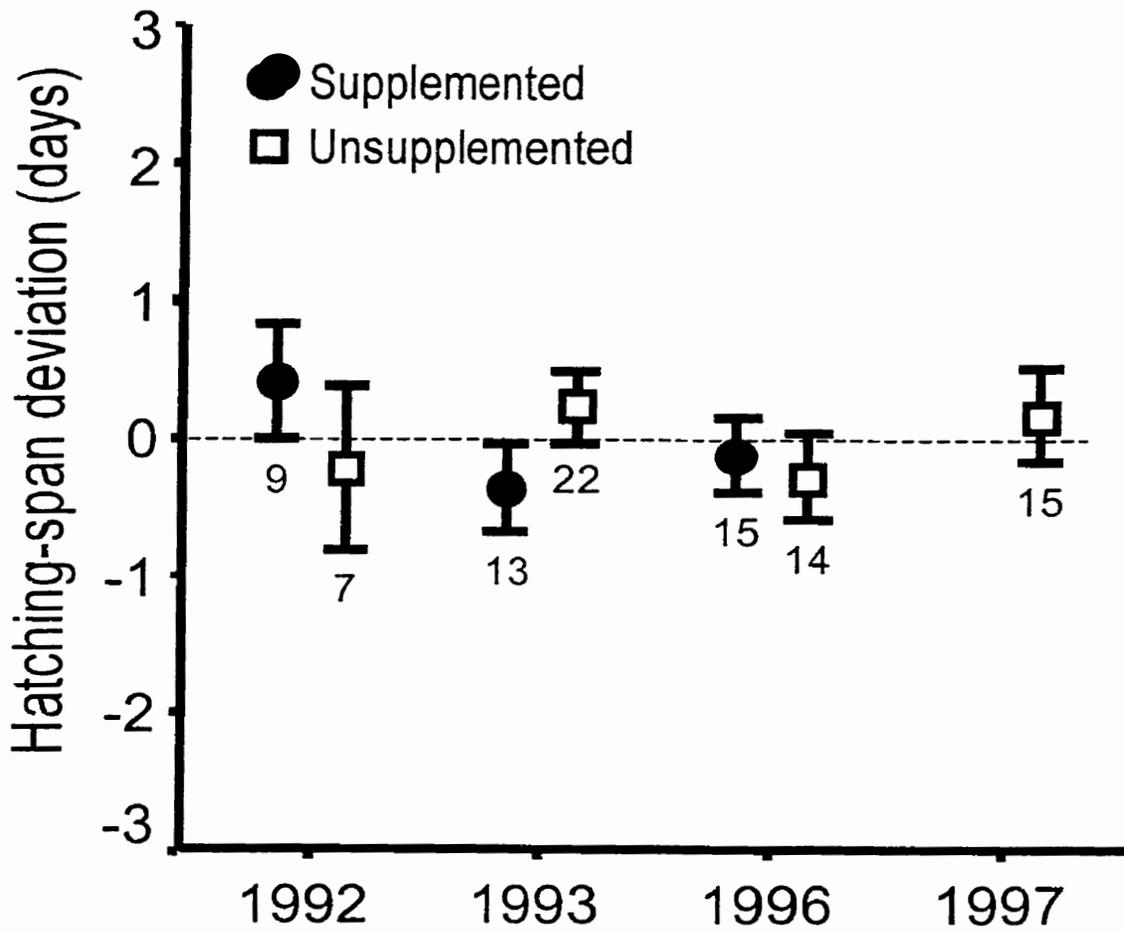


Figure 3-4. Mean (\pm SE) hatching-span deviations for food-supplemented and control pairs in 1992, 1993, and 1996. The mean (\pm SE) is also provided for unsupplemented pairs in a high-food year, 1997. Only nests with fewer than three unhatched eggs were included, and number of pairs is shown below each error bar. Y-axis is scaled to the range of observed values.

appeared to decrease; and in 1997, mean prey-cache size showed a substantial decrease between laying and hatching. This means, for example, that prey-cache sizes in 1997 and 1998 differed dramatically at the time of laying but were very similar after hatching.

I also assessed whether individual pairs could gain reliable information about post-hatch feeding conditions from their own food intake during laying. Within-year tests for a relationship between each pair's prey-cache size at laying and at hatching were non-significant (1992, $r = 0.81$, $P = 0.10$, $n = 5$; 1993, $r = 0.16$, $P = 0.61$, $n = 13$; 1996, $r = 0.76$, $P = 0.08$, $n = 6$; 1997, $r = -0.13$, $P = 0.84$, $n = 5$; 1998, $r = 0.45$, $P = 0.45$, $n = 5$); however, these results should be interpreted with caution as sample sizes were small. When unsupplemented pairs from all years were combined in the same analysis, the relationship approached significance ($r = 0.33$, $P = 0.06$, $n = 34$; Fig. 3-5), with individual prey-cache size at laying accounting for 11% of the variation in prey-cache size after hatching.

DISCUSSION

Effects of food on hatching asynchrony

Observed variation in hatching asynchrony was inconsistent with both the energy constraint and facultative manipulation hypotheses: hatching span (with effects of clutch size removed) was unrelated to prey-cache size for pairs at the time of egg laying, it was unaltered by a year of super-abundant food (1997), and it was unaffected by experimental provisioning of extra food during laying. This lack of food-effects could not be explained by reduced male foraging when food was good (*e.g.*, Poole 1985) because prey caches and pellet-regurgitation rates during laying were much higher in 1997 than in other years, and were significantly higher for supplemented pairs than for control pairs (Chapter 2).

The absence of energetic constraints at the start of incubation agrees with the absence of energetic constraints for other breeding parameters in the Burrowing Owl population; namely, laying date, clutch size, egg volume (Chapter 2), and hatching success (Table 3-2). Early in the nesting season, female birds of prey may typically be free of both time-conflicts and energy constraints, as nearly all of their diet is supplied by males from prelaying until the completion of brooding (Wiebe and Bortolotti 1994, Stoleson and Beissinger 1995). Male Burrowing Owls appear to have little trouble delivering enough food for females to simultaneously lay and incubate large clutches, even though eggs are produced at a more rapid rate than in other Strigiformes and Falconiformes, which typically lay eggs at intervals of ≥ 2 days (Lack 1968:187, Southern 1970, Newton 1977, Eckert 1987, Wilson *et al.* 1986). This lack of limitation on the timing of incubation

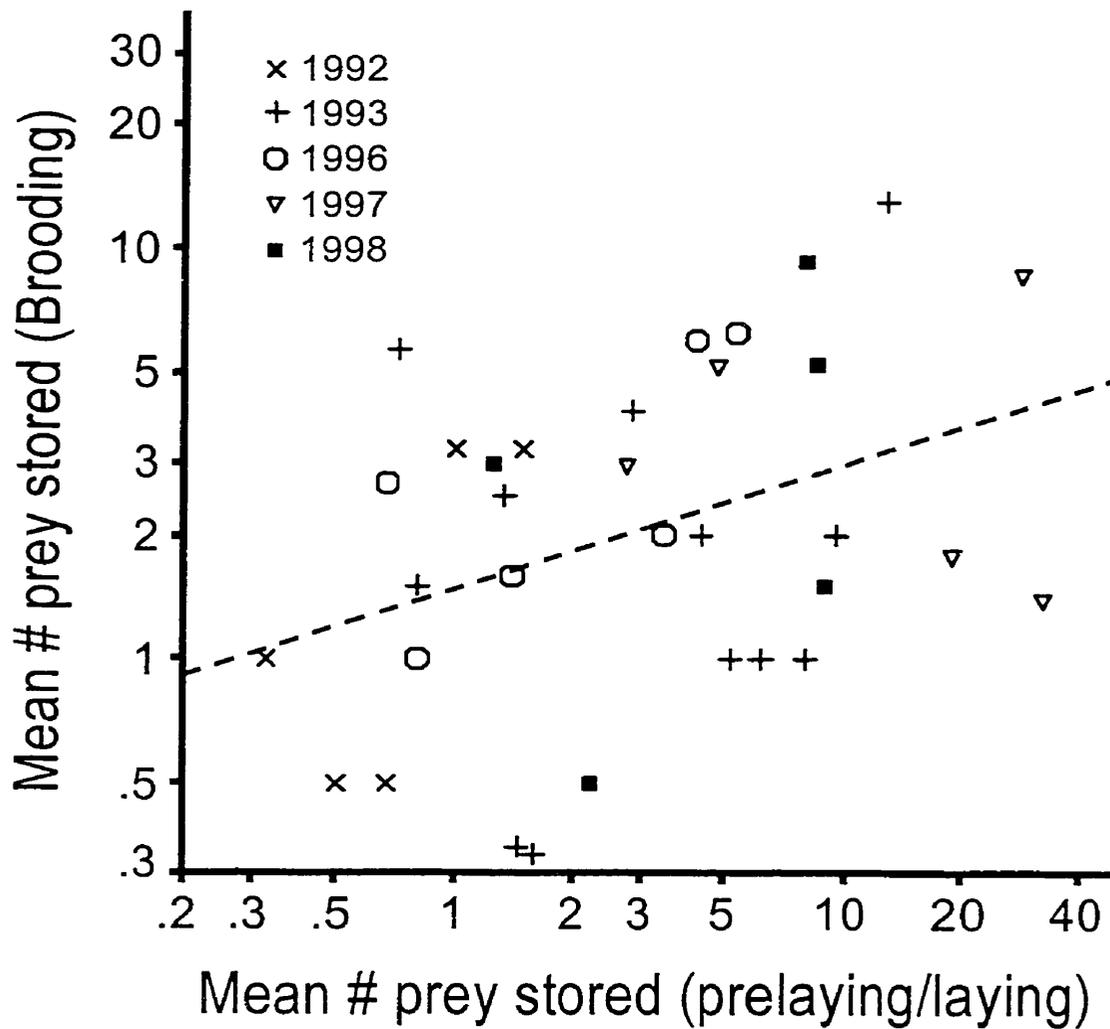


Figure 3-5. Relationship between prey-cache size at time of egg production and prey-cache size during brooding for each pair. Data are presented only for owls that were unsupplemented during both pre- and post-hatching. Dashed line calculated using least-squares linear regression for all years combined (equation: $Y = 0.11X + 0.35$). Each symbol indicates a single breeding event that is coded by year. Both axes are log scale.

contrasts with results from studies of passerines, which often delay incubation when food is scarce during laying (Slagsvold 1986, Enemar and Arheimer 1989, Slagsvold and Lifjeld 1989, Nilsson 1993, Nilsson and Svensson 1993).

The results of this investigation are also at odds with previous studies of raptors, which have shown that synchrony increases when food conditions are good (Wiebe and Bortolotti 1994, Green and Krebs 1995). These other experiments provided supplemental food during prelaying, so it is possible that Burrowing Owls did not react to supplementation because extra food was provided only during laying. This appears unlikely, however, because natural prey caches during prelaying and laying were between 3 and 16 times larger on average in 1997 than in other years (Fig. 1), yet hatching span showed no annual variation.

For facultative manipulation to evolve in Burrowing Owls, asynchronous hatching must provide food-dependent benefits during the nestling period (see 'nestling food-limitation hypotheses' in Table 3-1), and must also have associated costs. Asynchrony would then be optimal when food availability was low and synchrony optimal when food availability was high, so parents would do best by facultatively adjusting their hatching spans according to food intake (Wiebe 1995). Many of the conditions under which such beneficial adjustment is likely to develop exist in the Burrowing Owl study population. Nestling survival is strongly influenced by food intake during the nestling period (Chapter 4) and mortality is focussed on last-hatched chicks. Further, youngest nestlings from broods with naturally large hatching spans frequently die, even when provided with extra food from the time of hatching (unpubl. data). However, the clearest experimental test of costs and benefits of asynchrony in Burrowing Owls — the simultaneous manipulation of hatching spans and nestling food supply (Magrath 1989, Wiebe and Bortolotti 1995) — has not been conducted.

Food predictability

Another premise of the facultative manipulation hypothesis is that nestling food-availability is at least partially predictable at the start of incubation (Wiebe and Bortolotti 1994). In this scenario, one would expect a correlation between measures of food intake early in spring and food intake later in the season. Few studies of hatching asynchrony have tested the validity of this premise (Wiebe *et al.* 1998), but seasonal predictability of food has been confirmed for both species known to exhibit facultative manipulation of hatching asynchrony. Prey abundance in American Kestrels was correlated between spring and mid-summer (Wiebe 1995), and food-delivery rates in Osprey were correlated between prelaying and brooding (Green and Krebs 1995). In contrast, cache size for

Burrowing Owl pairs showed no (or very low) seasonal correlations. This suggests that food intake during egg production may not have been a reliable indicator of food intake during early brood-rearing, and could not serve as a proximate cue by which to adjust the onset of incubation. Facultative manipulation may, therefore, be unfeasible for Burrowing Owls. The lack of seasonal predictability of food intake may also explain the failure of Burrowing Owl pairs to adjust their clutch or egg sizes according to food intake during laying (Chapter 2). When birds are unable to predict future food conditions, their best option may be to exhibit a moderate level of asynchrony that balances future costs and benefits (*e.g.*, Mock and Ploger 1987), regardless of food conditions during laying (Wiebe 1995). Perhaps even if average conditions during the nestling period were predictable, Burrowing Owls might still show a fixed level of asynchrony given that short-term food shortages often result during the nestling period from rainy weather (Chapter 4) – a phenomenon that is presumably unpredictable.

Alternatively, rather than suggesting unpredictable seasonal food variation, the low correlation between food intake during laying and brooding may simply reflect the inadequacy of prey-cache size as an index for number of prey captured and eaten by owls. Annual variation in prey abundance agreed generally with annual variation in prey-cache size for the owl population (Chapter 4), and mean prey-cache size and pellet- regurgitation rate correlated positively within pairs during laying ($r = 0.54$, $P < 0.001$, $n = 59$; Chapter 2). However, I cannot exclude the possibility that prey-cache size (at the level of the individual) gave a poor indication of food intake during brooding. Male hunting yield would have been a better measure of energetic intake, but is extremely difficult to determine for wild birds (Masman et al. 1986), especially when they are nocturnal foragers (Wijdnants 1984). Difficulties in measuring food intake may explain why few avian studies have attempted to assess within-season predictability of food (Wiebe et al. 1998).

Other intraspecific variation

To illustrate extremes in the range of possible hatching patterns for birds with large clutches, I outline reproductive traits for four altricial species below. The first two species, with the highest degrees of asynchrony recorded for birds (Stoleson and Beissinger 1995), are the Barn Owl (*Tyto alba*) and the Green-rumped Parrotlet (*Forpus passerinus*). Barn Owl pairs in Mali lay eggs at 2-day intervals, producing clutches of 2–11 eggs (Wilson *et al.* 1986). Females apparently start incubation after their first eggs, as hatching is completely asynchronous within broods, varying between 2 to 22 days in direct proportion to clutch size. Green-rumped Parrotlets in Venezuela also begin incubation after laying first eggs, causing hatching spans to vary directly with clutch size

(4–10 eggs). However, because egg-laying intervals are between 1 and 2 days, the completely asynchronous hatch lasts only 6–15 days (Beissinger and Waltman 1991; Stoleson and Beissinger 1995). Marsh Tits (*Parus palustris*) and Blue Tits (*P. caeruleus*) in Sweden also lay large clutches (5–11, and 5–15 eggs, respectively; laying rates = 1 egg/day), but have hatching spans of only 0.5–2 days (Nilsson 1991, 1993; Nilsson and Svensson 1993). These tits typically start incubating on the ultimate or penultimate egg, so hatching spans are small and invariant with respect to clutch size, unlike the spans of Barn Owls and parrotlets.

Burrowing Owls in the present study exhibited hatching patterns intermediate to the two extremes illustrated by the above species. Incubation onset must not have been constant relative to the end of laying, or hatching asynchrony would have been invariant with respect to clutch size. Nor could incubation have begun consistently after a particular number of eggs were laid, or else each 1-egg increase in clutch size would have been associated with a 1.5-day increase in hatching span (Fig. 3-2). Instead, pairs seemed to adjust incubation behaviour, and hence hatching spans, differentially according to clutch size. Perhaps clutch size provides some indication of the potential levels of food stress that can be expected during the nestling period (Magrath 1992), or risk of complete nest-failure goes up with brood size, necessitating greater asynchrony with larger clutches (Wiebe *et al.* 1998). The fact that owls did not increase hatching span monotonically with increasing clutch sizes suggests that high levels of asynchrony are associated with high costs. Perhaps selection tends to ensure that incubation does not begin too early in relation to clutch completion, as mortality of last-hatched young likely increases steeply with increased age-difference within broods (see also Haftorn 1981). The rapid laying rate in Burrowing Owls may be another trait that allows large broods to hatch without extreme asynchrony.

The changes in hatching span that occurred as clutch size varied refutes one hypothesis proposed to explain hatching asynchrony – the hormonal hypothesis (Mead and Morton 1985). This hypothesis suggests that incubation onset in birds is controlled by the same hormone that causes termination of ovulation, in which case incubation should invariably begin on the penultimate egg and hatching span should equal the laying interval between the penultimate and ultimate eggs, regardless of clutch size. Because hatching asynchrony has now been shown to vary with clutch size in several species (reviewed in Magrath 1990, Stoleson and Beissinger 1995), the hormonal hypothesis appears to be generally unfounded.

Patterns of seasonal variation in hatching span in the present study also refute another hypothesis for asynchrony – the hurry-up hypothesis (Table 3-1). A main prediction of

this hypothesis is that hatching spans should increase late in the season, as parents attempt to save time for first-laid eggs by incubating and hatching them as early as possible. In some species, seasonal variation in hatching asynchrony (see Introduction) supports this prediction; however, hatching spans for Burrowing Owls actually decreased over the season when breeding events from all years were considered together. This association between hatching span and laying date disappeared once the influence of clutch size on hatching span was removed (see also Bryant 1978, and Wiebe *et al.* 1998). Thus, the hurry-up hypothesis was not supported by the findings in this study.

Burrowing Owls exhibited additional between-individual variation in hatching spans not accounted for by those proximate factors suggested to be most influential in birds – laying date, clutch size, and food conditions during laying. Future experimental manipulation of these main factors, and of other factors, in a variety of bird species, will likely provide considerable gains in our understanding of the proximate causes and ultimate functions of hatching asynchrony.

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CHAPTER 4

Energetic Bottlenecks for Breeding Burrowing Owls: Supplementation Experiments Comparing Food Limitation Among Three Nesting Stages

INTRODUCTION

Food supply is widely regarded as one of the most important factors determining the amount of investment in breeding by birds (Martin 1987, Nilsson 1994). Avian parental effort can be partitioned into three distinct stages: egg formation, incubation, and brood rearing. In theory, reproductive rates could be food-limited at any or all of these stages (Martin 1987). For altricial species, the predominant view is that parental feeding of young imposes the most severe energetic bottleneck (Murphy and Haukioja 1986, Bryant and Tatner 1988). This view stems primarily from the influential work of David Lack, who advocated that laying date, clutch size, hatching asynchrony, and brood reduction were all adapted to food limitation during the nestling period (Lack 1947, 1950, 1954, 1968). In contrast, other work with altricial species has shown reproductive limitation early in the breeding season, via proximate energetic constraints on egg-laying females (Perrins 1965, 1966, and 1970; Jones and Ward 1976; Murphy 1978; Pinowska 1979 in Murphy and Haukioja 1986; Hochachka and Boag 1987; Korpimäki 1987, 1989; Slagsvold and Lifjeld 1989; Nilsson 1993). Further still, some authors have used indirect evidence to argue that incubation is the most food-limited stage (*e.g.*, Mertens 1987, Siikamäki 1995, Gende and Willson 1997). For instance, Yom-Tov and Hilborn (1981) calculated energy stress for temperate birds, and suggested that incubation was the critical bottleneck during nesting. This half-century of debate underscores the need for experiments designed to compare the relative importance of food during each breeding stage in determining offspring number and quality.

Because manipulation of dietary intake is the most direct way to address questions of food limitation (Newton 1980, Martin 1987, Adams *et al.* 1994), supplemental feeding has been used frequently in avian breeding experiments (Boutin 1990). However, given that the nestling period is often assumed to be the most energy-limiting stage of breeding for altricial species, surprisingly few experiments have provided extra food solely during that stage. Rather, in most investigations, food supplementation started well before egg laying and continued through much of the reproductive cycle (Hogstedt 1981, Ewald and Rohwer 1982, Davies and Lundberg 1985, Arcese and Smith 1988, Dhindsa and Boag 1990, Soler and Soler 1996). Consequently, effects of food limitation during the nestling phase could not be separated from effects during earlier phases. Only a handful of studies in altricial species provided extra food to natural broods during the nestling period alone (Simons and Martin 1990, Richner 1992, Garcia *et al.* 1993, Verhulst 1994, Gende and

Willson 1997, and Wiehn and Korpimaki 1997). These food-supplementation studies ranged from 1 to 4 years in duration, and most found some evidence of food limitation. Unfortunately, demonstrating that food intake during the nestling period affects the number and/or size of fledglings gives no indication of the importance of food availability in the nestling stage relative to availability in other stages of the nesting cycle (Simons and Martin 1990, Wiehn and Korpimaki 1997). To accomplish this, supplementation must begin at different stages in the cycle for different breeding pairs, as first suggested by Hochachka and Boag (1987).

Here, I present results from food-supplementation experiments conducted over five years on the Burrowing Owl (*Athene cunicularia*). To test if food normally limits reproduction during the nestling period, I compared the quality (size, mass, condition) and quantity of fledglings between control pairs and pairs provided with extra food from hatching until fledging. In two of the years, I also fed a third subset of owl pairs from clutch initiation until fledging so that supplemental feeding started at different reproductive stages in the different treatments. To my knowledge, no previous experiment has shown how fledgling production is influenced by food during each nesting phase – egg-laying, incubation, and nestling-rearing. I also examined additional temporal aspects of food limitation by comparing the impact of long-term food shortage, during low food years, and short-term food shortage, during periods of adverse weather.

METHODS

Study area and study species

I studied Burrowing Owls in 1992, 1993, and 1996–1998 in the Grassland Ecoregion of Saskatchewan (Harris *et al.* 1983), on a 10 000 km² site (49°40'–50°35' N, 103°45'–105°40' E), containing the cities of Regina, Moose Jaw, and Weyburn. Rainfall data for each of these cities were obtained from Atmospheric Environment Service, Environment Canada. The owls in my study area nested in heavily-grazed pastures, which are interspersed amongst other agricultural fields. Normally, clutches are laid in underground chambers at the end of 2- to 3-m tunnels previously excavated by Richardson's ground squirrels (*Spermophilus richardsonii*) or by badgers (*Taxidea taxus*). In this investigation, most natural nest burrows were replaced with artificial nest burrows before egg laying each year (details in Wellicome *et al.* 1997). Some pairs in this study also nested in artificial nest burrows that had been installed in previous years. Artificial burrows were opened regularly to determine hatching date for each egg (see Chapter 3), numbers of hatched and fledged owlets, and numbers of prey items cached. Much of this information could not be collected at natural burrows because the nest chambers were inaccessible. I

was, however, able to count young at each natural burrow during three or more observation periods late in the nestling stage, when nestlings often stand outside of burrow entrances waiting for food deliveries from parents. Nestling mortality was quantified only for broods nesting in artificial burrows, and was diagnosed from evidence collected at the nest sites. Predation by large raptor species was established by the presence of large splatters of whitewash near plucked Burrowing Owl feathers or other remains close to nest burrows. Nestlings that died from starvation typically showed considerable weight-loss before death and any remains were always found inside nest burrows. Nestlings were often partially or completely eaten by other family members, as shown by the presence of Burrowing Owl body parts (feathers, bones, or leg bands) inside owl pellets.

Nesting chronology.— In the study population, clutches are typically initiated in the first half of May, with the laying period lasting from 8–17 days, depending on clutch size (see Chapter 2). First-hatch occurs 15–22 days after clutch completion, and hatching of all eggs in a clutch occurs over 1 to 7 days (Chapter 3). Nestlings are brooded for the first 2 weeks of their life, after which time they become very mobile, and can sometimes be seen standing out front of burrow entrances (Haug *et al.* 1993). At three weeks of age, owlets can walk between their nest burrow and nearby roost burrows (pers. observ.). By four weeks of age, most nestlings can complete short flights, and by five–six weeks, all are capable of sustained flight (Landry 1979, King 1996). It was not possible to establish exact fledging dates because, even after they are able to fly, nestlings seem to prefer to run along the ground and retreat into burrows upon approach. However, after approximately 40 days-of-age, most fledglings flew away from their burrow when approached, rather than retreating into it (pers. observ.). Therefore, for the purposes of this study, I considered each nestling to have fledged when it reached 41 days-of-age. I defined the nestling period as the time from hatching of the first egg until all surviving owlets had reached 41 days-of-age (age 0 = individual's hatch day). Because of nestling mortality and age disparities among siblings, the duration of the nestling period was a minimum of 41 days and a maximum of 47 days. Age of young was estimated at natural burrows based on feather development (Priest 1997) and ability to fly. Owlets were captured and measured at 17 natural burrows, in which cases the age of each nestling could be determined by comparing its morphometric measures to those of known-age owlets from artificial nest burrows (see *Nestling measurements* section). In these natural burrows, the calculated ages of oldest nestlings provided estimates of hatching date for each brood.

Nestling measures.— For individual identification, each bird that hatched in an artificial burrow was marked with a unique combination of colours by applying indelible ink to feathers on the insides of its legs. Colour-combinations were maintained until nestlings were approximately 16 days-of-age, and could be fitted with numbered U.S. Fish and Wildlife Service aluminum bands. Each nestling was weighed, and lengths of its tarsus, culmen, and wing chord were recorded every third day (1992) or every sixth day (1993 and 1996), from hatching until at least 41 days-of-age. Canadian populations of Burrowing Owls are not sexually dimorphic in mass or size (Clayton *et al.* in review), so nestling growth was analysed with both sexes combined. Because of time and funding constraints, nestlings were not measured in 1997 or 1998. As hatching was asynchronous within broods (Chapter 3), nestlings measured on the same day were often different ages. Therefore, to obtain same-age measures for all fledglings, I fitted each individual's data to a separate logistic growth curve (SPSS 1996), and used the resulting equation to calculate a measure for the individual at 41 days-of-age (see also Mock 1985). Two entire broods could not be measured in 1996 (one brood from each of the feeding treatments; see *Feeding experiments* section below for description of treatments) because they moved from their artificial nest burrow to nearby natural burrows while still quite young. These broods therefore had to be excluded from nestling growth comparisons. Measurements also could not be taken for a few other owlets that escaped capture near the end of the nestling period, but growth curves were successfully constructed for 90% of the nestlings in experimental broods included in 1992, 1993, and 1996 comparisons. Lengths of tarsus, culmen, and wing for each individual (at age 41 days) were then incorporated into a principal components analysis. Each bird's score on the first component (hereafter 'PC1') of the principal components analysis served as a measure of its structural size at fledging (Freeman and Jackson 1990). There was a significant positive association ($P < 0.001$) between mass and PC1 (both at age 41 days), but there was still substantial variation in mass not explained by PC1 ($r^2 = 0.49$). I used mass residuals from the linear regression of mass on PC1 as an index of fledgling condition (Brown 1996). Mass residuals measure deviation from expected mass given a bird's structural size: positive residuals indicate fledglings that are heavier than expected, and negative residuals indicate fledglings that are lighter (Hochachka and Smith 1991). Size, mass, and condition were averaged within broods before analysis, resulting in one value per nest for each of these measures. Growth and asymptotic mass have been shown to be greater for nestlings that hatch early in relation to their siblings (Landry 1979), and late-hatched nestlings are more likely to die than are their older nest-mates (pers. observ.). This means that broods with high nestling mortality likely contain older fledglings, on average, than

broods with low nestling mortality. Therefore, for each nest, I also calculated mean mass, size, and condition for only those fledglings that hatched early within each brood. I did this by averaging measures for fledglings that were among the first four hatchlings per nest (hereafter, 'oldest fledglings'; note that mean brood size at hatch was ≈ 8). I determined hatching order by recording both the extent of cracking on eggs that were pipping and the condition of down on recently hatched owlets (see Chapter 3).

Feeding experiments

Egg laying and incubation.— Every third pair, in 1993, and every second pair, in 1996, that began laying in an artificial burrow was assigned to be food-supplemented during laying; all other pairs in artificial burrows were not supplemented (see Chapter 2 and Appendix 1 for details). In 1996, additional pairs nesting in natural burrows, where laying date could not be determined, were included in the experiment. Each of these pairs in natural burrows was randomly assigned to either the supplemented or unsupplemented group according to their arrival date. Supplemental feeding began after the first egg (24 pairs) or the second egg (8 pairs) had been laid in artificial burrows, and started in the second week of May for pairs in natural burrows (2 pairs, 1996). Fed pairs were provided with 255 g of white laboratory mice every third day, equalling a rate of 85 g/day, which is more than three times the metabolic requirements for daily existence of an adult Burrowing Owl in captivity (mean = 26 g; Marti 1973). Dead laboratory mice were placed inside the tunnel of each nest, at least 60 cm beyond the burrow entrance. This placement ensured that only intended recipients had access to supplemented food, as Burrowing Owls vigorously exclude other birds from their nest (pers. observ.). Several lines of evidence showed that extra food was readily accepted: owls were often seen eating supplemented food immediately after it was provided, remains of laboratory mice (especially tails) were found inside nest chambers, and pure-white fur was found in regurgitated pellets at all fed nests. Supplemental feeding continued until all nestlings fledged or until the nesting attempt failed. Unfed pairs were also visited every third day and disturbed for the same duration as supplemented pairs.

Nestling period.— In 1992, 1993, 1996, and 1997, half of all pairs that were unfed during the pre-hatch periods, and that nested in artificial burrows, were assigned to be fed for the nestling period. To ensure that pairs supplemented only during the nestling period would have the same numbers of hatchlings as those pairs remaining unfed, nests were ranked by clutch size and by predicted hatching date, then alternately assigned to each experimental group. Assignment of pairs in artificial burrows in 1998 was similar to other years, except that approximately four-fifths of the previously unfed pairs were fed

after hatching to maximize the number of fed pairs for a separate, ongoing study (see Wellicome *et al.* 1997). Clutch size could be used as a criterion for assigning pairs to experimental groups only when nests chambers were accessible. Hence, for pairs in natural burrows, a coin toss determined whether each unfed pair from the pre-hatch period would remain unfed or become fed during the nestling period. Supplemental feeding of pairs in natural burrows began in the first week of June in 1992, 1997, and 1998, and in the second week of June in 1996. All supplemented pairs were provided with food at 3-day intervals, at a rate of approximately 85g/pair/day, for the duration of the nestling period. In the first half of the nestling period, only laboratory mice were used for supplemental feeding, but in the second half, a combination of laboratory mice and juvenile quail was used for each feeding ration. Food remains (tails, feathers, and bones) in all nests and regurgitated pellets of fed pairs confirmed that the owls were eating both quail and laboratory mice.

Natural prey

Vertebrate prey stored in the nest chambers of unfed pairs were counted at intervals of 2–6 days between the end of April and the beginning of August in each study year. When calculating cache means, I included all counts recorded inside an 80-day window (15 days before egg laying to 35 days after hatching date) at each unsupplemented nest. Virtually all vertebrate prey in caches were either deer mice (*Peromyscus maniculatus*) or meadow voles (*Microtus pennsylvanicus*). However, on occasion, caches also included passerines, sagebrush voles (*Lagurus curtatus*), prairie voles (*Microtus ochrogaster*), house mice (*Mus musculus*), shrews (*Sorex* spp.), northern grasshopper mice (*Onychomys leucogaster*), olive-backed pocket mice (*Perognathus fasciatus*), and tiger salamanders (*Ambystoma tigrinum*).

Relative abundance of small mammal prey was determined using Museum Special snap-traps baited with peanut butter. Trapped prey were predominantly deer mice and meadow voles, but sagebrush voles, prairie voles, house mice, shrews, northern grasshopper mice, and olive-backed pocket mice were also captured on occasion. Each trapline contained 10 snap-traps, spaced at 10-m intervals, and was checked every 24 hours for three consecutive days. The number of small mammals captured over each 3-day period was totalled and then standardised to the number of prey caught per 100 trap-nights. Traps triggered by something other than potential prey (*e.g.*, by cattle) were excluded from trap-night totals. Each trapline was run once in either June or July. Trapline locations were chosen at random within each of five habitat categories (see below). First, all fields within 875 m (average radius of foraging home ranges; Haug and

Oliphant 1990) of any nest site were classified according to habitat type. Then, a subset of fields was chosen at random from those available within each habitat category. One trapline was set in each randomly-chosen field. A total of 110 traplines were run in 1992, 95 traplines in 1993, and 46 traplines in 1997. Percentages of traplines in each habitat in 1992, 1993, and 1997, respectively, were as follows: 30, 31, and 35% in 'cereal crop'; 16, 14, and 15% in 'pasture'; 16, 14, and 13% in 'fallow/stubble'; 28, 29, and 26% in 'roadside ditches'; and 10, 12, and 11% in 'ungrazed grass or hayland'. The percentage of traplines set in each habitat type was thus very consistent over the three years. This allowed me to compare overall relative prey abundance among years by comparing annual means of number of prey captured per trapline (after conversion to number per 100 trap-nights) with all habitat types included.

Data analysis

A breeding attempt was recorded as failed if all eggs in a nest were found broken, buried or missing, or if an entire brood died or disappeared between successive nest checks well before the anticipated date of fledging. As hypotheses in this study concern the effects of food limitation on reproduction, and nest failures appeared to be random with respect to feeding treatments (Appendix 3), nest failures were excluded from analyses of reproductive parameters (see also Lack 1948, Simons and Martin 1990, Siikamaki 1998). In addition, one pair nesting in an artificial burrow in 1996, which received extra food starting at hatch time, was excluded after two of its feedings were inadvertently missed during the nestling period.

All statistical tests were performed using SPSS for Windows (SPSS 1996). Two-way ANOVAs were performed, with year and feeding treatment as factors, to test variation in the number of hatchlings, the percentage of hatchlings fledged, and the mass, size, and condition of owlets fledged by pairs nesting in artificial burrows. When examining differences in these variables between unfed pairs and pairs fed for the nestling period alone, data from all 5 years were included, except where fledgling mass, size, and condition were involved, as these data were collected in only 3 years (1992, 1993, and 1996). Because I collected data on hatching dates and number of fledglings for both natural and artificial burrows, I included 'type of nest burrow' as a factor in 3-way ANOVAs when comparing these two reproductive variables among the 5 years and between fed and unfed pairs. Since supplemental feeding of pairs from laying through to fledging was performed only in 1993 and 1996, I used data from those 2 years alone when testing for reproductive differences among all three experimental groups. Interaction terms were initially included in ANOVA models, but were subsequently excluded if non-

significant. In such cases, probability values for predictors were recalculated without interaction terms. Annual variation in prey abundance and prey-cache size was assessed using one-way ANOVAs (unfed pairs only). Test statistics for all ANOVAs were based on Type III sums-of-squares. When significant effects were detected, I performed pairwise multiple comparisons with Tukey's Honestly Significant Difference tests. Prior to parametric testing, prey-trapping and cache totals were transformed by $\log(X+1)$, and proportions of hatchlings fledged were arcsine transformed. However, untransformed data are presented in figures and tables for ease of interpretation. Because sample sizes were small, I chose to increase statistical power by setting α to 0.10 when testing fledgling measures. Because sample sizes were larger, in all other analyses P -values were considered significant only when less than 0.05. I calculated power (using observed parameter values) whenever P -values were non-significant but ≤ 0.20 .

RESULTS

Feeding experiments

Hatching.—Over the five study years, assigning nests to treatment and control groups according to clutch size and laying date successfully controlled for both initial brood size (number of hatchlings) and hatching date. Number of hatchlings did not differ among years or between controls and pairs fed during the nestling period (Table 4-1a). Similarly, hatching date did not differ between pairs assigned to be fed during the nestling period and those assigned to remain unfed, nor did it differ according to burrow type (artificial vs. natural). Hatching date differed among years (Table 4-1b), being later in 1996 than in any other year (Tukey tests, $P \leq 0.02$) except 1997 ($P = 0.29$), and later in 1997 than in 1998 ($P = 0.05$).

When some owls were supplemented for the entire breeding season, number of hatchlings and hatching date were unaffected by extra food during laying and incubation. Number of hatchlings did not differ among the three experimental groups or between the two years (1993 vs. 1996; Table 4-1c). Likewise, hatching date did not differ among the experimental groups, but it was generally later in 1996 than in 1993 (Table 4-1d).

Fledging.—Supplemental feeding during the nestling period had a dramatic influence on the number of fledglings produced by owl pairs (Fig. 4-1). Pairs that were fed from the time of hatching until fledging produced more young than did unfed controls ($F = 56.9$, $P < 0.001$; no influence of burrow type: $F = 0.61$, $P = 0.44$). The overall mean number of fledglings differed among years, as well ($F = 16.3$, $P < 0.001$). In 1997, fledgling production was higher than in any of the other 4 years (Tukey tests, $P \leq 0.02$ for all pair-wise comparisons), and pairs raised more fledglings overall in 1992 than in 1993 ($P = 0.01$). There was a significant interaction between year and treatment ($F = 9.22$, $P <$

Table 4-1. Mean \pm 1 SE number of hatchlings, hatching dates, and percentages of hatchlings fledged by food-supplemented and control Burrowing Owl pairs over five years. Pairs with failed nesting attempts have been excluded (see Appendix 3). Values in parentheses indicate number of owl pairs for which information was collected. *Number of hatchlings* and % of hatchlings fledged were determined for all pairs nesting in artificial burrows. *Hatching date* was determined for all nests in artificial burrows, and was also estimated for 17 additional pairs nesting in natural burrows (see *Methods*). Proportions of hatchlings fledged were arcsine-transformed for statistical analyses. The dashed rectangle labeled “c)” outlines data used in a 3-way ANOVA testing effects of year, feeding treatment, and burrow type (artificial vs. natural). The other dashed rectangles outline data used in 2-way ANOVAs, with year and feeding treatment as factors.

Treatment	1992	1993	1996	1997	1998
Number of hatchlings					
Unfed controls	8.3 \pm 0.9 (4)	8.1 \pm 0.5 (11)	7.8 \pm 0.5 (6)	8.8 \pm 0.6 (6)	7.8 \pm 0.6 (4)
Fed (hatching to fledging)	7.4 \pm 0.6 (5)	8.2 \pm 0.4 (10)	7.7 \pm 0.3 (6)	8.6 \pm 0.4 (9)	8.2 \pm 0.3 (20)
Fed (laying to fledging)	--	8.5 \pm 0.4 (14)	8.1 \pm 0.4 (16)	--	--
Hatching date (in June)					
Unfed controls	6.7 \pm 2.8 (6)	8.0 \pm 1.6 (11)	17.0 \pm 3.7 (6)	10.3 \pm 1.9 (10)	7.8 \pm 1.5 (8)
Fed (hatching to fledging)	8.4 \pm 1.0 (5)	9.3 \pm 1.5 (10)	13.8 \pm 2.9 (9)	11.8 \pm 1.8 (12)	5.9 \pm 1.1 (21)
Fed (laying to fledging)	--	10.3 \pm 1.8 (14)	17.3 \pm 1.5 (16)	--	--
% of hatchlings fledged					
Unfed controls	81.0 \pm 8.7 (4)	35.8 \pm 9.6 (11)	51.8 \pm 5.1 (6)	94.8 \pm 2.3 (6)	50.3 \pm 9.5 (4)
Fed (hatching to fledging)	100.0 \pm 0.0 (5)	93.8 \pm 2.1 (10)	79.9 \pm 8.0 (6)	96.3 \pm 1.9 (9)	88.2 \pm 3.5 (20)
Fed (laying to fledging)	--	93.5 \pm 2.7 (14)	80.8 \pm 2.7 (16)	--	--

^a year, $F = 1.11$, $P = 0.36$; treatment, $F = 0.06$, $P = 0.81$; year-by-treatment interaction, $F = 0.39$, $P = 0.82$.
^b year, $F = 1.13$, $P = 0.29$; treatment, $F = 0.52$, $P = 0.60$; year-by-treatment interaction, $F = 0.04$, $P = 0.97$.
^c year, $F = 6.26$, $P < 0.001$; treatment, $F = 0.07$, $P = 0.79$; burrow type, $F = 1.04$, $P = 0.31$; all interaction terms non-significant.
^d year, $F = 16.5$, $P < 0.001$; treatment, $F = 0.70$, $P = 0.50$; year-by-treatment interaction, $F = 0.50$, $P = 0.61$.
^e year, $F = 8.41$, $P < 0.001$; treatment, $F = 40.16$, $P < 0.001$; year-by-treatment interaction, $F = 4.11$, $P = 0.005$.
^f year, $F = 1.45$, $P = 0.23$; treatment, $F = 26.5$, $P < 0.001$; year-by-treatment interaction, $F = 3.90$, $P = 0.03$.

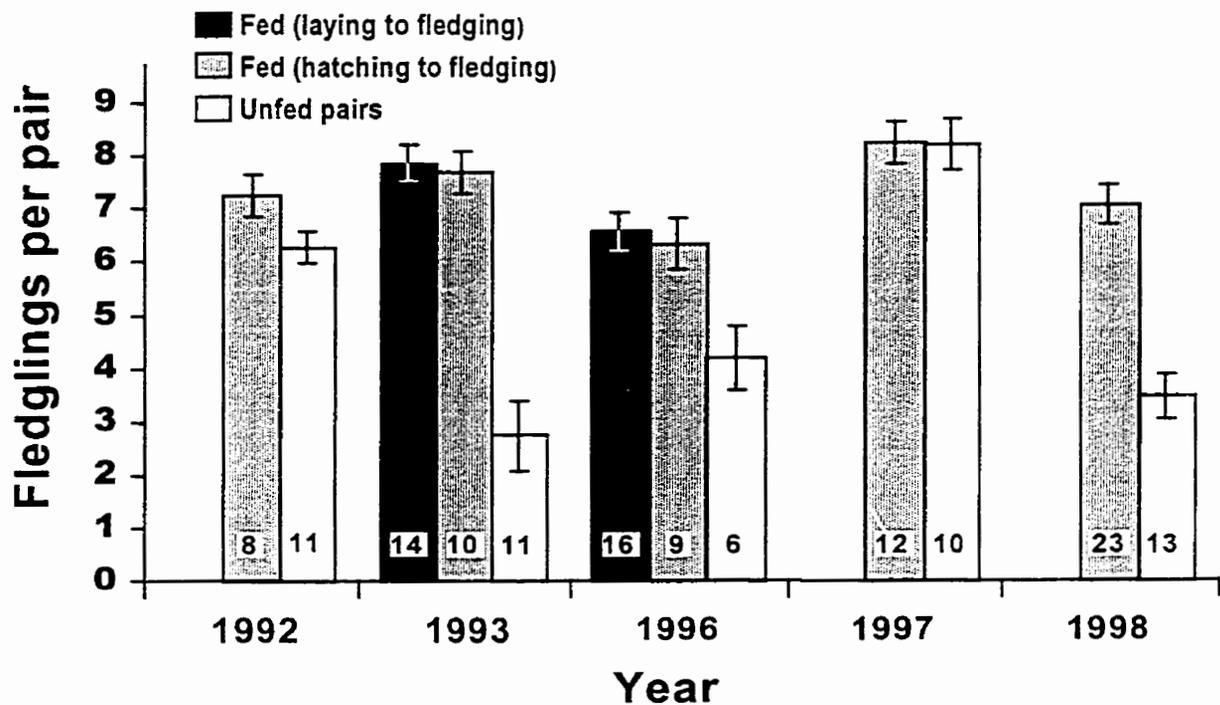


Figure 4-1. Mean number of fledglings (\pm SE) per Burrowing Owl pair, after exclusion of nest failures (see Appendix 3). Averaging over the five seasons, pairs supplemented after hatching fledged 47% more young than controls. Effects were much more dramatic in low-food years (mean = 70% for 1992, 1993, 1996, and 1998) than in the year with naturally high food (< 1% for 1997). Also, feeding throughout the breeding season caused no further increase in fledging rate over that resulting from supplementation during the nestling period alone. Number of pairs included in each year and experimental group is indicated at the base of each bar. Fledging data are combined for pairs in both natural and artificial burrows. See Table 4-1 for numbers of nests in artificial burrows.

0.001), indicating that the degree of food limitation differed substantially among the 5 breeding seasons. In 1993 and 1996, when some pairs were also fed from egg laying through to fledging, there was a significant effect of treatment on number of fledglings ($F = 33.8$, $P < 0.001$). Pairs in both fed groups fledged significantly more young than did unfed pairs (Tukey tests, $P < 0.001$ for the two pair-wise comparisons); whereas, offspring production for pairs fed through the egg-laying, incubation, and nestling periods was no higher than for pairs fed in the nestling period alone ($P = 0.97$). The 2-way ANOVA did not show a difference in fledgling output between the two years ($F = 1.04$, $P = 0.31$) but revealed a significant year-by-treatment interaction ($F = 4.73$, $P = 0.01$), suggesting that the degree of food limitation differed between the two years.

Among-year and among-treatment variation in the percentage of hatchlings fledged mirrored variation in the number of fledglings. Over the five years in which birds were supplemented with extra food during the nestling period, fed pairs fledged a higher percentage of their hatchlings than did unfed pairs (Table 4-1e; artificial burrows only). The overall percentage of hatchlings fledged differed among years, as well, being lower in 1993 and 1996 than in 1992 and 1997 ($P \leq 0.02$ for each pair-wise comparison), and lower in 1993 than in 1998 ($P = 0.02$; $P > 0.10$ for all other between-year comparisons). In addition, there was a significant year-by-treatment interaction. Examining only 1993 and 1996 data, the percentage of hatchlings fledged per brood did not differ between years, but did differ among treatments (Table 4-1f). Percentages were lower for unfed broods than for broods in either fed treatment ($P < 0.001$ for both pair-wise comparisons), but were very similar for pairs fed all season and pairs fed only during brood-rearing ($P = 0.87$). There was also a significant year-by-treatment interaction.

Nestling-survivorship curves further illustrate the effects of supplemental feeding on fledging success and show the ages at which nestling mortality occurred (Fig. 4-2). Unfed owlets died in only the first half of the nestling period in 1992, 1997, and 1998, but mortality appeared to be unrelated to age in 1993 and 1996. Of all deaths ($n = 176$), 2 (1%) resulted from leg-joint infections, 2 (1%) from navel infections (yolk-sacs did not fully retract), 3 (2%) from predation by large raptors late in the nestling period (when owlets were away from their burrows), and 169 (96%) from food shortage. Of the 169 nestlings that died from food shortage, 13 (8%) were found emaciated but otherwise intact, 32 (18%) were partially eaten, and 124 (73%) were completely consumed by their siblings or parents. Ninety-six of these 169 nestlings had been weighed within 5 days of their death. Fourteen nestlings (15%) showed normal patterns of weight gain prior to death, but 82 nestlings (85%) experienced weight loss, or a reduced rate of weight gain, before they died.

Fledgling measures.— Mean fledgling mass per brood (Table 4-2) was not significantly

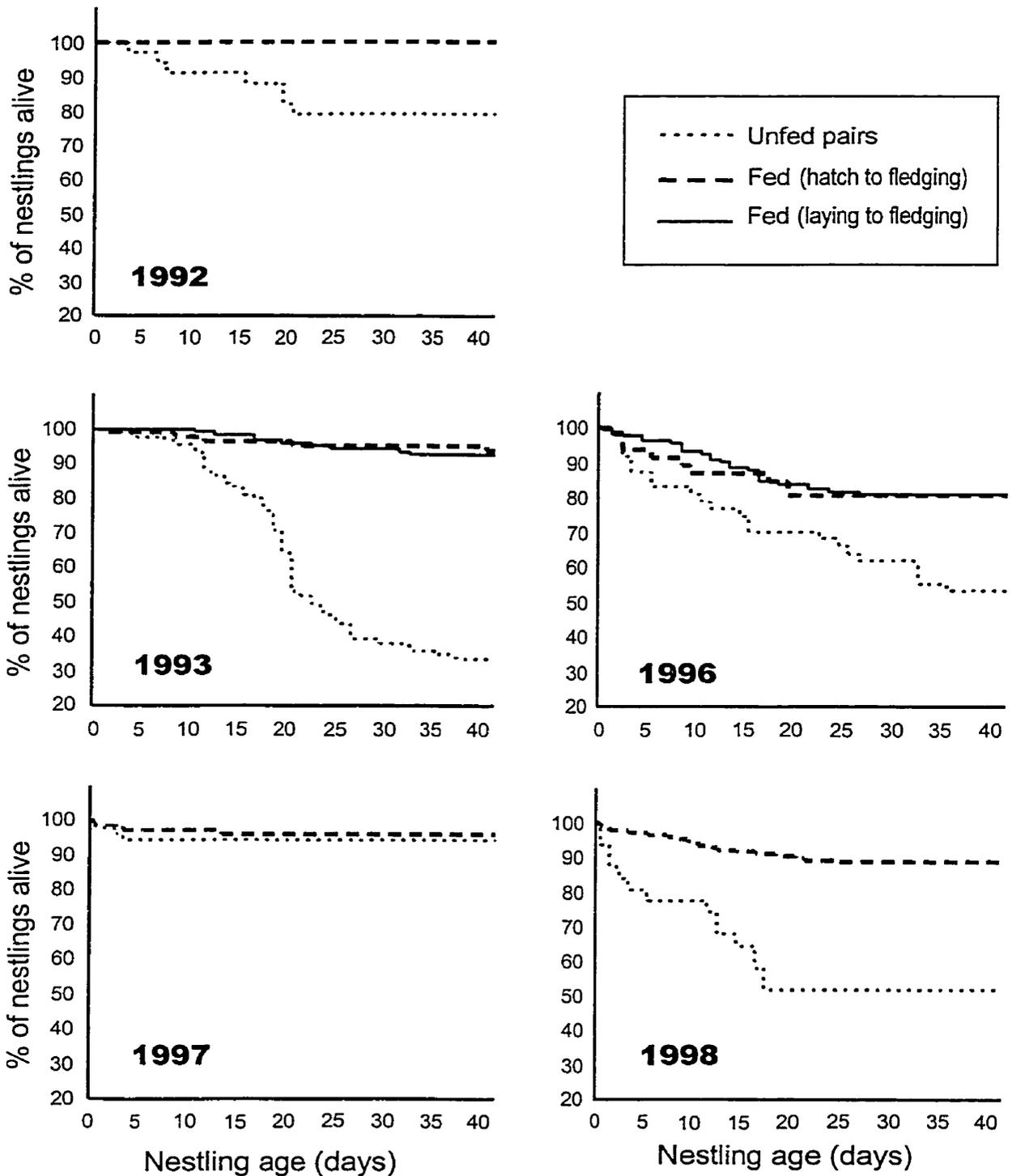


Figure 4-2. Survival of nestlings in artificial burrows from age 0 to 41 days (age 0 = individual's hatch day) in 5 years and 2 or 3 experimental groups. The numbers of hatchlings in 'Unfed' and 'Fed (hatching to fledging)' groups, respectively, were 33 and 37 (1992), 89 and 82 (1993), 47 and 46 (1996), 53 and 77 (1997), and 31 and 164 (1998). The number of hatchlings in the 'Fed (laying to fledging)' treatment was 119, in 1993, and 130, in 1996.

affected by year or supplemental feeding, whether two experimental groups over three years were examined (Table 4-3a) or three experimental groups over two years (Table 4-3b). *P*-values for year-by-treatment interactions were non-significant but somewhat suggestive for both tests (Table 4-3a, b), likely because fledglings in 1993 control broods tended to be slightly heavier on average than those in fed broods but slightly lighter on average in the other years. When only oldest fledglings were included in brood averages (Table 4-2), supplemental feeding during the nestling period increased average fledging mass significantly over that of controls in the three study years (Table 4-3a). However, when mass of oldest nestlings was examined for all three experimental groups in 1993 and 1996 alone, no significant effects of treatment or study year were apparent (Table 4-3b). Interaction terms were non-significant in both of the above analyses, as effects were in the same direction in every year.

Whether all fledglings or only oldest fledglings were included in brood means (Table 4-2), owlets were structurally smaller in unfed broods than in broods receiving extra food from hatching until fledging in all three years (Table 4-3a). Likewise, when all three treatments in 1993 and 1996 were analysed, supplemental feeding had a significant influence on fledgling size, mainly because fledglings from broods fed for the entire season were larger than fledglings from unfed broods (Table 4-3b). When only oldest fledglings in broods were examined, fledglings in both feeding treatments were significantly larger than fledglings in control broods. Owlets from broods fed from laying until fledging were similar in size to owlets from broods fed from hatching to fledgling, whether all fledglings were examined or only oldest fledglings (Table 4-2, Table 4-3b).

In 1992, 1993, and 1996, owlet condition was unaffected by year or by food supplementation during the nestling period (Table 4-2, Table 4-3a). However, when all three experimental groups were examined, fledgling condition was significantly better overall in 1993 than in 1996, and there was also a non-significant overall tendency for fledglings from control broods to be in slightly better condition than fledglings from fed broods (Table 4-3b).

Annual comparisons

Further interpretation of annual differences in reproductive food limitation required an assessment of yearly variation in key environmental factors.

Precipitation.— Mean monthly rainfall during the breeding season in the Regina area over the past 50 years (1948–1998) has typically been highest in June and July, and lowest in August and May (Fig. 4-3). Total monthly precipitation during the 5-year study varied substantially within and among years (Fig. 4-3). All months in 1992 experienced near-average rainfall, except for June, which had approximately half the usual amount.

Table 4-2. Fledgling mass (g), structural size, and condition, in relation to year and treatment (only birds in artificial nest burrows). Means (± 1 SE) of brood means are given for 'All fledglings' and for '1st four hatched' fledglings (oldest siblings within each brood). Size values are scores from the first-axis of a principal components analysis (PC1), incorporating length of tarsus, wing, and culmen at 41 days-of-age. Condition values are residuals (in grams) from a linear regression of fledgling mass on PC1 at 41 days: zero represents the overall mean condition after size has been taken into account; a value < 0 indicates poorer condition than expected; and a value > 0 indicates better condition than expected. '# Broods' was used as sample size for statistical comparisons.

Treatment	Mass (g)		Size (PC1)		Condition		# Broods
	All fledglings	1 st four hatched	All fledglings	1 st four hatched	All fledglings	1 st four hatched	
1992							
Unfed controls	125.7 \pm 6.0	127.1 \pm 6.3	-0.92 \pm 0.56	-0.75 \pm 0.62	0.04 \pm 3.27	0.08 \pm 3.45	4
Fed (hatching to fledging)	138.5 \pm 3.0	139.4 \pm 3.0	0.37 \pm 0.18	0.51 \pm 0.22	1.92 \pm 2.15	1.61 \pm 1.91	5
1993							
Unfed controls	137.5 \pm 5.7	136.1 \pm 5.6	-0.60 \pm 0.60	-0.61 \pm 0.68	9.13 \pm 3.02	7.82 \pm 2.33	9
Fed (hatching to fledging)	132.2 \pm 3.4	136.3 \pm 3.6	-0.27 \pm 0.25	0.00 \pm 0.26	1.05 \pm 2.30	2.85 \pm 2.67	10
Fed (laying to fledging)	135.2 \pm 1.9	136.6 \pm 2.2	0.02 \pm 0.16	0.12 \pm 0.16	1.62 \pm 1.49	2.07 \pm 1.67	14
1996							
Unfed controls	126.5 \pm 3.6	126.8 \pm 4.1	-0.70 \pm 0.44	-0.69 \pm 0.44	-1.02 \pm 2.67	-0.77 \pm 3.38	6
Fed (hatching to fledging)	137.4 \pm 7.9	141.5 \pm 7.2	0.43 \pm 0.34	0.76 \pm 0.25	0.27 \pm 6.47	1.59 \pm 6.78	5
Fed (laying to fledging)	133.0 \pm 1.6	132.8 \pm 2.1	0.21 \pm 0.21	0.26 \pm 0.19	-2.22 \pm 1.41	-2.86 \pm 1.38	15

Table 4-3. Two-way ANOVA tables for the effects of treatment (*unfed, fed from hatching to fledging, and fed from laying to fledging*) and study year (1992, 1993, and 1996) on fledgling mass, structural size, and condition. Tests were performed on brood means for all fledglings and also on means for the first four fledglings to hatch within each brood (see Table 4-2). Because sample sizes were small, I lowered the probability of Type II errors in these analyses by accepting *P*-values as significant (underlined) when they were less than 0.10. Interaction terms were initially included in ANOVA models, but were all subsequently excluded because they were non-significant. Values presented for Treatment and Year were calculated without interaction terms.

	Mass (g)		Size (PC1)		Condition	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
a) Two Experimental Groups (1992, 1993, and 1996 data)						
All fledglings						
Treatment	0.64	0.43	4.48	<u>0.04</u>	1.28	0.27
Year	0.19	0.83	0.26	0.77	1.55	0.23
Interaction	2.01	0.14 ⁱ	0.70	0.50	1.55	0.23
1st four hatched						
Treatment	3.05	<u>0.09</u>	7.08	<u>0.01</u>	0.21	0.65
Year	0.13	0.88	0.31	0.74	1.32	0.28
Interaction	1.33	0.28	0.50	0.61	0.76	0.48
b) Three Experimental Groups (1993 and 1996 data)						
All fledglings						
Treatment	0.07	0.93	2.76	<u>0.07</u> ^{iv}	2.22	0.12 ⁱⁱⁱ
Year	0.85	0.36	0.82	0.37	5.49	<u>0.02</u>
Interaction	1.95	0.15 ⁱⁱ	0.57	0.57	1.44	0.25
1st four hatched						
Treatment	0.94	0.40	4.01	<u>0.02</u> ^v	1.41	0.25
Year	1.02	0.32	0.76	0.39	5.78	<u>0.02</u>
Interaction	1.50	0.23	0.67	0.52	0.76	0.47

^{i, ii, iii} POWER = 0.53, 0.52, and 0.57, respectively

^{iv} Tukey tests: Unfed vs. Fed (hatching to fledging), *P* = 0.23; Unfed vs. Fed (laying to fledging), *P* = 0.05; Fed (hatching to fledging) vs. Fed (laying to fledging), *P* = 0.88.

^v Tukey tests: Unfed vs. Fed (hatching to fledging), *P* = 0.05; Unfed vs. Fed (laying to fledging), *P* = 0.03; Fed (hatching to fledging) vs. Fed (laying to fledging), *P* = 0.98.

Overall, 1993 was a very wet year with above-average precipitation in August and near-record rainfall in July. Rainfall was generally above average in 1996, but well below average for much of 1997. In 1998, precipitation was extremely high in June, but below average in the latter half of the season.

Prey.— Annual means of the mean number of vertebrates cached at unsupplemented nests varied considerably among years (Fig. 4-4a; ANOVA on log-transformed data, $F = 9.192$, $P < 0.001$). Mean prey caches were between 3 and 12 times larger in 1997 than in 1992, 1993, or 1996 (Tukey; $P < 0.02$ for each comparison), and were twice as large in 1997 as in 1998, but the latter difference was not statistically significant ($P = 0.31$). Caches were significantly larger in 1998 than in 1992 ($P = 0.03$), but were not significantly larger in 1998 than in 1993 or 1996 ($P = 0.30$ and 0.82 , respectively). Mean annual prey-cache size was unrelated to total annual rainfall during the nesting season ($r^2 = 0.36$, $P = 0.28$).

The relative abundance of small mammals varied significantly among the three years that prey were trapped (Fig. 4-4b; ANOVA with log-transformed data, $F = 11.15$, $P < 0.001$). Mean relative abundance of prey was much higher in 1997 than in either 1993 (Tukey, $P = 0.03$) or 1992 ($P < 0.001$), and was also significantly higher in 1993 than in 1992 ($P = 0.03$). The ranking of relative prey abundance in 1992, 1993, and 1997 was the same as the ranking of mean annual prey caches among those three years (Fig. 4-4), suggesting that annual prey-cache sizes are largely a reflection of annual prey abundance.

Production of fledglings.— To understand better proximate causes of observed reproductive food limitation, I examined annual variation in the mean number of fledglings (unfed pairs only) with respect to annual variation in two environmental factors potentially affecting the owls' intake of natural prey. First, because annual means of prey-cache size for unfed pairs appeared to provide a reasonable index of relative prey abundance among years (Fig. 4-4), I tested the relationship between mean annual fledging rate and mean number of prey cached (Fig. 4-5a). Yearly values for these two variables showed no association ($r^2 = 0.35$, $P = 0.30$). However, when I examined mean annual fledging rate (unfed pairs) with respect to total annual rainfall during the nesting season, there was a negative linear relationship between the two variables ($r^2 = 0.91$, $P = 0.01$; Fig. 4-5b). Also, the within-year difference in fledgling production between control pairs and pairs fed during the nestling period showed a significant positive relationship with total annual rainfall ($r^2 = 0.91$, $P = 0.01$), but not with annual prey caches ($r^2 = 0.22$, $P = 0.43$). Thus, annual variation in fledgling production, and the degree of food limitation during the nestling period, was influenced more by total rainfall than by measures of relative prey abundance.

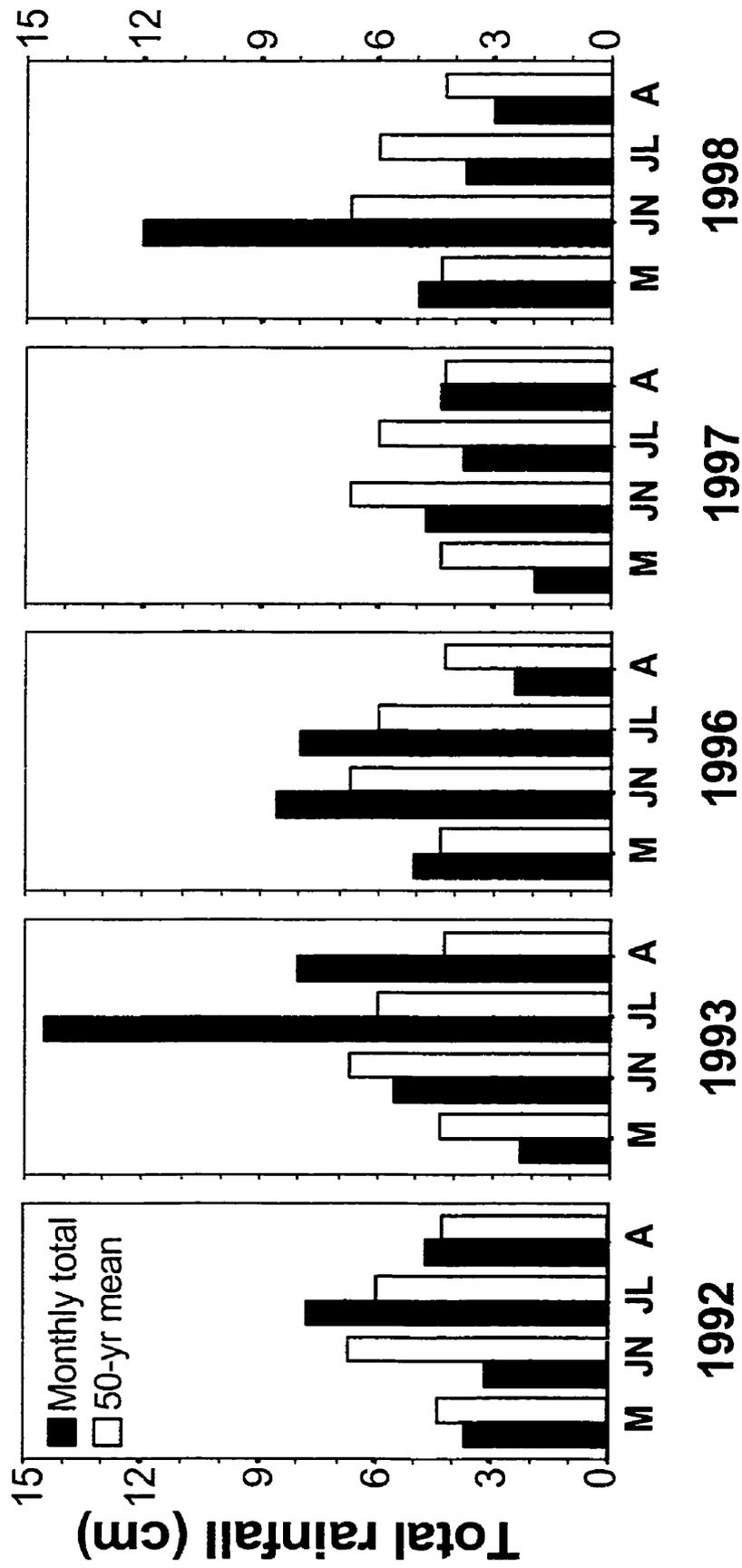


Figure 4-3. Monthly rainfall near Regina, Saskatchewan, in May (M), June (JN), July (JL), and August (A) of each study year. For comparison, mean monthly rainfall for 1948–1998 is also indicated. Data were obtained from Atmospheric Environment Service, Environment Canada.

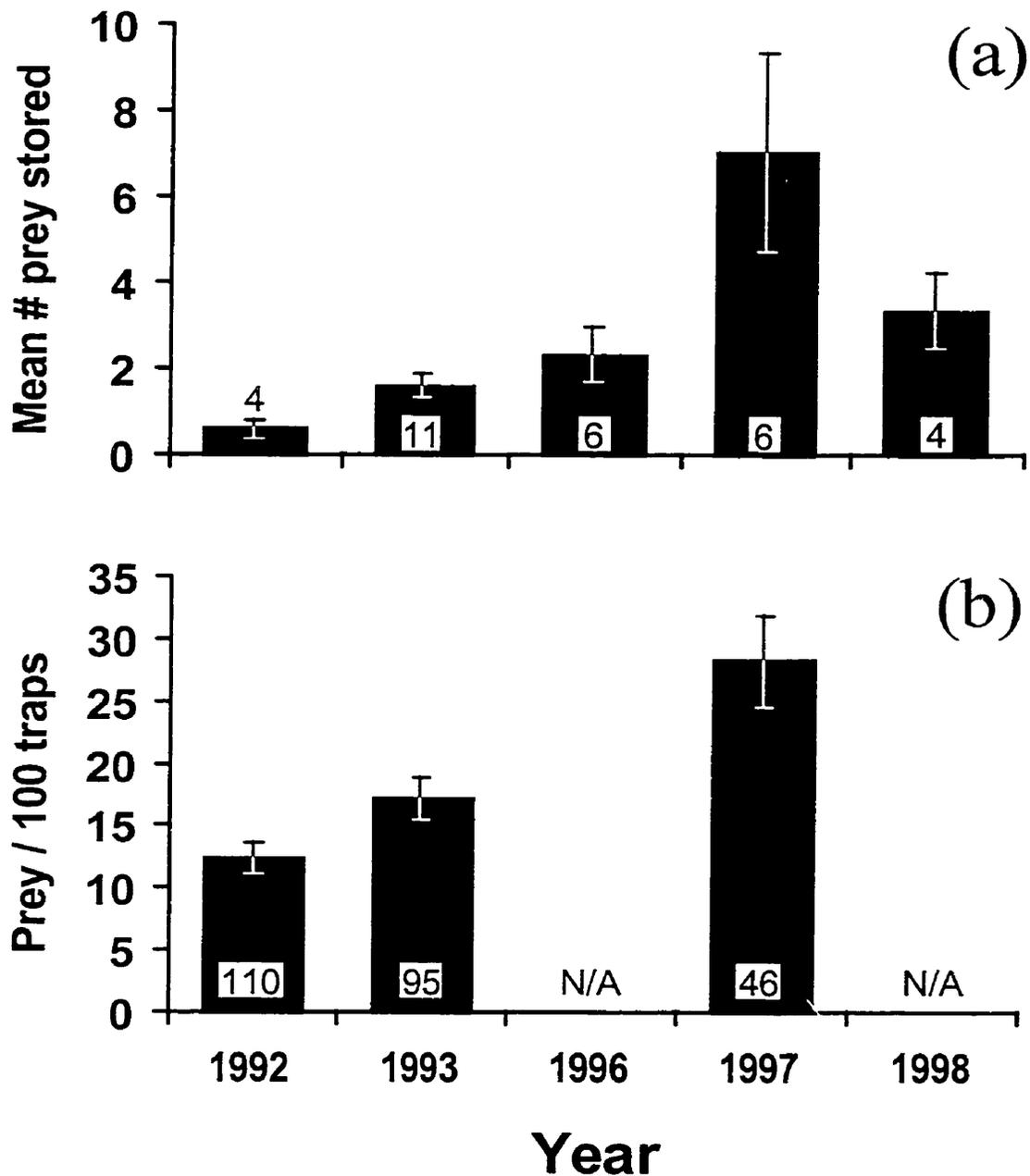


Figure 4-4. Annual variation in (a) mean number of prey items (mean \pm SE) cached by unfed Burrowing Owl pairs during five breeding seasons (May–July), and (b) relative prey abundance (mean number of small mammals per 100 traps \pm SE) in June and July of 1992, 1993, and 1997 (trapping not conducted in 1996 or 1998; N/A = not available). Values at the base of each bar in (a) show the number of pairs for which prey-cache information was collected, and values on each bar in (b) indicate number of traplines.

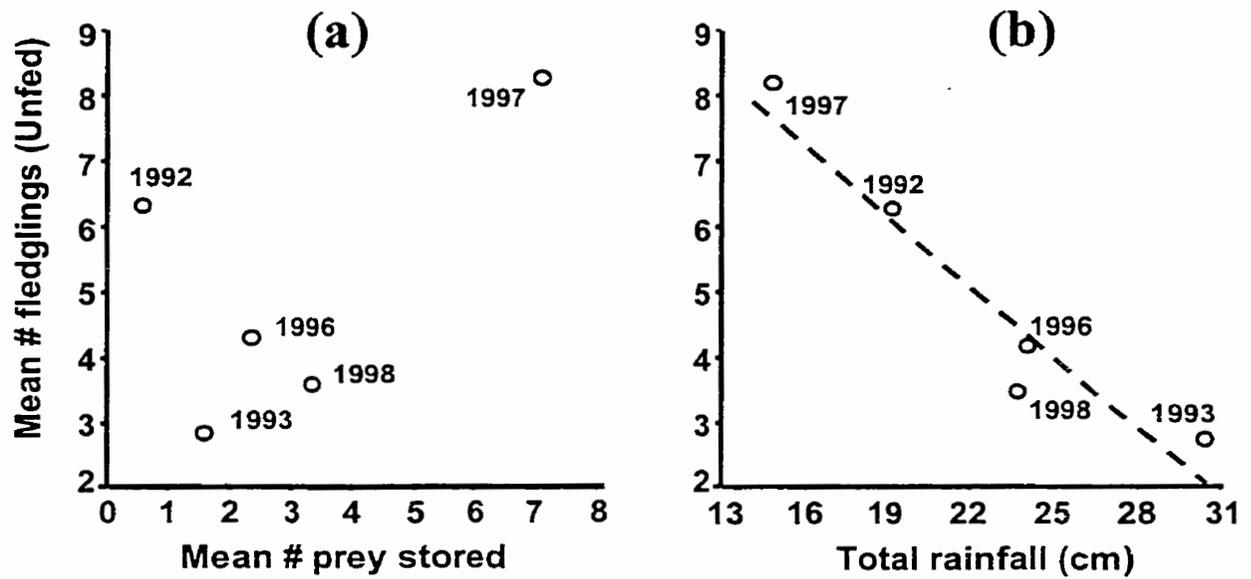


Figure 4-5. Mean number of fledglings for unsupplemented pairs in relation to (a) mean prey-cache size for unsupplemented pairs and (b) total rainfall in each study year. Total annual rainfall was obtained by summing rainfall for all 4 months of each breeding season (May-August, Fig. 4-3). Mean annual rainfall (May-August), from 1948 to 1998, was 21.3 cm. Regression line calculated using ordinary least-squares.

DISCUSSION

Timing of food limitation

Results from this study show that Burrowing Owls are commonly food limited during the nestling period. Supplemental feeding increased average size for all fledglings, and increased both mass and size for oldest fledglings (first four hatched per brood), in all three years that owlets were measured. Moreover, even though fed and control pairs started with an equivalent number of hatchlings, fed pairs produced more fledglings than control pairs in four of five years. This difference in fledging success was due to a much higher frequency of starvation within control broods than within fed broods.

Observational studies have shown that partial-brood loss, through starvation, occurs in a wide variety of bird species (reviewed in O'Connor 1978, Howe 1978). More recent investigations have demonstrated that partial-brood loss is reduced by food supplementation during the breeding season (Hogstedt 1981, Arcese and Smith 1988, Dhindsa and Boag 1990, Soler and Soler 1996). However, because such feeding experiments extend from well before egg laying through to fledging, their results are difficult to interpret. Firstly, extra food prior to clutch-initiation almost always causes early laying (reviewed in Arcese and Smith 1988). Thus, effects on reproductive output late in the season could be attributed either to supplemental feeding or to an advance in breeding date (Nilsson and Svensson 1993; Nilsson 1994), as nestling survival often decreases with time of year (Perrins 1970, Ewald and Rohwer 1982, Daan *et al.* 1989, Siikamaki 1998). Secondly, when supplemental feeding is conducted throughout the breeding season, it is unclear if observed increases in fledging success result from alleviation of food limitation during the nestling period or alleviation during earlier stages (Nilsson 1994). For instance, supplemental feeding during prelaying and laying can increase egg size (Hogstedt 1981, Hill 1988, Wiebe and Bortolotti 1995), which can in turn increase hatchling size and nestling survival (Martin 1987, Bolton 1991, Magrath 1991, Perrins 1996). Benefits of supplementation can also carry over from one phase to the next if adult condition is affected (Hochachka and Boag 1987) or if extra food is stored in caches (Korpimaki 1989). Hence, for many reasons, the strongest test of food limitation during the nestling stage is supplementation during that stage alone. Five of the six studies that supplemented solely during the nestling period found evidence for food limitation (Simons and Martin 1990, Richner 1992, Garcia *et al.* 1993, Verhulst 1994, and Wiehn and Korpimaki 1997; but see Gende and Willson 1997). Results from these feeding experiments, and from the present experiment on Burrowing Owls, demonstrate that the ability of parents to meet the energy requirements of nestlings often

limits the number of offspring that parents raise, as originally suggested by Lack (1947, 1954). However, studies that supplement food in only the nestling phase do not explicitly test Lack's supposition that brood-rearing is more energetically limiting than the other stages of nesting.

The Burrowing Owl feeding experiments conducted in 1993 and 1996 showed that food limitation was more influential during the nestling stage than during either egg laying or incubation. Pairs supplemented through all three stages fledged the same number of young as pairs fed for the nestling period alone, and showed similar patterns of nestling survival in relation to nestling age. Furthermore, average nestling mass, size, and condition were all very similar for these two treatments (Table 4-2). Accordingly, supplemental feeding during egg laying showed no effects on clutch or egg size (Chapter 2), and pre-hatch feeding did not influence number of hatchlings (Table 4-1b; see also Chapter 3). Pairs were assigned to treatments alternately by their laying date, so hatching dates were similar for the two experimental groups. Results thus demonstrated that there were no lagged or cumulative effects of extra food during egg-laying and incubation on fledgling quality or quantity, and provided the first experimental support for Lack's contention that the nestling period is the most food-limited phase of the nesting season.

For Burrowing Owls, food consistently limited fledgling structural size. Also, in 1992 and 1996, fledgling mass and condition appeared to be higher in supplemented broods than in unsupplemented broods. However, in 1993, when supplemented pairs had more than 2.5 times the number of fledglings that unsupplemented pairs had, average fledgling condition was slightly (but not significantly) better in unsupplemented broods. This means that control owlets in 1993, although smaller, tended to be heavier for their size; whereas, supplemented owlets in 1992 and 1996 seemed to be both larger and heavier than unsupplemented owlets. The tendency for both mass and condition effects to be of opposite direction in 1993 than in other years probably explains why *P*-values for interaction terms were fairly low. Statistical power for interactions in mass tests was only moderate (0.52 and 0.53; Table 4-3), so perhaps interaction terms would have been significant if power had been higher. The tendency, in 1993, for fledglings from unsupplemented broods to be heavier and in better condition than those from supplemented broods may, in part, be explained by better growth and asymptotic weight in owlets that hatch early in relation to their siblings (see Landry 1979). As late-hatched nestlings are more likely than their older siblings to die (pers. observ.), broods that experience high nestling mortality likely contain older fledglings, on average, than broods with low nestling mortality. This may explain why, when only oldest fledglings (first four hatchlings in each nest) were included in brood averages, both mass and size were significantly higher in broods supplemented from hatching to fledging than in unsupplemented broods.

It is unclear which of the three variables measured for Burrowing Owl fledglings provides the

best measure of offspring quality, as post-fledging survival and the subsequent probability of becoming a breeder were not determined in this study. Hochachka and Smith (1991) demonstrated that nestling condition in Song Sparrows (*Melospiza melodia*) did not affect mortality after independence. Simons and Martin (1990) found that supplementing Cactus Wrens (*Campylorhynchus brunneicapillus*) during the nestling period increased fledgling mass and size, and enhanced post-fledging survival in one of two years. Richner (1992) showed that nestling Carrion Crows (*Corvus corone*) provided with extra food were larger and heavier at fledging than were control nestlings. Though these differences did not affect post-fledging or over-winter survival, larger body size increased the probability that a juvenile crow would acquire a territory and become a breeder. Whether larger structural size would confer this same advantage for supplemented Burrowing Owl young is unknown. Regardless, none of the potential measures of quality were lower for fed fledglings than for controls, particularly when the oldest 'half' of each brood was compared, so there was no indication that food-supplemented owlets were less likely to survive and breed. Therefore, given that supplemented pairs fledged substantially more nestlings than did control pairs, supplemented pairs most likely produced more recruits, as well.

Annual variation

Of six previous studies that supplemented food solely during the nestling period, only two examined annual variation in the degree of food limitation. Simons and Martin (1990) found that fledgling output was more limited in the first year of their study than in the other year, but were uncertain what factor might explain this disparity. They suggested availability of prey may have differed between the two study years, but had not measured food supply. Wiehn and Korpimäki (1997) showed that reproductive food limitation was constant for the three years of their study, even though prey densities varied substantially among years (*i.e.*, annual variation in natural food abundance did not lead to annual variation in food limitation).

In the present study, annual fledgling production at control nests, and within-year differences in production between fed and unfed broods, were better explained by total rainfall than by mean prey-cache size. These latter two variables relate to potential food shortage at different temporal scales. Year-to-year shortfalls in food can be thought of as chronic food shortages; whereas, day-to-day shortfalls can be considered acute food shortages (Bortolotti *et al.* 1991, Forbes and Mock 1996). For Burrowing Owls, mean prey-cache size provided an index of the annual availability of vertebrate prey. Therefore, had chronic food shortage been important in this study, its effects would most likely have surfaced in the worst food-year, 1992 (Fig. 4-4), yet control pairs had high reproductive

output in that year. I interpret total rainfall as an index for the frequency of acute food shortages. Owlets in control broods experienced considerable weight loss during periods of heavy rain, and their mortality seemed especially high when rain fell for several consecutive days (pers. observ.). It was clear that these deaths resulted from food limitation rather than exposure because mortality of food-supplemented nestlings was very low, even though they experienced the same bouts of rain (Fig. 4-2). What remains unclear, however, is whether rainfall reduced activity levels of prey (Falls 1968, Baumler 1975, Lehmann and Sommersberg 1980) or simply hampered the owls' foraging ability (Hirons 1982, Wijnandts 1984).

In an observational study of Red-tailed Hawks (*Buteo jamaicensis*), Adamcik *et al.* (1979) showed that nestling mortality was largely attributable to frequency of rain and suggested that low prey abundance became critical to nestling survival only when associated with above-average rainfall after hatching. This may be the case for many carnivorous birds (Newton 1979), including insectivores (Lack and Lack 1951, Hogstedt 1981, Murphy 1983, Reynolds 1996, Siikamaki 1996) and piscivores (Reese 1977, Braun and Hunt 1983), or indeed any other bird whose foraging success is severely hampered by excessive amounts of rain.

Reproductive strategy

Many bird species show changes in clutch size that correspond to changes in food levels during prelaying and laying periods (reviewed in Martin 1987). This pattern of high clutch-size variation, coupled with a low rate of nestling mortality, has been recorded in various owl species (*e.g.*, *Strix uralensis*, Lundberg 1981, and Pietiainen *et al.* 1986; *Bubo virginianus*, Rohner 1994, Houston *et al.* 1998), indicating that either these birds are adjusting their clutches to a size appropriate for predictable post-hatch food limitation or their clutches are proximately limited by food. In contrast, Burrowing Owls are free from food limitation prior to hatching (see also Chapter 2), and produce many more hatchlings than they are normally able to rear. But why would parents consistently produce extra hatchlings, when they could presumably conserve energy by avoiding such overproduction?

Mock and Forbes (1995), in their review of this apparently anomalous behaviour, present potential functions for the production of superfluous nestlings, three of which may be relevant in Burrowing Owls. First, extra offspring may serve as "insurance" against unforeseen losses of eggs or hatchlings that result from infertility, accidents, or congenital defects. These insurance eggs act as substitutes only when their nest-mates

prove unviable. Burrowing Owls in my study, on average, failed to hatch nearly one egg per successfully incubated clutch (Chapter 3). Also, a total of four hatchlings died from infections early in the nestling period and were survived by their younger siblings. In these cases, extra eggs appeared to benefit parents by replacing unviable offspring, as proposed by the insurance hypothesis. However, one prediction of this hypothesis is that redundant offspring are eliminated when primary siblings survive. Thus, if extra eggs were purely for insurance purposes, annual variation in the percentage of eggs producing fledglings would have been low, which was not the case. It appears, therefore, that extra hatchlings must serve other functions in addition to insurance.

The second potential benefit of having an over-sized family applies only to cannibalistic species. The prevalence of cannibalism (*sensu* Bortolotti et al. 1991) within Burrowing Owl broods implies that this behaviour may be important for the owls. The ice-box hypothesis (Alexander 1974), which can be thought of as a special kind of food caching, states that extra nestlings may provide core nestlings with a critical meal in times of temporary food shortages. Forbes and Mock (1994) largely dismissed this hypothesis for birds, suggesting “there are easier ways of finding a meal”. However, studies of species that frequently undergo short-term fasts (*e.g.*, when foraging success is severely affected by inclement weather) could provide substantive support for this hypothesis (Bortolotti et al. 1991, Reynolds 1996, Wiebe 1996). For nestling birds that are forced to do without food for days, even a single meal may mean the difference between life and death.

The third function of surplus hatchlings may be to provide parents with extra reproductive value in years when food availability proves unexpectedly high during the nestling period. When availability turns out to be average or below-average, food shortage leads to the culling of an appropriate number of marginal offspring (Lack 1947). This method of adjusting offspring number is most commonly referred to as the brood reduction strategy (Ricklefs 1965). An inherent characteristic of this strategy is marked annual variation in fledging success in concert with changes in food availability. The fact that partial-brood loss for Burrowing Owls varied substantially among years, and was virtually eliminated in 1997 (the year with the best feeding conditions) and when food was supplemented during the nestling period, lends support to the brood reduction hypothesis. As emphasized by Lack (1947), a seasonally unpredictable food supply, such as that for the Burrowing Owl (Chapter 3), favours brood reduction as a means for adjusting offspring number; whereas, predictable seasonal variation in food favours clutch-size adjustment.

Preliminary information presented here suggests the large clutch of the Burrowing Owl

may, at times, serve each of the three functions discussed above. However, further research and experimentation is required to thoroughly assess the adaptive significance of the Burrowing Owl's apparently oversized family.

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CHAPTER 5

General Discussion and Conclusions

Burrowing Owls showed considerable intrapopulation variation in all reproductive parameters measured in this study. I used observational and experimental approaches to investigate the role of food availability in governing this variation. I isolated potential effects of food by statistically, or experimentally, controlling for important seasonal factors, such as spring arrival and laying dates.

Measures of food intake were unrelated to laying date (Chapter 2). In contrast, date of female arrival in spring explained 91% of the overall variation in laying date. Age showed an indirect effect on laying date through arrival date; first-year females arrived 8 days later, and then laid 8 days later, on average, than older females. In general, females appeared to lay eggs as soon as possible after arrival and pairing, with other factors having little influence.

None of the evidence in this study suggested egg size was appreciably larger when food intake was higher (Chapter 2). Likewise, clutch size varied little among years, showed no correlation with measures of food intake for individuals, and was unaffected by supplemental feeding during egg laying. This lack of food-effects could not be explained by reduced foraging in males when food was high because prey caches and pellet-regurgitation rates were much higher in the year that voles were superabundant (1997) than in other years and were higher for supplemented pairs than for control pairs.

Mean egg volume was unrelated to laying date in every year. Conversely, clutch size declined over the season by an average of 0.63 eggs/week, and laying date explained 41% of the total variation in clutch size. The seasonal clutch-size decline occurred in every year, and was remarkably consistent among years, despite obvious annual fluctuations in measures of food intake (Chapter 2) and adverse weather (Chapter 4). Regressions of clutch size on laying date were also similar for both yearlings and older owls (Chapter 2). Furthermore, the seasonal clutch decline did not differ between food-supplemented and control groups, which had the same distributions of laying dates. These results indicate the seasonal clutch-size decline in Burrowing Owls does not result from differential food intake of pairs laying on different dates.

Hatching success was unaffected by natural and experimental variation in food availability during laying and incubation (Chapter 3). Hatching span increased with increases in clutch size, and decreased over the season. However, when clutch size was controlled for statistically, the seasonal decrease in hatching span disappeared. With effects of hatching success and clutch size removed, hatching span was unrelated to prey-

cache size for pairs at the time of egg laying, it was unaltered by a year of super-abundant food (1997), and it was unaffected by experimental provisioning of extra food during laying. Observed variation in hatching asynchrony was, therefore, inconsistent with both the energy constraint and facultative manipulation hypotheses (Chapter 3; Fig. 1-1).

Supplemental feeding during the nestling period increased fledgling size, and to a lesser extent mass, relative to controls in all three years that owlets were measured (Chapter 4). Moreover, even though fed and control pairs started with an equivalent number of hatchlings, fed pairs produced more fledglings than control pairs in four of five years. This difference in fledgling success was due to a much higher frequency of starvation within control broods than within fed broods. For pairs that experienced partial-brood loss, 96% of all nestling deaths (169/176) resulted from food shortage. In 1993 and 1996, a third subset of owl pairs was given extra food from clutch initiation until fledging (Appendix 1). Pairs fed through all three periods of the nesting season fledged the same number of young as pairs fed for the nestling period alone, and showed similar patterns of nestling survival in relation to nestling age. Fledglings in these two treatments were also similar with respect to average mass, structural size, and condition (Chapter 4). On the whole, the feeding experiments showed Burrowing Owls were commonly food limited during the nestling period, and demonstrated there were no lagged or cumulative effects of extra food during egg-laying and incubation on fledgling quality or quantity. This is the first experimental support for the contention (Lack 1947, 1954) that the nestling period is the most food-limited phase of avian breeding seasons.

Together, evidence from Chapters 2, 3, and 4 suggests that Burrowing Owls are free from food limitation prior to hatching, and produce many more hatchlings than they are normally able to rear. But why would parents consistently produce extra hatchlings, when they could presumably conserve energy by avoiding such overproduction? The answer to this question probably relates to the predictability of food.

Food intake for Burrowing Owl pairs showed no (or very low) seasonal correlations (Chapter 3). This means food intake during egg production was not a reliable indicator of food intake during early brood-rearing, and could not serve as a proximate cue by which to adjust clutch size, or the onset of incubation, to future food availability. For this reason, reproductive adjustments early in the season may be impractical for Burrowing Owls (Fig. 1-1b). When birds are unable to predict future food conditions, their best option may be to exhibit a moderate level of asynchrony that balances potential future costs and benefits (*e.g.*, Mock and Ploger 1987). A moderate nestling-size hierarchy probably makes food shortage, which precedes partial-brood loss, less costly in terms of growth of surviving brood members.

Lack (1947, 1954) emphasized that seasonal unpredictability, caused by temporal variation in food supply, favoured the use of brood reduction as a means of adjusting offspring numbers during the nestling period; whereas, predictable seasonal variation in food favoured the adjustment of clutch size. Clutch size varied little for Burrowing Owls among years. However, partial-brood loss varied substantially among years, and was virtually eliminated in the year with the best feeding conditions (1997) or when food was supplemented during the nestling period. Also, partial-brood loss tended to occur in the first half of the nestling period (Fig. 4-2). This evidence lends support to Lack's suggestion that some species of birds use brood reduction as a means of adjusting family size to suit food conditions in the nestling period (Fig. 1-1b).

Food limitation observed in this study must not have been related to average food abundance alone, as annual fledgling production at control nests, and within-year differences in production between fed and unfed broods, were closely associated with total rainfall (Chapter 4). I interpreted total rainfall as an index for the frequency of acute food shortages. Owlets in control broods experienced considerable weight loss during periods of heavy rain, and their mortality seemed especially high when rain fell for several consecutive days (pers. observ.). It was clear that these deaths resulted from food limitation rather than exposure because mortality of food-supplemented nestlings was very low, even though they experienced the same bouts of rain (Fig. 4-2). Partial-brood loss associated with rain probably reflects proximate food limitation (Fig. 1-1a), rather than brood-size adjustment in anticipation of future food shortage (Fig. 1-1b). O'Connor (1978) referred to the seasonal correlation of food availability as predictability, distinguishing it from the degree of day-to-day variation, which he called stability. Partial-brood loss occurs when food conditions during the nestling period are unstable or are unpredictable at the time of laying. Birds are expected to exhibit asynchronous hatching in either of these situations (O'Connor 1978). Food conditions for nestling Burrowing Owls appeared to be unstable due to rain (Chapter 4) and also unpredictable at the time of laying (Chapter 3). Partial-brood loss in Burrowing Owls may therefore have reflected both adaptive brood reduction (*sensu* Mock 1994), when food was chronically short, and simple proximate food limitation (Fig. 1-1), when food shortage was acute.

The substantial annual variation in reproductive food limitation also suggests conclusions drawn from short-term food-supplementation studies on Burrowing Owls would vary, depending on the years experiments were done. For example, had food supplementation been conducted only in 1997, one would have concluded that Burrowing Owls were not limited by food during the nestling period. Considerable annual variation thus increases the importance of conducting long-term studies when asking questions about food limitation.

In the years that I studied Burrowing Owls, small mammals contributed far more dietary biomass than any other prey (Appendix 2). However, in the 1980s, grasshoppers were often very abundant in Saskatchewan (James and Fox 1987) and were eaten in large quantities by Burrowing Owls during the late-nestling period (Haug 1985). The large clutches of Burrowing Owls probably allow them to take advantage of any unpredictable 'windfall' of food, whether it is a peak in voles, grasshoppers, or any other potential prey.

The availability of food to the owls in my study area was influenced strongly by rainfall. In other regions, other weather variables may be more important in affecting food conditions for Burrowing Owls. For example, drought is thought to be a critical factor in more arid systems (*e.g.*, Gleason 1978). It would be interesting to study reproduction and the timing of food limitation in other regions, where Burrowing Owls rely on a different prey base and experience different weather conditions. Food availability may be more predictable in other regions than on the Regina Plain, and this difference may allow the owls to exhibit alternative strategies of reproductive adjustment.

It may be common for altricial birds to be limited by food during the nestling period (Martin 1987). The experimental design used in the present study could be the first component in a suite of experiments allowing researchers to characterize timing of food limitation and reproductive adjustments in almost any altricial species. If supplemental feeding during the nestling period alone results in just as many fledglings as supplementation throughout the entire nesting period (Group A = Group B; Appendix 1), and if pairs in both treatments fledged more young than unfed controls (Group A & B > Group C), then food limitation is more important during the nestling period than during the egg-laying and incubation periods. If no differences occur among any of the three experimental groups, supplemental feeding could be conducted during the post-fledging period or the prelaying period, although in the latter case laying date might be affected by supplemental feeding (Arcese and Smith 1988). If pairs that are supplemented through all three periods of the nesting season fledge more young than those fed only during the nestling period (Group A > Group B), then additional experiments are required to ascertain whether birds are proximately limited by food during one of the pre-hatch stages or are using food supply as a cue to adjust reproduction in anticipation of future food levels (Fig. 1-1). For example, one could supplement pairs only during egg laying (Group D). If these pairs laid more eggs and subsequently fledged *more* young than controls, one could be certain that the experiment helped the birds overcome food limitation during egg laying. Conversely, if these pairs laid more eggs but fledged *fewer* young than controls, it would show they had adjusted clutch size in expectation of good feeding conditions during the nestling period and had done worse because their brood size was too large for

natural food availability. Reproductive adjustments such as these may be expected when food for a given species is normally somewhat predictable. Therefore, experiments examining reproductive food limitation will be most convincing when they also measure within-season correlations in food (Wiebe 1995).

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APPENDIX 1

Summary of Food-supplementation Experiments

The feeding experiments conducted for this thesis (Fig. A-1) varied among years. The amount of funding for the project varied and the number of Burrowing Owl pairs declined between 1992 and 1998. Consequently, sample sizes and the number of field staff allowed inclusion of three experimental groups only in 1993 and 1996. Also, in 1992, Burrowing Owl pairs were provided with dead laboratory mice every third day during egg laying (Group D). Supplemental feeding began for each pair on their estimated laying date (Chapter 2) and ended after laying had ceased. Because of time constraints and a lack of funding for transportation in the first field season, these pairs were not monitored regularly once all owlets had hatched. In 1996 every second pair, and in 1993 every third pair, was supplemented at three-day intervals, from the time of their first egg until they fledged their young (41 days after hatching; Group A). In 1992, 1993, and 1996–1998, all pairs not receiving extra food during laying or incubation were ranked by clutch size and predicted hatching date, then alternately assigned to be supplemented or unsupplemented between hatching and fledging (Groups B and C, respectively). As a result, pairs nesting in artificial burrows in all experimental groups (Groups A–D) had equal distributions of laying dates within years. When examining fledging rate in 1992, 1993, 1997, and 1998, pairs nesting in natural burrows (where laying date and clutch size were unknown) were also included in feeding experiments (Groups A, B, and C). These pairs were assigned to groups based on their pairing date, which was usually the same date as female arrival.

In Chapter 2, I compared clutch size, mean egg volume, mean cache size, and pellet production rate between pairs supplemented during laying and pairs not supplemented during laying (1992: Group D *versus* Groups B + C; 1993 and 1996: Group A *versus* Groups B + C). I combined data from 1992, 1993, and 1996 to compare seasonal clutch declines between supplemented and unsupplemented pairs (Chapter 2). I made within-year comparisons of hatching success and hatching-span deviation for these same supplemented and unsupplemented pairs (Chapter 3), excluding those that failed before their eggs hatched. In 1992, 1993, and 1996–1998, I examined nest failures (Appendix 3) and the number of fledglings per successful nest (Chapter 4) for pairs supplemented with food during the nestling period (Group B) and for pairs remaining unsupplemented (Group C). In 1993 and 1996, I also examined nest failures and fledgling numbers for pairs fed from laying until fledging (Group A; Appendix 3). For pairs nesting in artificial burrows in these same treatments, I compared hatching date, number of hatchlings, patterns of nestling survival, and percent of hatchlings fledged (Chapter 4). In

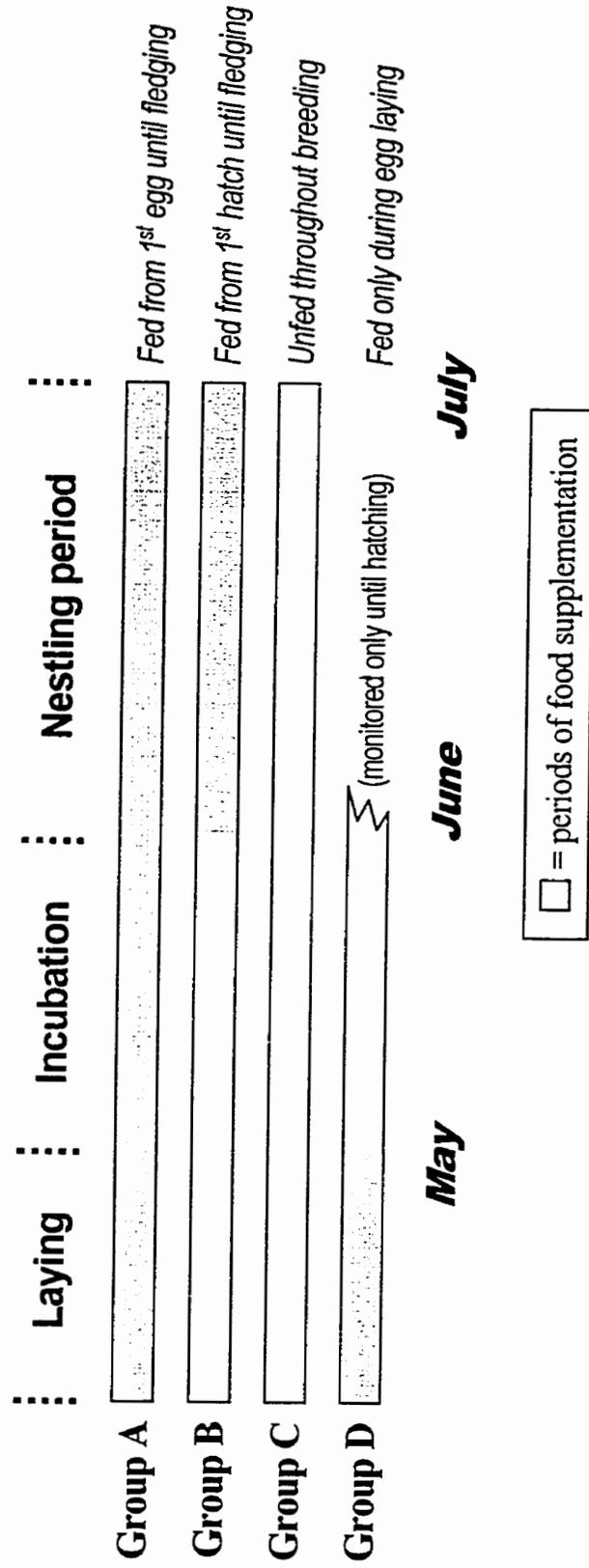


Figure A-1. Schematic showing the various food-supplementation experiments in this study.

1992, 1993, and 1996, I measured nestling structural size, mass and condition (Chapter 4), comparing these parameters for each experimental group (1992: Group B *versus* C; 1993 and 1996: Groups A *versus* B *versus* C). Because of time and budget constraints, these parameters were not measured in 1997 and 1998.

APPENDIX 2

Proportions of Prey in Burrowing Owl Food-pellets

Food-pellets were collected at nest entrances or on the ground within 10-15 m of Burrowing Owl nests, throughout the 1992, 1993, 1996, and 1997 breeding seasons (see Chapter 2 *Methods*). An attempt was made to collect all pellets at nests from the start of laying until fledging, at 3- to 6-day intervals.

The percent volume of each prey type was visually estimated for each pellet and then averaged for each nest. Fur and mammal bones, feathers and passerine bones, and chitinous exoskeletons constituted mammal, bird, and insect remains, respectively. In the unsupplemented pairs for which pellet proportions were estimated (Fig. A-2), yearly averages for bird remains were between 0 and 3%, and for insect remains between 3 and 15%. In contrast, small mammal remains averaged between 82 and 97% annually. These percentages provide a rough estimate of the biomass each prey type provided for Burrowing Owls during this study. However, the dietary importance of insects may be somewhat exaggerated by this measure because insects are poorly digested in comparison to small mammals and birds (Akaki and Duke 1998). Hence, a greater volume of remains was probably egested per calorie of insects than per calorie of vertebrates.

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Akaki, C., and G.E. Duke. 1998. Egestion of chitin in pellets of American Kestrels and Eastern Screech Owls. *Raptor Research* 32:286-289.

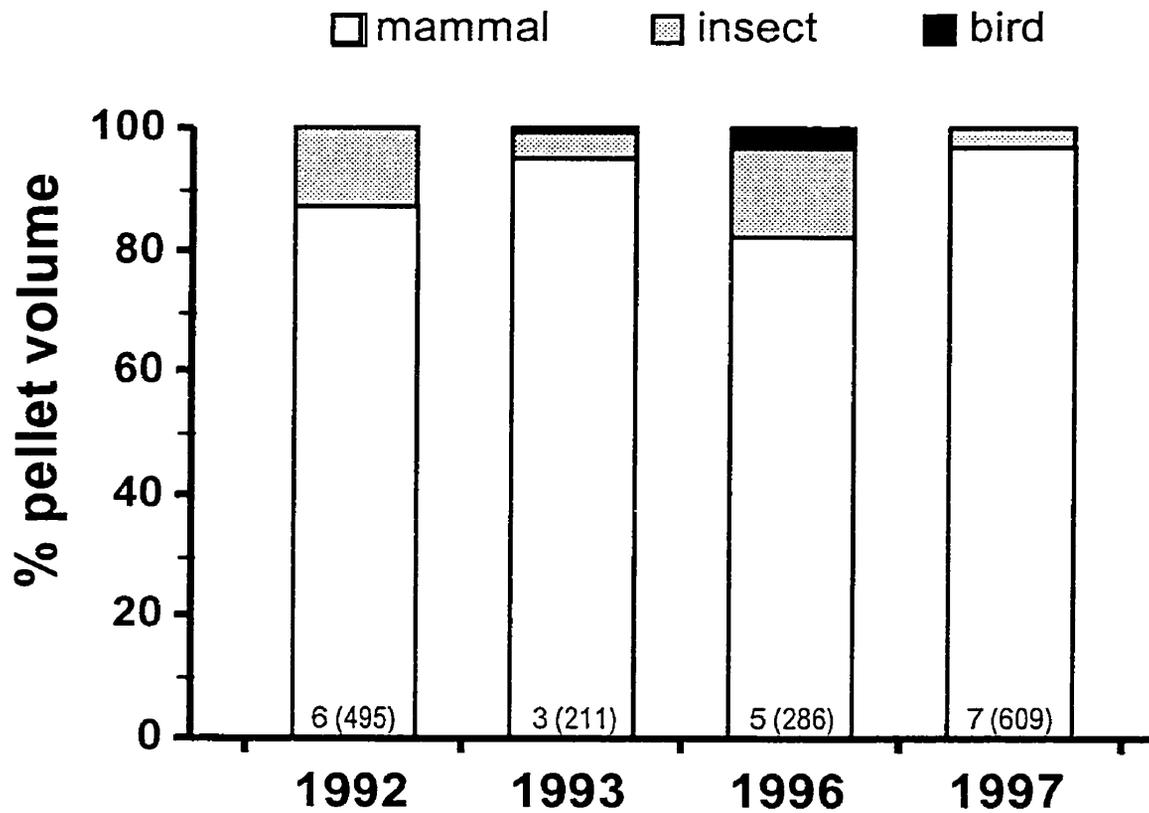


Figure A-2. Mean annual proportions of prey contained in Burrowing Owl food-pellets. The percent volume of each prey type was estimated for each pellet collected between the start of egg laying and fledging, then averaged for each nest. Number of nests per year is shown at the base of each bar with the number of pellets in parentheses. Only nests that remained unsupplemented throughout the breeding season were included.

APPENDIX 3

Nesting Failures in Relation to Supplemental Feeding

In this study, a breeding attempt was recorded as failed if all eggs in a nest were found broken, buried or missing, or if an entire brood died or disappeared (when too young to fly) between successive nest checks. Nest failures caused by various mammalian carnivores usually showed characteristic signs, such as digging or teeth imprints on eggshells.

To assess whether food supplementation affected rate of nesting failure, I present frequency and causes of nest failures for all nests in Chapter 4 experiments. In 1993, all 41 pairs involved in supplementation experiments during egg laying nested in artificial burrows (see Wellicome et al. 1997 for design). In 1996, 34 pairs nested in artificial burrows and 7 pairs nested in natural burrows. For the latter nests, the stage (egg-laying, incubation, or nestling) of any nesting failures was determined based on date, breeding behaviour of adults (particularly of females), and remains at burrow entrances and in food-pellets (e.g., egg shells or nestling feathers).

Failures during the egg-laying and incubation periods of 1993 and 1996 are presented in Table A-1 with respect to feeding treatment, burrow type, and year. The overall frequency of nest failures observed during egg laying and incubation did not differ (Fisher's exact test, $P = 0.69$) between pairs provided with extra food (3 failures out of 34 pairs) and unfed control pairs (3 out of 48; 1993 and 1996 combined).

Failures during the nestling periods of 1992, 1993, 1996, 1997, and 1998 are presented in Table A-2. There were no abandonments during the nestling period, but of the 165 nests active at the time of hatch, 22 (13%) failed before fledging. Nest failures occurred for numerous reasons, some of which had the potential to be associated with food limitation and some of which did not. The cultivation, flooding, or trampling of burrows resulted in nest failures that were obviously unrelated to food limitation. One additional breeding attempt failed when an adult female died in her nest, even though ample food was cached within her reach. These incidents accounted for 7 (39%) of the 18 failures with known causes. Predation, which could conceivably be related to food limitation (Martin 1992), was the most common cause of failure for Burrowing Owls, explaining 11 (61%) nest failures (predation of adult males and of nests, combined). However, predation did not differ (Fisher's exact test, $P = 1.0$) between pairs fed during the nestling period alone (6 of 74 nests) and unfed control pairs (4 of 60 nests; all 5 years combined). Likewise, predation during the nestling period did not differ ($\chi^2 = 0.87$, $P = 0.96$) among the three experimental groups (unfed: 1 of 21; fed from laying to fledging: 1 of 23; fed

Table A-1. Number of failed nesting attempts, during egg laying and incubation, in relation to total number of pairs in each year, treatment, and burrow type (artificial versus natural). Causes of failures: *a* = clutch abandoned for unknown reasons, *p* = clutch destroyed by predator, *r* = pair relocated from this burrow during egg laying and re-nested in an artificial burrow, *u* = unknown cause of failure (but smashed eggs found in burrow entrance and eggshell fragments found in the pairs' food pellets).

Year	Treatment	Artificial nest burrows			Natural nest burrows			All burrows	
		%	failed/ total	Cause(s)	%	failed/ total	Cause(s)	%	failed/ total
Egg-laying period									
1993	Unfed controls	8	2/26	<i>p, p</i>	-	-	-	8	2/26
1993	Fed (laying to fledging)	0	0/15	-	-	-	-	0	0/15
1996	Unfed controls	0	0/17	-	0	0/5	-	0	0/22
1996	Fed (laying to fledging)	0	0/17	-	50	1/2	<i>r</i>	5	1/19
Incubation period									
1993	Unfed controls	4	1/24	<i>a</i>	-	-	-	4	1/24
1993	Fed (laying to fledging)	7	1/15	<i>p</i>	-	-	-	7	1/15
1996	Unfed controls	0	0/17*	-	0	0/5	-	0	0/22
1996	Fed (laying to fledging)	0	0/17	-	100	1/1	<i>u</i>	6	1/18

* One of these 17 nests was later excluded from the post-hatching experiment after two feedings were inadvertently missed during the nestling period (see *Data analysis* in *Methods* section of *Chapter 4*)

Table A-2. Number of failed nesting attempts, between hatching and fledging, in relation to total number of broods hatched in each year, treatment, and burrow type (artificial *versus* natural). Causes of failures: *c* = burrow accidentally cultivated, *d* = brood drowned when burrow flooded, *f* = adult female and brood died even though ample food was cached in the nest, *m* = adult male killed by raptor, *p* = predation of entire brood, *t* = both adults and brood died after cow trampled entrance of nest burrow trapping them inside, *u* = unknown cause of failure.

Year	Treatment	Artificial nest burrows			Natural nest burrows			All burrows	
		%	failed/ total	Cause(s)	%	failed/ total	Cause(s)	%	failed/ total
1992	Unfed controls	0	0/4	–	30	3/10	<i>p, p, p</i>	21	3/14
1992	Fed (hatching to fledging)	0	0/5	–	25	1/4	<i>p</i>	11	1/9
1993	Unfed controls	8	1/12	<i>p</i>	–	–	–	8	1/12
1993	Fed (hatching to fledging)	9	1/11	<i>d</i>	–	–	–	9	1/11
1993	Fed (laying to fledging)	0	0/14	–	–	–	–	0	0/14
1996	Unfed controls	14	1/7	<i>t</i>	100	2/2	<i>c, u</i>	33	3/9
1996	Fed (hatching to fledging)	33	3/9	<i>f, p, u</i>	0	0/3	–	25	3/12
1996	Fed (laying to fledging)	6	1/17	<i>p</i>	–	–	–	6	1/17
1997	Unfed controls	0	0/6	–	0	0/4	–	0	0/10
1997	Fed (hatching to fledging)	0	0/9	–	40	2/5	<i>m, p</i>	14	2/14
1998	Unfed controls	20	1/5	<i>d</i>	10	1/10	<i>u</i>	13	2/15
1998	Fed (hatching to fledging)	9	2/22	<i>m, u</i>	50	3/6	<i>d, d, p</i>	18	5/28

from hatching to fledging: 1 of 31; data combined for 1993 and 1996).

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