HATCHING ASYNCHRONY, BROOD REDUCTION, AND FOOD LIMITATION IN A NEOTROPICAL PARROT

SCOTT H. STOLESON AND STEVEN R. BEISSINGER[1]

School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut 06511 USA

Abstract. A number of hypotheses for hatching asynchrony suggest that the size hierarchy among nestlings produced by hatching asynchrony is adaptive and confers benefits to parents. We assessed the costs and benefits of asynchronous hatching in the Green-rumped Parrotlet (*Forpus passerinus*), a small Neotropical parrot that hatches large clutches very asynchronously. We manipulated eggs to create broods of four, six, or eight young that hatched synchronously or asynchronously. In a second experiment, we tested whether food limits offspring survival by experimentally feeding later hatched young in large asynchronous broods. We also examined the premise that food varies unpredictably by sampling seeds throughout several breeding seasons.

Experimentally synchronized broods generally fledged as many or more young than asynchronous broods. Synchrony particularly outperformed asynchrony in broods of eight, where food demands should have been greatest. Nestlings had a higher probability of fledging from synchronous broods than from asynchronous broods, from small rather than medium or large broods, and if they were early hatched rather than later hatched. Most mortality in asynchronous broods occurred within 12 d of hatching, and a significantly greater proportion of later hatched chicks died with empty crops than did early hatched chicks. Later hatched chicks grew more slowly than their earlier hatched nestmates, but at fledging they were as heavy or heavier than earlier hatched chicks. Chicks from asynchronous broods were slightly heavier at fledging than synchronous chicks, but there was no correlation between fledging mass and the likelihood of being resighted in subsequent years. Cormack-Jolly-Seber model estimates revealed no significant differences in annual survival rates between young fledged from synchronous and asynchronous broods. Female chicks fledged from synchronous broods were recruited into the study population at a lower rate than those from asynchronous broods. Older chicks from reduced broods were less likely to fledge than chicks from broods that fledged all their young. Parents of large synchronous and asynchronous broods provisioned their young at similar rates and did not differ significantly in their subsequent survival. Females that raised experimentally synchronous and asynchronous broods showed no significant differences in the likelihood, timing, or success of their next breeding attempt. A marginally higher proportion of last-hatched chicks that received supplemental food survived to fledging than last-hatched control chicks, but feeding had no effect on penultimate chicks. Seed densities showed a high degree of autocorrelation over spans of 30–50 d. Asynchronous hatching appears to result in the mortality of the smallest young, due in part to the inequitable distribution of food among nestmates, rather than to food limitation, and as a direct result of the size disparities among nestmates. Thus, parrotlet parents appeared to derive no detectable short- or long-term benefits from the staggered hatching of their young through increased nestling growth and survival, reduced parental efforts, or increased parental survival. Although other adaptive benefits from hatching asynchrony are possible that were not tested directly in these experiments (e.g., "insurance" that some nestlings will survive), they seem insufficient to account for the extreme hatching asynchrony observed in the parrotlet. Instead, benefits to egg survival derived from the early onset of incubation may offset the costs of asynchronous hatching.

Key words: brood reduction; fledging success; food limitation; Forpus passerinus; *Green-rumped Parrotlet; growth rate; hatching asynchrony; mark–recapture; parrot; reproductive effort; survival; Venezuela.*

INTRODUCTION

A variety of altricial and semiprecocial bird species begin to incubate their eggs before the clutch is complete, causing their eggs to hatch asynchronously (Clark and Wilson 1981, Stoleson and Beissinger 1995). Asynchronous hatching produces chicks of different sizes within a brood (Lack 1968, Stokland and Amundsen 1988). Because of the size disparity among nestlings, later hatched chicks can be competitively inferior to their nestmates, and frequently die (Parsons 1975, Lamey and Mock 1991, Seddon and van Heezik 1991a). This mortality presents a paradox in that parents appear to opt for a hatching pattern that reduces fledging success (Stoleson and Beissinger 1995).

Understanding the function of parental care patterns requires an assessment of the costs and benefits of care to animals and their offspring (Clutton-Brock 1991). Parents face numerous trade-offs, such as quantity vs. quality of the offspring they raise (Trivers 1972, Andersson 1978, Lloyd 1987), reproduction vs. survival (Stearns 1976, Bryant 1979, Pugesek 1987, Henrich 1988), and investment in current vs. future reproduction (Williams 1966, Askenmo 1979, Gustafsson and Sutherland 1988, Nur 1988, Stearns 1989). Thus, to resolve the apparent paradox of hatching asynchrony requires a thorough assessment of the costs and benefits of initiating incubation early and hatching eggs asynchronously.

Numerous hypotheses have been proposed to explain hatching asynchrony (reviewed in Magrath 1990, Stoleson and Beissinger 1995). David Lack (1947, 1954) provided a resolution to the paradox by suggesting that when food resources vary unpredictably from the time of laying, parents may benefit by laying the maximum number of eggs that they can raise under ideal conditions and initiating incubation before the clutch is completed. In the event of an unpredictable food shortage, parents can adjust their brood size to the number of young that they can feed by eliminating the smallest chick(s). If hatching occurred synchronously, all nestlings would be equally competitive and would suffer undernourishment or starvation (Lack 1966, 1968). Thus, hatching asynchrony is thought to increase the number or quality of young produced relative to synchronous hatching. The benefits derived by adjusting brood size offset the costs of producing and briefly maintaining surplus young. This hypothesis is known as the Brood Reduction Hypothesis (Ricklefs 1965, Mock 1994) or the Resource Tracking Hypothesis (Forbes 1991).

The Brood Reduction Hypothesis has been tested experimentally numerous times by assessing the effect of manipulated hatch spreads on the reproductive success of parents. Most studies found that broods with decreased hatch spreads fledged as many or more young than normal asynchronous broods (Amundsen and Slagsvold 1991b, Stoleson and Beissinger 1995). Although results have provided little support for the hypothesis, most studies have examined the consequences of hatching asynchrony using only short-term measures, such as the number of fledglings produced. Few studies have quantified postfledging survival or recruitment, which may be better measures of reproductive success (Stoleson and Beissinger 1995). Parents of experimentally synchronized broods may increase their level of parental effort to raise all the young in a brood, thereby reducing their own survivorship or reducing or delaying future reproduction (Nur 1988, Stearns 1989). A long-term, life history perspective may be more appropriate for evaluating the costs and benefits of asynchrony (Mock and Forbes 1994, Stoleson 1996b).

Sixteen alternatives to the Brood Reduction Hypothesis have been proposed (Stoleson and Beissinger 1995). Like that hypothesis, most consider the size hierarchy among nestlings to have some adaptive value. Several are based on food limitations. Size disparities among nestmates may serve to increase parental efficiency by spreading out the peak food demands of a brood (the Peak Load Reduction Hypothesis; Hussell 1972, Mock and Schwagmeyer 1990), or the demand for a limited food resource (the Dietary Diversity Hypothesis; Magrath 1990). Asynchrony may serve to prioritize chicks within a brood, enabling parents to accelerate the fledging of first-hatched young in the face of diminishing food resources (the Hurry-up Hypothesis; Hussell 1985), or selectively eliminate later hatched individuals of the more expensive sex in sexually dimorphic species (the Sex Ratio Manipulation Hypothesis; Slagsvold 1990). Alternatively, asynchrony may be unrelated to food supply, and function to reduce sibling rivalry by imposing a dominance hierarchy based on size among nestmates (the Sibling Rivalry Hypothesis; Hahn 1981), or to facilitate the elimination of surplus nestlings that function as insurance against the loss of older sibs (the Insurance Hypothesis; Stinson 1979, Forbes 1991).

Although the function of the nestling size hierarchy differs among the preceding hypotheses, all posit that parents derive benefits by hatching their eggs asynchronously, and that asynchronous hatching addresses constraints on reproductive success that occur during the nestling period (Stoleson and Beissinger 1995). This suite of hypotheses may be collectively labeled as *adaptive hatching pattern* hypotheses. All share general predictions about the relative effects of synchronous and asynchronous hatching on reproductive success and the costs of reproduction. Compared to chicks in asynchronously hatched broods, chicks in synchronously hatched broods may (1) have a lower probability of fledging; (2) be of lower quality as measured by growth rate or fledging mass; or (3) experienced reduced postfledging survival. Compared to parents of

asynchronously hatched broods, parents of synchronously hatched broods may (1) invest greater levels of effort to raise their broods; (2) experience lower survival; (3) be less likely to raise a second brood; (4) experience delays in laying a second clutch; (5) lay fewer eggs in a second clutch; or (6) fledge fewer young from a second brood. For species that hatch their eggs asynchronously, these potential benefits should exceed the costs of offspring mortality associated with asynchrony.

In addition, several hypotheses make specific predictions. The Brood Reduction Hypothesis predicts differences between synchronous and asynchronous broods only when food resources are scarce. Furthermore, the Brood Reduction Hypothesis is based on the premise that food supplies vary unpredictably. All food-dependent hypotheses (Brood Reduction, Peak Load Reduction, Dietary Diversity, and Hurry-up) predict that food availability limits fledging success. The Brood Reduction and Insurance hypotheses view mortality of the smallest offspring as an adaptive adjustment of brood size to fit parental ability. Therefore, surviving young in asynchronous nests should benefit from the mortality of their younger sibs through increased growth rates, higher fledging masses, or a greater probability of fledging.

In this paper, we report the results of experiments that assessed the costs and benefits of hatching asynchrony in a color-banded population of Green-rumped Parrotlets (*Forpus passerinus*), a small Neotropical parrot that lays large clutches that hatch completely asynchronously (Beissinger and Waltman 1991). Because parrotlets feed their young the same variety of seeds throughout the nestling period (Waltman and Beissinger 1992; S. H. Stoleson and S. R. Beissinger, *unpublished data*), the Dietary Diversity Hypothesis does not pertain to this species. Likewise, the Sex Ratio Manipulation Hypothesis is irrelevant because this species does not show sexual dimorphism in size at fledging (Forshaw 1989, Waltman and Beissinger 1992). We experimentally tested the remaining hypotheses by manipulating broods to hatch relatively synchronously or asynchronously, and assessed the effects of synchrony on nestling quality, fledging success, postfledging survival, parental effort, and other costs of reproduction. Because one premise of the food-dependent hypotheses is that the quantity of food limits nestling survival, we conducted a second experiment in which we provided supplemental food to a subset of later hatched nestlings to test whether starvation was the primary cause of mortality for these young. Although we were not able to limit or augment food availability in the wild, this study included 1 yr of normal abundant rainfall (1550 mm in 1990) and 1 yr of record-breaking drought (988 mm in 1989). Thus, it is likely that seeds were limited in one of the two years. We also tested the premise that food supplies vary unpredictably and are correlated with rainfall by sampling densities of seeds eaten by parrotlets.

Methods

Study site and species

This study was conducted at Hato Masaguaral, a working cattle ranch 45 km south of Calabozo, in Guárico, Venezuela (8°34′ N, 67°35′ W). The habitat is primarily flat brushy savanna, or llanos, with scattered clumps of larger trees. Rainfall averages 1485 mm/yr (Troth 1979), but is highly seasonal, and large areas flood during the rainy season (May–November). See Troth (1979) and Beissinger et al. (1988) for detailed descriptions of the area. Field work was conducted from May through December of 1989 and 1990. During the course of other studies from 1991 through 1993, we attempted to identify all banded individuals seen within the study site, and opportunistically identified individuals sighted outside of the study area.

The Green-rumped Parrotlet is a small (24–36 g) granivorous Neotropical parrot that inhabits savanna, pasture, and forest edge (Forshaw 1989). It feeds principally on the seeds of herbaceous plants or fruits (Waltman and Beissinger 1992). The sexes are plumage dimorphic. Parrotlets breed during the rainy season and frequently raise two broods per year (Waltman and Beissinger 1992). Parrotlets lay large clutches that hatch and fledge very asynchronously (Plate 1). Clutch size averages 7 eggs (range 4–11 eggs) and observations suggest that most females initiate incubation with their first egg (Beissinger and Waltman 1991). Complete clutches hatch over an interval of 6–14 d ($\overline{X} = 8.6$ d), and hatch spread is positively correlated with clutch size (Beissinger and Waltman 1991). Extreme hatching asynchrony in Green-rumped Parrotlets leads to low survivorship of penultimately hatched and last-hatched young (Beissinger and Waltman 1991). See Beissinger and Waltman (1991), Waltman and Beissinger (1992), and Stoleson (1996a) for further details of parrotlet breeding biology. The study population of parrotlets nested in 100 nest boxes made from polyvinyl chloride tubing attached to fence posts (Beissinger and Bucher 1992).

Hatching asynchrony experiment

We assessed costs and benefits of asynchronous hatching in the Green-rumped Parrotlet by randomly assigning nests with complete clutches to synchronous and asynchronous treatments (hereafter SYNC and ASYNC). During the latter half of the incubation period, eggs of known laying dates were moved among nests to create broods that hatched relatively synchronously (within 2–3 d), or asynchronously, with a hatch spread typical of this species (from 6 to 14 d depending on clutch size; Beissinger and Waltman 1991). A hatch spread of 2–3 d was used for SYNC nests because incubation time can vary among eggs by several days,
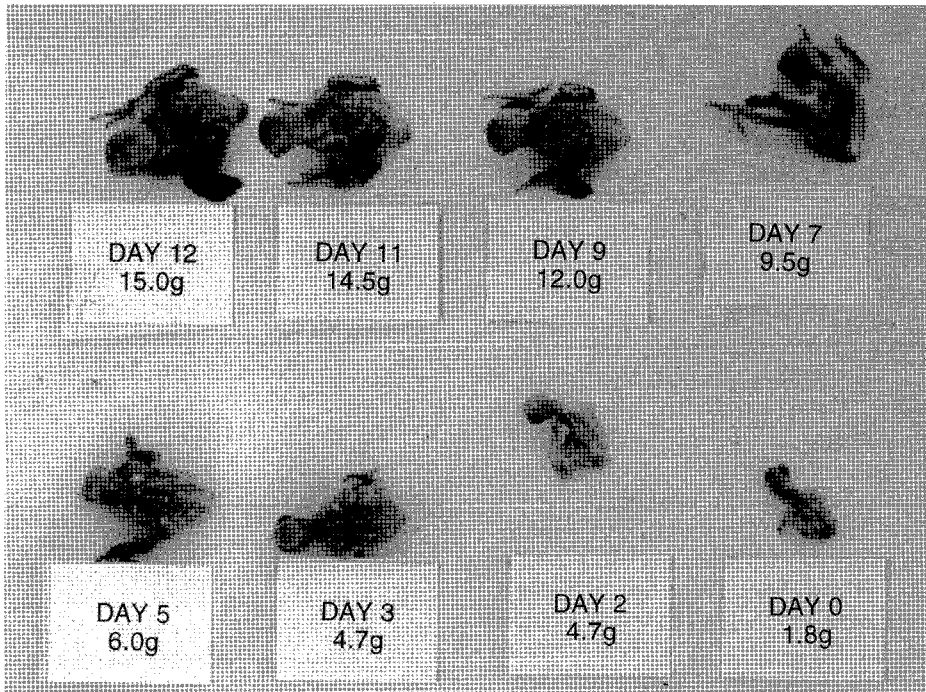
PLATE 1. Typical hatching asynchrony for a brood of eight young in a Green-rumped Parrotlet (*Forpus passerinus*) nest in Venezuela. The age and mass of each chick are shown. Hatching of the brood occurred over a 12-d period. On the birthday of the eighth chick (day 0), its oldest sibling was an order of magnitude larger in mass and halfway to fledging. Last and penultimately hatching chicks frequently die during their first week of life from starvation and other causes resulting directly from this size disparity.

which makes more precise synchronization difficult, and because spreads of <48 h never occur in this species and would represent an unnaturally extreme degree of synchrony. ASYNC nests contained eggs from several source nests to control for possible effects of manipulation (Götmark 1992). In 1989 both brood size and hatching asynchrony were manipulated to determine how these factors interacted: experimental broods ($n = 52$) contained either four, six, or eight chicks that hatched either synchronously or over 6–7, 9–10, or 12–14 d, respectively. In 1990 we created another 26 experimental broods. All contained eight chicks, because for most nests this constituted a slight brood enlargement, thus potentially exacerbating food limitations (Forbes 1994), and because in 1989 differences between treatments occurred only among large broods.

Nests were checked daily until all eggs hatched to determine hatching dates. Because SYNC nests frequently had more than one egg hatch in a day, pipped eggs were injected with 0.01 mL of nontoxic food dye to identify individuals during hatching. Eggs that failed to hatch on schedule were replaced with newly hatched chicks from unmanipulated nests. Nestlings were individually marked at hatching and every 2–4 d thereafter with nontoxic paints, and uniquely marked with a combination of colored plastic and metal bands ≈5 d before fledging. Approximately every 4th d nestlings were weighed (within ±0.1 g) with Pesola spring scales or an Ohaus electronic scale. Nestlings that died were

not removed by parrotlet parents; we examined them to determine whether their crops contained food and removed them from the nest. Nestlings were considered to have fledged if they survived in the nest until at least 25 d after hatching. Nests were checked daily after day 25 to determine exact dates of fledging.

The rates at which parents provisioned their young were used to measure parental effort. In 1990, experimental nests were observed from 30–60 m away with spotting scopes or 10-power binoculars. Nests were watched for 3-h periods ≈4, 8, 12, 16, and 23 d after the hatching of the first chick. Watches of 3 h were found to be of sufficient length to detect differences in provisioning rates (Waltman and Beissinger 1992, Curlee and Beissinger 1995). During nest watches, the frequency and duration of visits by either parent to feed young were recorded. We followed the criteria of Waltman and Beissinger (1992) to define feeding trips. Parents of experimental broods were marked with a unique combination of colored aluminum and plastic to allow individual identification. Following these experiments, all banded birds within the study site were identified to individual whenever possible. These resightings were used for estimates of survival of fledglings and parents.

Supplemental feeding experiment

When results from the synchrony manipulations suggested food supplies may not limit reproductive suc-

cess, a second experiment was designed to better understand the mechanisms of nestling mortality in large parrotlet broods. In 1990, we moved eggs among nests to create 20 asynchronous broods of eight young, with hatch spreads of 12–14 d. At 10 nests ("fed nests") we fed fifth-, seventh-, and eighth-hatched young three times per day (0800–1000, 1200–1400, and 1600–1800) with a formula recommended for parrotlet nestlings by aviculturalists (R. Conser, *personal communication*). The formula was a puree of commercial monkey chow, powdered Roudybush parakeet feed, oatmeal, eggs, mixed fruit baby formula, and water. Fifth-hatched chicks were fed to test for possible negative effects of feeding procedures. Feeding began when the last nestling hatched and continued for 17 d. At all feedings, nestlings were given enough formula through a ball-tipped feeding tube to fill the crop completely. Nestlings retained some food in their crops throughout the day. Ten control nests were visited and checked at the same frequency as fed nests, but chicks did not receive food. All nestlings from fed and control nests were weighed each morning and crop contents were noted at each visit for fifth-, seventh-, and eighth-hatched young.

Seed sampling

We did not quantify food availability during the two years of these experiments, but we estimated the predictability of food resources available to parrotlets by sampling seed density approximately every 10 d throughout the nesting periods of 1992 and 1993 and for 3 mo in 1994. Four fixed transects were established in two different locations used for foraging by parrotlets: two in dry pasture and two in wet savanna. For each sampling session, we chose 10 points at random along each transect. Within a radius of 0.5 m of each point, we counted the number of stems bearing seeds and the mean number of seeds per plant for species known to be eaten by parrotlets (Waltman and Beissinger 1992; S. H. Stoleson and S. R. Beissinger, *unpublished data*).

Analyses

We examined the effects of synchrony treatment and brood size on per-brood fledging success. Because the hypotheses do not pertain to extraneous causes of mortality such as predation or infanticide, nests that failed due to predation ($n = 10$), infanticide ($n = 5$), or abandonment ($n = 2$) were excluded from all analyses. We analyzed the effects of synchrony treatment, brood size, and hatching order on growth parameters, fledging probability, and postfledging survival of individual nestlings. Because all chicks within a brood are subject to the same effects of nest site and parentage, they may be considered pseudoreplicates (J. T. Rotenberry, *personal communication*). Multivariate analyses based on individual nestlings therefore included individual nest as a variable to partition out nest-specific variance (M.

Dennis, *personal communication*). To examine the effects of relative hatching order, chicks were assigned to one of four categories: first-hatched, middle, penultimately hatched, and last-hatched (Beissinger and Stoleson 1991, Beissinger and Waltman 1991). For some analyses, first- and middle-hatched chicks were pooled as early-hatched, and penultimate and last-hatched chicks as late-hatched. Data from 1989 and 1990 were analyzed both separately and pooled. Results are presented for individual years only when significant differences existed between years.

Nestling growth.—Logistic curves and growth parameters were fit to mass data of 337 individual nestlings that fledged from experimental broods, using the equation

$$\text{MASS} = \frac{A}{1 + e^{-K(\text{age}-I)}}$$

where A is the asymptotic mass, K is the growth constant, and I is the inflection point, using the SAS NLIN procedure (SAS Institute 1988). Growth parameters of parrotlets did not differ between the sexes (Waltman and Beissinger 1992), so data from males and females were pooled. We used ANOVAs to test for significant effects of synchrony treatment, brood size, and hatching sequence on growth parameters.

Fledgling survival and recruitment.—Logistic regression was used to examine the effects of fledging mass, brood size, synchrony treatment, hatching sequence, sex, and year on the probability of a nestling ever being seen after fledging. Brood size and hatching sequence were treated as continuous variables; other variables were treated as categorical. Logistic models employed a forward selection–backward elimination methodology using a critical value of 0.05 to enter or remove variables from the model. The probability of resighting a marked bird at time i depends not only on the probability that it is alive and in the study population at time i (ϕ_i), but also on the probability that it is seen if alive (p_i). We therefore employed maximum likelihood models to obtain separate estimates of survival rate, ϕ, and resighting probability, p, for nestlings from each treatment following the methods of Lebreton et al. (1992). See Loery and Nichols (1985), Krementz et al. (1989), Spendelow and Nichols (1989), Blondel et al. (1992), Kanyamibwa et al. (1993), and Brawn et al. (1995) for other examples of this approach. Postfledging survival rates of young produced from experimental ASYNC and SYNC nests were estimated using resighting data from 1990 through 1993 in a modified Cormack-Jolly-Seber mark–recapture model using the program SURGE, version 4 (Clobert et al. 1987, Lebreton et al. 1992).

Maximum likelihood survival models assume that (1) ϕ_i and p_i are homogeneous within any subgroup of individuals, (2) marking is accurate and permanent, and (3) the resighting or death of any individual is independent of the fate of other individuals (Burnham et

al. 1987). We used goodness-of-fit tests of the program RELEASE (TEST 2 and TEST 3; Burnham et al. 1987) on a fully parameterized model to test the first assumption. All nestlings were marked with at least one permanent metal band, so no individuals were "lost." We were not able to test the final assumption of independent fates. It might not be met for birds fledging from the same nest because fledglings may remain together while receiving parental care after leaving the nest (Krementz et al. 1989). However, we believe any brief dependence among broodmates would have little effect on parameter estimates because the period of postfledging care appears to be short in the parrotlet (Waltman and Beissinger 1992), and because our resightings were considered on an annual basis.

Model selection followed the step-down strategy suggested by Lebreton et al. (1992). We began with a fully parameterized model and progressively examined models with reduced parameters. We assessed the effects of year (y), age class (a), and synchrony treatment (s) on survival and resighting rates. We defined two age classes (first year vs. after-first year) because first-year birds appear to experience high rates of mortality, emigration, or both (S. H. Stoleson and S. R. Beissinger, *unpublished data*). We modeled resighting probabilities first to retain as much power as possible for tests of survival parameters. For similar reasons we tested for effects of year and age class before synchrony treatment. The final most parsimonious model structure that fit the data was determined using Akaike's Information Criterion (AIC; Lebreton et al. 1992). The AIC is the sum of the maximum log-likelihood plus two times a model's number of estimable parameters. Because it is an objective optimization function, the AIC avoids the increased risk of Type I errors resulting from multiple statistical tests between models (Lebreton et al. 1992). The fit of the data to the most parsimonious model was assessed using a χ^2 goodness-of-fit test.

For all models, brood sizes and sexes were pooled to boost sample sizes and increase power to detect differences between SYNC and ASYNC young. We tested for differences in fledgling survival rates or resighting probabilities due to the effects of year, age, or synchrony treatment using a likelihood ratio test (LRT) between a complex model with separate values for the parameter of interest and a neighboring, reduced-parameter model with a common value (Lebreton et al. 1992). Model estimates of survival and resighting rates tend to have relatively large sampling variances that reduce the power of tests that use these estimates. We therefore used a significance level of $P \leq 0.10$ to increase the power of these LRT tests to take advantage of the relation between the probabilities associated with Type I and Type II errors (Krementz et al. 1989, Lebreton et al. 1992). In cases where the null hypothesis of no difference in survival rates could not be rejected, the statistical power of tests was approximated by generating expected frequencies under the alternative hy-

pothesis of different rates (Burnham et al. 1987:214–217). These expected counts were analyzed using SURGE as if they were real data. The χ^2 test statistic produced in contrasts of the alternative hypothesis against the null hypothesis approximates lambda, the noncentrality parameter of the corresponding chi-square power curve for the parameters used to generate the expected data (Burnham et al. 1987:214–217).

To measure recruitment of young into the population, the proportions of fledglings known to have bred within the study site in subsequent years were compared using χ^2 tests.

Effects of brood reduction on surviving siblings.— We tested the prediction that the early loss of younger chicks in asynchronous broods resulted from adaptive reduction of brood size to alleviate food stress. For these analyses we considered broods to be reduced in size if one or more later hatched nestlings died in the nest within 12 d of hatching. This age was chosen because the timing of mortality of later hatched young was bimodal in distribution: 87% of the mortality occurred within 12 d of hatching, and the remainder occurred after 21 d of age, when the potential benefits of brood reduction were unlikely to accrue. Analyses included ASYNC nests from synchrony manipulation experiments and control nests from the food supplement experiments, but excluded nests in which nestlings died from extraneous causes such as infanticide or predation. If brood reduction is an adaptive strategy, then chicks in reduced broods should no longer be food stressed, and should therefore show growth parameters and fledging success similar to or greater than chicks from broods with ample food. We have assumed that broods that fledged all their young had received ample food.

Costs of reproduction.—We also assessed possible costs of reproduction due to synchrony treatment. Small sample sizes precluded separate analyses by year. We estimated survival and resighting rates of males and females separately with mark–recapture models using the methods described for fledglings. We assessed the effects of year and synchrony treatment on survival and resighting rates. Because most parents were of unknown age, we could not assess the effect of age on survival. Parents that raised both synchronous and asynchronous experimental broods in different nesting attempts within a single year were excluded from survival analyses.

The nesting histories of females that raised experimental broods were followed to assess potential impacts of treatments on subsequent reproduction. For females that had an experimental first brood, we calculated both the proportion of females that laid second clutches and the number of days between the fledging of the last young in their first experimental broods and the laying of the first egg in second broods for each female. For females that raised an experimental second brood, we examined the effect of treatment on the tim-

ing of the first brood in the following year by comparing deviances from the mean starting date for that year. For all females that raised experimental broods, the clutch size and number of young fledged from their next nesting attempt were recorded. We did not assess effects beyond the next breeding attempt because most pairs were subsequently subjected to other experimental manipulations that may have affected later reproductive success.

Seed sampling.—Seed data from wet and dry sites were analyzed separately because the areas differed in species composition and fruiting phenology. We averaged the 20 points at each location (dry and wet) to obtain a mean density of seeds (seeds per square meter). We excluded three nonconsecutive sample sessions at one of the dry sites when the pasture was freshly mowed. We calculated Pearson correlations between the mean seed density at time 0 and the density at 30, 40, and 50 d as a crude measure of environmental predictability (Beissinger and Gibbs 1993). These intervals bracket the time span in which most brood reduction occurs; they represent the average intervals between the initiation of egg-laying and the hatching of the seventh egg, the time when an eighth-hatched chick would be 8 d old, and the time when an eighth-hatched chick would be 18 d old, respectively. We tested the assumption of a relationship between rainfall and seed availability by calculating Pearson correlations between mean seed density and total rainfall in the 10 d prior to the seed sampling session.

Statistical analyses.—Data were analyzed using SYSTAT (Wilkinson 1990) and SAS (SAS Institute 1988). Means are reported with standard deviations except where noted. When assumptions of normality and homogeneity of variances were not violated, means were compared using analyses of variance (ANOVA) or t tests; otherwise, appropriate nonparametric tests were used. Specific predictions were tested using one-tailed tests. Where significant effects existed ($P < 0.05$), we used Tukey HSD post-hoc tests to identify differences between groups. Frequency data were analyzed using χ^2 tests of independence, except when one or more expected cell counts in 2 × 2 tables were <5, when Fisher's exact tests were used. Where statistical tests of specific predictions failed to reject null hypotheses, the statistical power of those tests was estimated using $\alpha = 0.05$ and observed effect sizes (Cohen 1988, Wickens 1989).

RESULTS

Effects of experimental synchrony on fledging success and nestling mortality

A total of 337 young parrotlets fledged from 61 experimental ASYNC and SYNC nests. The ratio of male to female fledglings was similar (ASYNC; 0.99:1; SYNC; 0.87:1) for both treatments ($\chi^2 = 0.32$, df = 1, $P = 0.572$). A two-way ANOVA using synchrony treat-
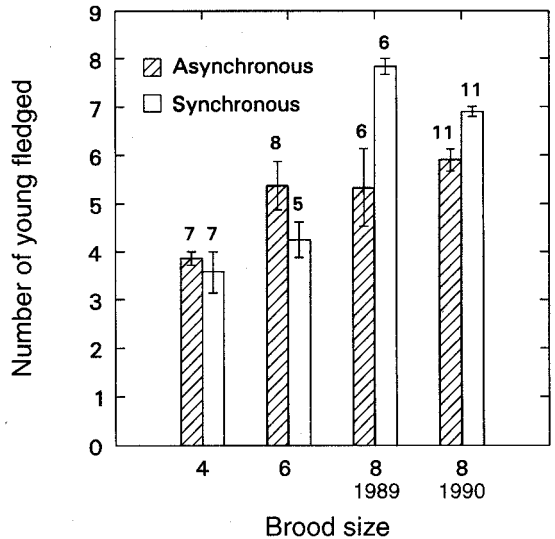

FIG. 1. Fledging success in 61 experimentally asynchronous and synchronous parrotlet nests of four, six, and eight young in 1989 and 1990 (in 1990 all nests had eight young). Bars indicate ± 1 SE of the mean, and sample sizes are given above each bar. Only nondepredated nests are included.

ment and brood size as factors revealed that fledging success in experimental nests was related to both brood size and hatching asynchrony (Fig. 1). Large broods (eight young) fledged more young than medium (six young) or small (four) broods for both SYNC and ASYNC treatments ($F_{2,55} = 20.4$, $P < 0.001$). Hatching asynchrony alone had no effect on fledging success ($F_{1,55} = 0.003$, $P = 0.95$), but the interaction of brood size and hatching asynchrony did affect the number of young fledged ($F_{1,55} = 4.8$, $P = 0.01$). Synchrony treatment had no significant effect on the number of young fledged in small (Tukey HSD test, $P = 0.98$) or medium broods (Tukey HSD test, $P = 0.70$). But large SYNC broods fledged significantly more young (Fig. 1) than large ASYNC broods overall (Tukey HSD test, $P = 0.03$) and in 1989 (Tukey HSD test, $P = 0.01$), although not in 1990 (Tukey HSD test, $P = 0.15$).

Logistic regression indicated that an individual chick's probability of survival to fledging was a function of the size and degree of synchrony of its brood, and of its hatch order within the brood (Fig. 2, Table 1). First- through sixth-hatched young fledged at a uniformly high rate regardless of brood size or synchrony treatment (Fig. 2). Seventh- and eighth-hatched chicks also had a high probability of fledging from SYNC broods, but few fledged from large ASYNC broods (Fig. 2). Thus, treatments differed in the number of young fledged from large broods due to the low survival of penultimate and last-hatched chicks in ASYNC broods (Fig. 2). Generally, chicks were more likely to fledge from SYNC broods than from ASYNC broods, from small rather than medium or large broods, and if
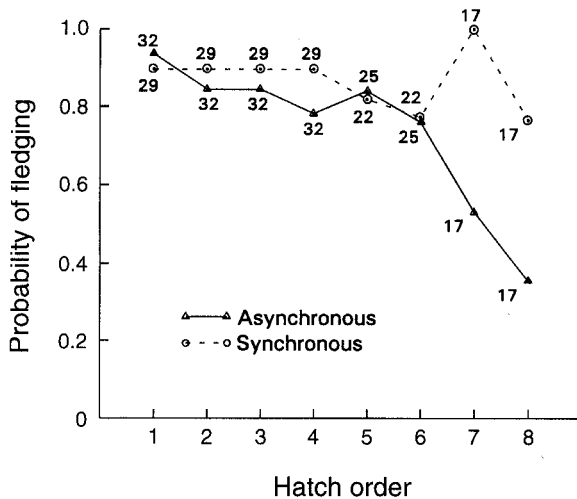
FIG. 2. The probability of fledging for 406 parrotlet chicks from 61 experimental broods in relation to asynchrony treatment and hatch order. All brood sizes are pooled. Sample sizes are given and indicate nondepredated nests only.

they were early-hatched rather than late-hatched chicks.

Effects of brood reduction on surviving nestlings.— The loss of younger siblings did not appear to increase the probability of fledging for nestlings that survived to 13 d of age in asynchronous broods. The proportions of first- through sixth-hatched nestlings fledged from reduced and unreduced broods did not differ significantly when considered individually (Table 2). Overall, however, a significantly lower proportion of older chicks fledged from broods after brood reduction (0.81) than from unreduced broods (0.93; Table 2), contrary to predictions.

Nestling mortality.—Excluding complete nest failures due to predation or infanticide, 71 (17.4%) nestlings from experimental broods died. A significantly higher proportion ($\chi^2 = 5.3$, df $= 1$, $P = 0.02$) of ASYNC chicks (21.7%) died than SYNC chicks (12.8%). Partial brood losses included 21 nestlings that were victims of predation ($n = 16$) or infanticide ($n = 5$). We observed no wounds, fights, behaviors, or other evidence that overt sibling aggression, fatal or otherwise, occurred in this species.

Mortality of the remaining 50 nestlings found in nests was potentially due to food limitations. Of these, 8 were too decomposed when examined to determine whether they died with food in their crops. Crop contents of chicks found dead in the nest ($n = 42$) suggested that starvation may have been a major cause of early mortality for later hatched nestlings in ASYNC broods. The majority (77.8%) of offspring found dead in ASYNC nests died before reaching 13 d of age ($n = 21$). Of these, a significantly higher proportion of later hatched nestlings (73.0%) died with empty crops than did earlier hatched nestlings (20.0%; Fisher's exact test, one-tailed, $P = 0.02$). Too few offspring died

TABLE 1. The effects of synchrony treatment, brood size, and hatching sequence on the probability of fledging, based on a mixed logit model.

Effect	df	Chi-square	P
Intercept	1	12.55	0.001
Synchrony treatment	1	9.32	0.023
Brood size	1	3.89	0.048
Hatching sequence†	1	3.22	0.048
Synchrony × size	1	12.66	0.001
Synchrony × sequence	1	2.57	0.109
Size × sequence	1	5.75	0.017
Synchrony × size × sequence	1	3.15	0.076
Likelihood ratio	4	4.80	0.309

† First-hatched through antepenultimately hatched chicks are pooled as early-hatched, penultimate and last-hatched as late-hatched.

in SYNC nests before 13 d of age ($n = 8$) to analyze statistically. Nevertheless, the single later hatched nestling that died had food in its crop. Few offspring died after 13 d of age in ASYNC ($n = 6$) or SYNC ($n = 9$) broods, and in neither case was there an association of crop contents with hatching order. The mean age of mortality for chicks found dead in the nest was significantly higher ($t = 3.38$, df $= 29$, $P = 0.002$) for SYNC chicks ($\overline{X} = 18.8 \pm 11.7$ d) than for ASYNC chicks ($\overline{X} = 8.5 \pm 8.2$ d).

Effects of experimental synchrony and brood reduction on nestling growth

Nestling parrotlets grew slowly and growth curves were sigmoidal in shape (Fig. 3). Average curves for SYNC and ASYNC young diverged primarily at later ages, in part because ASYNC chicks peaked in mass well before fledging, while SYNC chicks peaked near fledging (Fig. 3). In large broods, later hatched chicks grew more slowly than their earlier hatched nestmates, especially in ASYNC broods (Fig. 4). At fledging, however, later hatched chicks were as heavy or heavier than earlier hatched chicks.

Growth constants (K) for all experimental chicks averaged 0.23 ± 0.04. Growth constants declined with increasing brood size (Table 3). Chicks in large broods

TABLE 2. The proportion of surviving young in experimental asynchronous broods that fledged, in relation to hatching order and whether or not the brood experienced brood reduction. Sample sizes include only young that survived to 13 d of age.

Hatching order	Proportion fledged (N)		P
	Reduced	Not reduced	
1	0.95 (19)	0.95 (22)	1.00
2	0.80 (20)	0.95 (22)	0.17
3	0.80 (20)	0.91 (22)	0.40
4	0.75 (20)	0.91 (22)	0.23
5	0.84 (19)	0.93 (14)	0.62
6	0.74 (19)	0.93 (15)	0.20
Total	0.81 (117)	0.93 (117)	0.006

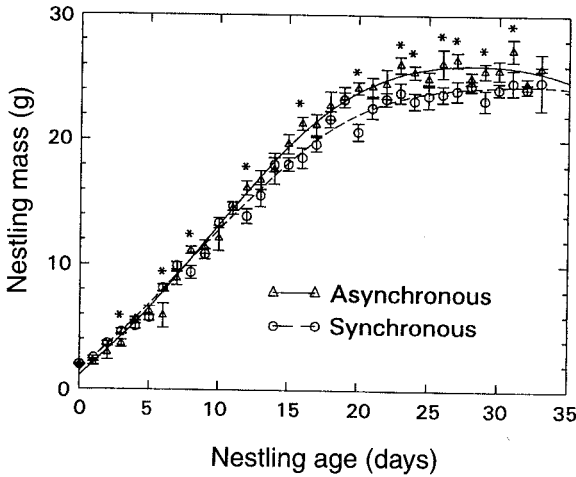*Note:* Level of significance for hatching order 1–6 derived from Fisher's exact tests; total: $\chi^2 = 7.49$, df $= 1$.

FIG. 3. Average growth curves of 337 young from experimentally asynchronous and synchronous broods of eight young. Bars represent ±1 SE of the mean. Lines were fitted to the points using a distance-weighted least squares algorithm. Significant differences (t test with $P < 0.05$) are indicated by asterisks above the upper line.

grew more slowly (0.23 ± 0.4, $n = 222$) than chicks in small (0.25 ± 0.03, $n = 52$; Tukey HSD test, $P = 0.002$) or medium broods (0.25 ± 0.05, $n = 63$; Tukey HSD test, $P = 0.001$). Growth constants declined with hatching sequence (Table 3), indicating that later hatched chicks grew more slowly than their earlier hatched nestmates (Fig. 4). A significant interaction occurred between hatching sequence and brood size (Table 3), because the disparity in growth constants within broods was greater in large broods than in small or medium broods. Synchrony alone had no effect on K (Table 3).

Chicks from ASYNC broods generally fledged at higher masses than SYNC chicks (Table 3). Chicks from SYNC broods reached a lower average asymptotic mass (24.8 ± 2.5 g, $n = 171$) than ASYNC chicks (26.3 ± 3.2 g, $n = 166$). Brood size and hatching se-

quence also influenced asymptotic mass (Table 3). Chicks from broods of four achieved higher asymptotic masses (26.7 ± 1.9 g) than chicks from broods of six (25.3 ± 3.1 g; Tukey HSD test, $P = 0.007$) or eight (25.6 ± 3.1 g; Tukey HSD test, $P = 0.009$). Last-hatched chicks tended to be heavier (25.9 ± 3.3 g) than first (25.4 ± 2.7 g; Tukey HSD test, $P = 0.038$) or middle chicks (25.2 ± 2.9 g; Tukey HSD test, $P = 0.001$). Differences between peak masses and fledging masses were significantly smaller for SYNC chicks (0.79 ± 1.0 g) than for ASYNC chicks (1.2 ± 1.3 g; ANOVA with synchrony treatment and nest as factors: $F_{1,276} = 12.11, P < 0.001$). ASYNC chicks were slightly but significantly ($F_{1,276} = 16.44, P < 0.001$) heavier at fledging (24.9 ± 2.9 g) than SYNC chicks (24.1 ± 2.2 g).

The inflection point (I) of the sigmoid growth curve of nestling parrotlets averaged 10.19 ± 2.26 d. Brood size influenced the value of inflection points (Table 3). Chicks from medium broods reached the inflection point of their growth curves earlier (9.62 ± 1.76 d) than chicks in large broods (10.46 ± 2.54 d; Tukey HSD test, $P = 0.013$). SYNC chicks reached their inflection points at a younger age (9.95 ± 1.66 d) than ASYNC chicks (10.44 ± 2.73 d) (Table 3). Later hatched chicks reached their inflection point at a greater age (11.45 ± 3.05 d, $n = 92$) than earlier hatched chicks (9.72 ± 1.66 d, $n = 245$), especially in large broods and in ASYNC broods (Table 3).

Nestlings that eventually died before fledging generally grew more slowly than chicks that fledged (Fig. 5). In large ASYNC broods, the mean mass of chicks that eventually died was significantly less than the mean mass of those that lived for almost every age up to 14 d of age, suggesting death was due to starvation. After 14 d of age there were few differences in the average masses of chicks that fledged and those that died.

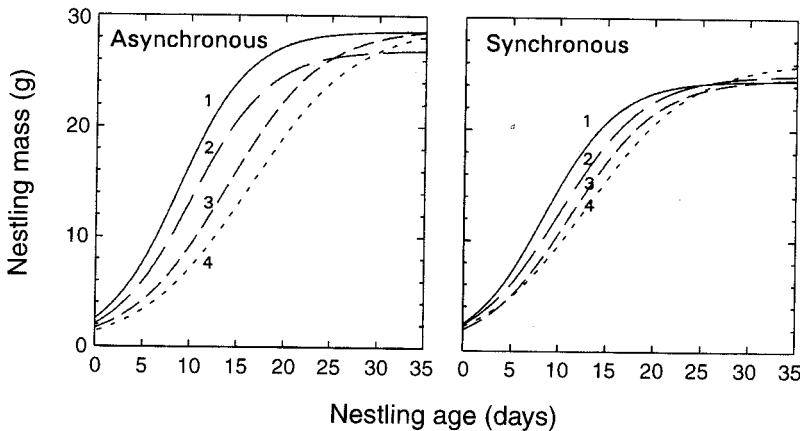The early loss of siblings had little effect on growth

FIG. 4. Average growth curves of young from experimentally asynchronous and synchronous broods of eight young in relation to hatching sequence: 1 = first-hatched, 2 = middle (second- through sixth-hatched), 3 = seventh-hatched, and 4 = last-hatched. Logistic curves were plotted from parameter means.

TABLE 3. Four-way analyses of variance of asymptotic mass (A), growth constant (K), and inflection point (I) for nestling parrotlets from small, medium, and large experimental synchronous and asynchronous broods in 1989 and 1990. Nest was included as a category to control for brood-specific variation.

Effect	df	A		K		I†	
		F	P	F	P	F	P
Synchrony	1	42.65	0.01	0.86	0.35	6.41	0.02
Brood size	2	11.62	0.01	18.84	0.01	10.63	0.01
Hatch sequence‡	3	3.92	0.01	28.10	0.01	37.36	0.01
Nest	54	6.42	0.01	3.65	0.01	1.86	0.01
Synchrony × brood	2	0.89	0.41	0.03	0.97	1.67	0.19
Synchrony × sequence	3	3.25	0.02	3.67	0.02	4.56	0.01
Brood × sequence	6	1.48	0.18	5.44	0.01	7.29	0.01
Synchrony × brood × sequence	6	0.55	0.77	0.39	0.88	1.08	0.37
Error	253						

† Log-transformed.
‡ Nestlings were categorized by hatching sequence as first, middle, penultimate, and last.

parameters of parrotlet nestlings in asynchronous broods. Asymptotic masses of chicks from reduced and unreduced broods did not differ significantly (ANOVA with brood reduction, hatching sequence, and nest as factors, $F_{1, 169} = 2.5$, $P = 0.12$). Neither growth constants (K) (0.22 vs. 0.24; $F_{1, 169} = 0.03$, $P = 0.85$) nor inflection points ($F_{1, 169} = 0.01$, $P = 0.92$) differed significantly between chicks from reduced and unreduced broods.

Age at fledging. Parrotlet chicks fledged at ages that ranged from 26 to 41 d of age ($\overline{X} = 31.7$, $n = 335$; Table 4). An ANOVA with brood size, synchrony, hatching order, and nest as factors showed that nest, brood size, hatching order, the interaction of brood size and synchrony treatment, and the three-way interaction of brood size, synchrony, and hatching order influenced

FIG. 5. Average growth curves of parrotlet nestlings up to 14 d of age for chicks that eventually fledged or died. Bars represent ±1 SE of the mean. Lines were fitted to the points using a distance-weighted least squares algorithm. Significant differences (*t* test with $P < 0.05$) are indicated by asterisks above the upper line.

the age at fledging (Table 5). Nestlings in large broods generally took more time to fledge ($\overline{X} = 32.6 \pm 2.5$ d, $n = 220$) than those in small ($\overline{X} = 30.5 \pm 1.6$ d, $n = 51$, Tukey HSD test, $P < 0.001$) and medium ($\overline{X} = 31.2 \pm 2.3$ d, $n = 64$, Tukey HSD test, $P = 0.022$) broods (Table 4). First-hatched nestlings generally fledged at a younger age ($\overline{X} = 30.6 \pm 1.6$ d, $n = 56$) than penultimate- ($\overline{X} = 32.0 \pm 2.9$ d, $n = 49$, Tukey HSD test, $P = 0.031$) and last-hatched nestlings ($\overline{X} = 32.5 \pm 3.0$ d, $n = 42$, Tukey HSD test, $P = 0.015$). Penultimate- and last-hatched chicks in large ASYNC broods required more time to fledge than all other nestlings (all Tukey HSD tests $P < 0.05$; Table 4). Synchrony treatment alone had no detectable effect on age at fledging, but nestlings in large ASYNC broods took more time to fledge than nestlings in large SYNC broods, as indicated by a significant interaction effect (Table 5).

Effects of experimental synchrony on postfledging survival and recruitment

Most fledglings from experimental broods were never seen again (77%), in part because the study population acts as a source population and many young may emigrate. A much higher proportion of male (41%) than female (10%) fledglings were seen again ($\chi^2 = 44.3$, df $= 1$, $P < 0.001$). The probability of a fledgling ever being resighted was significantly affected by sex, but not by fledging mass, brood size, experimental synchrony, hatching sequence, or year of fledging (Table 6).

Because brood size did not affect the probability of resighting, we pooled brood sizes for estimates of nestling survival. Results of RELEASE TEST 2 and 3 suggested that resighting data for young fledged from SYNC and ASYNC broods did not violate assumptions of homogeneity of data (SYNC: $\chi^2 = 1.24$, df $= 1$, $P = 0.27$; ASYNC: $\chi^2 = 2.24$, df $= 1$, $P = 0.13$), indicating that the general mark–recapture model was appropriate.
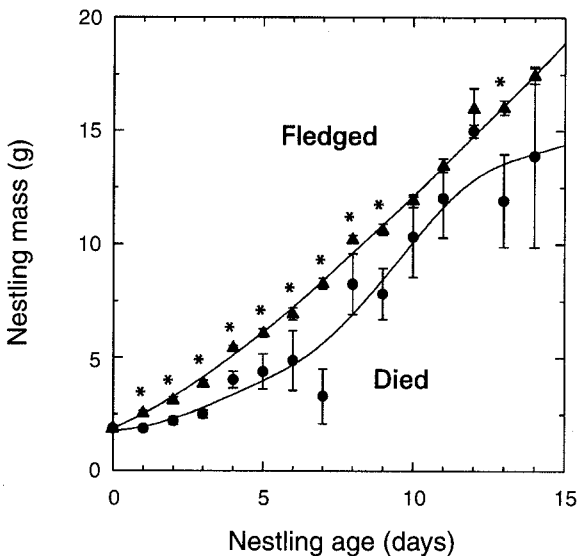
Young fledged from SYNC and ASYNC nests dif-

TABLE 4. The age at fledging (d) of nestling parrotlets from 61 experimental asynchronous (A) and synchronous (S) broods of four (small), six (medium), and eight (large) young in 1989 and 1990, as a function of hatching sequence. Means are presented with standard deviations and sample sizes (N = number of nestlings).

Hatch sequence	Syn-chrony	Brood size								
		Small			Medium			Large		
		$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N
First	A	31.2	1.0	6	30.0	1.4	7	30.8	2.1	17
	S	29.8	1.1	6	31.3	2.8	3	30.6	1.3	17
Middle	A	30.3	0.8	7	30.4	2.7	21	32.3	2.6	65
	S	30.8	2.1	6	32.2	1.5	13	31.7	2.0	76
Penul-timate	A	30.7	2.1	7	33.0	2.9	8	34.1	2.5	8
	S	30.5	2.6	6	32.5	2.1	3	32.7	3.2	17
Last	A	30.3	1.4	7	32.0	2.6	6	35.1	3.8	7
	S	30.7	1.8	6	31.7	0.0	3	33.5	2.7	13

fered significantly in their probabilities of being resighted (Table 7). Likelihood ratio tests between alternate models indicated that neither year (model 1 vs. 3, Table 7) nor age (model 1 vs. 4, Table 7) had a significant effect on resighting probabilities. A model with separate resighting probabilities for SYNC and ASYNC young (model 1, Table 7) fit the data significantly better than an otherwise equivalent model with a common resighting probability (model 2, Table 7). Young fledged from SYNC broods were less likely to be resighted if alive than young fledged from ASYNC broods (Table 7), apparently due to irregular sightings of some SYNC young (see *Discussion*).

Model estimates suggested that young from SYNC and ASYNC broods survived at similar rates that varied between years. Likelihood ratio tests between neighboring models indicated that survival rates were not significantly affected by age (model 5 vs. 8, Table 7) or synchrony treatment (model 5 vs. 7, Table 7). Survival rates varied significantly among years (model 5 vs. 6, Table 7). An otherwise identical model with treatment-specific survival rates (model 7, Table 7) did not fit the data significantly better than the final model with a common survival rate (model 5, Table 7). This test had a power of ≈0.75 with α = 0.10. The model with separate survival rates (model 7, Table 7) suggested survival rates of SYNC young may have been nonsig-

nificantly higher than those of ASYNC young. The parameters of this model are presented in Table 8 for comparative purposes, although they are based on a nonparsimonious model. Akaike's Information Criterion confirmed that the most parsimonious structure for the data (model 5, Table 7) had year-dependent survival rates that did not differ between treatments and treatment-specific resighting probabilities (ϕ_y, p_s). Both data sets fit this model well according to goodness-of-fit tests (ASYNC χ^2 = 1.19, df = 3, P = 0.76; SYNC χ^2 = 2.50, df = 3, P = 0.47), indicating that observed resighting frequencies did not differ significantly from model predictions.

The overall proportions of fledged young that subsequently bred within the study site did not differ significantly between treatments. A slightly greater proportion of ASYNC young (0.10, n = 166) than SYNC young (0.05, n = 171) later bred within our study site, but the difference was not quite statistically significant (χ^2 = 3.13, df = 1, P = 0.08, power = 0.46). With this small difference in recruitment rates, a sample of > 850 fledglings would have been required to achieve a statistical power of 0.8 for this test. The sexes differed in their probability of recruitment, however. Similar

TABLE 5. Analysis of variance of age at fledging for parrotlet chicks from experimental synchronous and asynchronous broods of four, six, and eight young in 1989 and 1990.

Effect	df	F	P
Synchrony	1	1.28	0.260
Brood size	2	21.50	0.001
Hatch sequence†	3	11.85	0.001
Synchrony × size	2	6.59	0.002
Synchrony × sequence	3	1.68	0.172
Size × sequence	6	1.20	0.306
Synchrony × size × sequence	6	3.13	0.006
Nest	54	2.16	0.001
Error	253		

† Nestlings were categorized by hatching sequence as first, middle, penultimate, and last.

TABLE 6. Logistic regression of sex, fledging mass, brood size, synchrony treatment, hatching sequence, and year on the probability of a fledgling parrotlet ever being resighted. R = partial correlation coefficient between the dependent variable (resighted) and the independent variables in the model.

	Partial χ^2	df	P	R
Variable in model				
Sex	36.09	1	0.001	−0.306
Variables not in model				
Fledging mass	0.84	1	0.36	<0.001
Brood size	0.16	1	0.69	<0.001
Synchrony treatment	0.60	1	0.44	<0.001
Hatching sequence	0.84	1	0.36	<0.001
Year	2.10	1	0.15	0.017
Constant	−1.33			
Complete model	43.76	6	<0.001	

SCOTT H. STOLESON AND STEVEN R. BEISSINGER

TABLE 7. Potential models† for estimating resighting (p) and survival (ϕ) rates of 337 nestling Green-rumped Parrotlets fledged from experimental SYNC and ASYNC nests.

Model	np	DEV	AIC	Model effects	Comparisons between models
Modeling resighting rates (p)					
1. ($\phi_{y \times a \times s}$, p_s)	16	524.72	556.72	Synchrony-specific variation in p	
2. ($\phi_{y \times a \times s}$, p)	15	536.72	556.72	Constant p	Synchrony treatment effect on p, model 1 vs. 2: $\chi^2_1 = 12.00$, $P < 0.001$
3. ($\phi_{y \times a \times s}$, $p_{y \times s}$)	21	515.65	557.65	Year $\times$ synchrony interaction on p	Year effect on p, model 1 vs. 3: $\chi^2_5 = 9.07$, $P = 0.11$
4. ($\phi_{y \times a \times s}$, $p_{a \times s}$)	18	520.44	556.44	Age $\times$ synchrony interaction on p	Age effect on p, model 1 vs. 4: $\chi^2_2 = 4.28$, $P = 0.12$
Modeling survival rates (ϕ)					
5. (ϕ_y, p_s)	6	531.14	543.14‡	Year-specific variation in ϕ	Age $\times$ synchrony interaction effect on ϕ, model 1 vs. 5: $\chi^2_{10} = 6.42$, $P = 0.78$
6. (ϕ, p_s)	3	539.29	545.29	Constant ϕ	Year effect on ϕ, model 5 vs. 6: $\chi^2_3 = 8.15$, $P = 0.04$
7. ($\phi_{y \times s}$, p_s)	8	527.42	547.42	Year $\times$ synchrony interaction on ϕ	Synchrony treatment effect on ϕ, model 5 vs. 7: $\chi^2_2 = 3.72$, $P = 0.16$
8. ($\phi_{y \times a}$, p_s)	9	530.90	548.90	Year $\times$ age interaction on ϕ	Age effect on ϕ, model 5 vs. 8: $\chi^2_3 = 0.24$, $P = 0.97$

Note: For each model we present the number of estimable parameters (np), the deviance (DEV = $-2 \ln L$), and the Akaike's Information Criterion (AIC = 2 np + DEV). Effects of year (y), age class (a), and synchrony treatment (s) were tested by comparing neighboring models using likelihood ratio tests (LRT χ^2 = DEV$_1$ − DEV$_2$, with df = np$_2$ − np$_1$).

† Model 5 was the best model based on the lowest AIC value among all models examined. Likelihood ratio tests between alternate models illustrate critical tests of effects. See *Methods: Analyses: Fledgling survival and recruitment* for details of model selection strategy.

‡ The boldface number is the lowest AIC value among all models examined.

proportions of males that fledged from ASYNC (0.11, $n = 80$) and SYNC broods (0.09, $n = 81$) eventually bred within the study site ($\chi^2 = 0.31$, df = 1, $P = 0.59$). This test had relatively high power (≈ 0.7). A significantly higher proportion of ASYNC females (0.08, $n = 86$) than SYNC females (0.01, $n = 90$) eventually were found breeding within the study site (Fisher's exact test, $P = 0.032$).

Effects of experimental synchrony on costs of reproduction

We found no detectable differences in parental effort or other costs of reproduction. Male and female parents of large SYNC and ASYNC broods provisioned their young at similar rates at 4, 8, 12, 16, and 23 d after hatching (Fig. 6). The mean feeding rate for either sex did not differ between treatments at any nest age (all comparisons, t tests on square-root transformed data, all $P > 0.30$). The total feeding rate was similar at each nest age as well (all comparisons, t tests on square-root transformed data, all $P > 0.24$).

Parental survival.—After raising experimental broods, parents from SYNC and ASYNC nests survived at similar rates that varied between the sexes. Resighting data for both female and male parents met assumptions of internal homogeneity (females: RELEASE TEST 2 and 3, $\chi^2 = 0.19$, df = 2, $P = 0.91$; males: $\chi^2 = 0.58$, df = 1, $P = 0.75$), which indicated that the general mark–recapture model was appropriate for both data sets.

Female parents appeared to have a resighting probability near unity (Table 9). Likelihood ratio tests be-

tween alternate models revealed no significant effects of year (model 1 vs. 3, Table 10) or synchrony treatment (model 1 vs. 2, Table 10) on resighting probabilities. Tests between the most parsimonious model (model 4, Table 10) and neighboring models could not reject the null hypotheses of no significant effect of year (model 4 vs. 6, Table 10) or synchrony treatment (model 4 vs. 5, Table 10) on survival. The test for differences in survival based on treatment had relatively low power (≈ 0.40, with $\alpha = 0.10$).

Akaike's Information Criterion confirmed that the most parsimonious model for the data, (ϕ, p), had constant probabilities of resighting and survival that were not significantly different for SYNC and ASYNC females (Table 10). The model fit the data well for both ASYNC ($\chi^2 = 0.59$, df = 2, $P = 0.74$) and SYNC ($\chi^2 = 0.21$, df = 2, $P = 0.90$) females based on goodness-of-fit tests. An otherwise identical model with treatment-specific survival rates (model 5, Table 10) suggested that SYNC females may have had a nonsignificantly lower survival rate than ASYNC females (Table 9).

Male parents of SYNC and ASYNC broods differed in resighting rates but not in survival rates (Table 11). Based on likelihood ratio tests, resighting rates of males did not vary significantly by year (model 1 vs. 3, Table 11), but differed significantly between treatments (model 1 vs. 2, Table 11). ASYNC males were significantly more likely to be seen if alive in any given year than SYNC males (Table 9), apparently due to the loss of color bands by a few individuals (see *Discus-*

TABLE 8. Estimates of survival and resighting rates† for 337 parrotlets fledged from experimental SYNC and ASYNC broods in 1989 and 1990, based on resightings of marked birds from 1990 through 1993.

Model	Parameter	Treatment	
		SYNC	ASYNC
5. (ϕ_y, p_s)‡	Survival rate		
	1990	0.29 ± 0.05	0.29 ± 0.05
	1991	0.45 ± 0.06	0.45 ± 0.06
	1992	0.26 ± 0.06	0.26 ± 0.06
	1993	0.63 ± 0.19	0.63 ± 0.19
	Resighting probability	0.38 ± 0.07	0.74 ± 0.09
7. $(\phi_{y \times s}, p_s)$§	Survival rate		
	1990	0.41 ± 0.11	0.24 ± 0.05
	1991	0.47 ± 0.11	0.45 ± 0.07
	1992	0.20 ± 0.08	0.28 ± 0.08
	1993	1.00 ± 0.01	0.50 ± 0.22
	Resighting probability	0.32 ± 0.09	0.77 ± 0.08

Note: Estimates are presented for the most parsimonious model (model 5, Table 7), and for an otherwise identical model (model 7, Table 7) with nonsignificant differences in treatment-specific survival rates for illustrative purposes.

† Rates derived from a Cormack-Jolly-Seber capture–recapture model are presented with standard errors of parameter estimates. See *Methods: Analyses: Fledgling survival and recruitment* for model selection strategy and notation.

‡ Most parsimonious model based on Akaike's Information criterion and LRT tests.

§ Nonparsimonious model presented only to show the trend for survival rates of ASYNC and SYNC nestlings.

sion). Survival rates were not significantly affected by synchrony treatment (model 1 vs. 4, Table 11). The test for differences by treatment had a power of ≈0.30 with $\alpha = 0.10$. Survival rates differed significantly by year (model 4 vs. 5, Table 11). The neighboring model with separate survival rates by treatment (model 1, Table 11) suggested that SYNC males may have survived at nonsignificantly higher rates than ASYNC males in some years (Table 9).

The AIC confirmed that the most parsimonious model structure for male parents, (ϕ_y, p_s), suggested a year-specific common survival rate and treatment-specific resighting rates (Table 11). The final model fit both data sets well (SYNC males: $\chi^2 = 1.10$, df = 2, $P = 0.58$; ASYNC: $\chi^2 = 1.00$, df = 2, $P = 0.61$). Average survival probabilities for males were somewhat higher than for females (Table 9).

Future reproduction.—Synchrony treatments had no detectable effect on subsequent reproduction by females (Table 12). Female parrotlets that raised experimental SYNC first broods were equally likely to lay a second clutch as those that raised experimental ASYNC first broods. Synchrony treatment had no detectable effect on the timing, clutch size, or success of a females' next breeding attempt, either within or between years (Table 12). Four of these five results were in the opposite direction from that predicted by the hypotheses. Because the original predictions and subsequent tests were unidirectional, these tests were one-tailed and therefore had no power to detect results inconsistent with the predictions (Cohen 1988:5). The t test of differences in mean clutch size of next breeding attempt had a power of approximately 0.10, probably because the apparent effect size was very small. To achieve a power of 0.80 with an effect of this magnitude would require >3000 females per treatment.
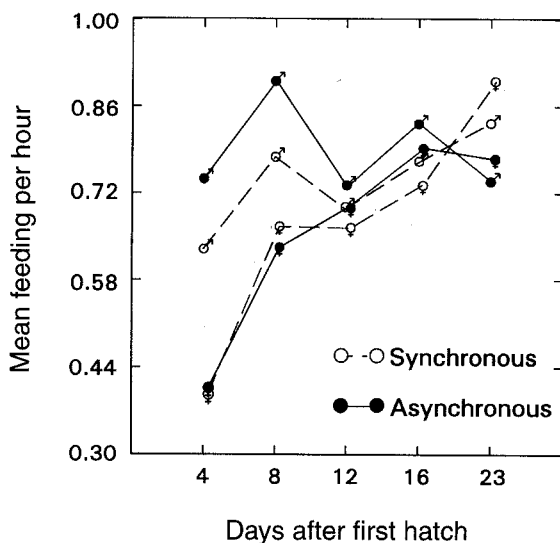
Effects of supplementary food on survivorship of last-hatched young

To be certain that experimental feeding procedures did not adversely affect nestling growth or survival, we examined these characteristics for fifth-hatched chicks. Fifth-hatched nestlings that received supple-

FIG. 6. Feeding rates by male and female parent parrotlets through the course of the nestling period at experimentally asynchronous ($n = 11$) and synchronous ($n = 11$) broods of eight young in 1990.

TABLE 9. Mark–recapture model estimates of suvival and resighting rates (±1 SE) for parent parrotlets from experimental SYNC and ASYNC broods in 1989 and 1990, based on resightings of marked birds during 1990–1993.

Model	Parameter	Treatment	
		SYNC	ASYNC
Females	n	19	17
(ϕ, p)†	Survival rate	0.66 ± 0.06	0.66 ± 0.06
	Resighting probability	1.0 ± 0.02	1.0 ± 0.02
(ϕ_s, p)‡	Survival rate	0.64 ± 0.08	0.68 ± 0.07
	Resighting probability	1.0 ± 0.005	1.0 ± 0.005
Males	n	15	19
(ϕ_y, p_s)§	Survival rate: yr 1	1.00 ± 0.67	1.00 ± 0.67
	yr 2	0.62 ± 0.11	0.62 ± 0.11
	yr 3	0.67 ± 0.14	0.67 ± 0.14
	yr 4	0.63 ± 0.18	0.63 ± 0.18
	Resighting probability	0.45 ± 0.12	0.93 ± 0.07
$(\phi_{y \times s}, p_s)\|$	Survival rate: yr 1	0.98 ± 0.30	1.00 ± 0.08
	yr 2	0.79 ± 0.30	0.57 ± 0.12
	yr 3	0.54 ± 0.26	0.67 ± 0.16
	yr 4	1.00 ± 0.06	0.63 ± 0.18
	Resighting probability	0.39 ± 0.14	0.93 ± 0.05

Note: Estimates are presented for the most parsimonious models and for otherwise identical models with nonsignificant differences in treatment-specific survival rates to display nonsignificant trends in survival rates. Notation is as in Table 7.

† Most parsimonious model for females based on AIC and LRT tests, this is model 4, Table 10.

‡ This nonparsimonious model for females is model 5, Table 10.

§ This most parsimonious model for males is model 4, Table 11.

‖ This nonparsimonious model for males is model 1, Table 11.

mental food until 14 d of age attained significantly higher asymptotic masses ($\overline{X} = 28.0 \pm 1.2$ g) than fifth-hatched control nestlings ($\overline{X} = 25.6 \pm 2.5$ g; Mann-Whitney U Test, $U = 55.0$, $n = 10$, $P = 0.016$). Growth constants and inflection points did not differ significantly between treatments. Similar proportions of fifth-hatched nestlings survived at control (0.9) and fed (0.8) nests (Fisher's exact test, $P = 1.0$). Thus, fifth-hatched chicks were included with first through sixth-hatched chicks as early-hatched chicks in the following analyses.

Supplemental feeding had mixed effects on the survival and growth of later-hatched nestlings (Fig. 7). A marginally higher proportion of last-hatched chicks that received food supplements survived to fledging than last-hatched control chicks (Fisher's exact test, one-tailed, $P = 0.085$), but fledging success of penultimate chicks did not differ between control and fed nests (Fisher's exact test, one-tailed, $P = 0.5$; Fig. 7). Supplemental feeding of last-hatched chicks increased their probability of fledging to the level of penultimate chicks in control nests (60%), but still well below that

TABLE 10. Potential models† for estimating resighting (p) and survival (ϕ) rates of female parent Green-rumped Parrotlets from experimental SYNC ($n = 16$ birds) and ASYNC ($n = 14$ birds) nests.

Model	np	DEV	AIC	Model effects	Comparisons between models
Modeling resighting rates p					
1. $(\phi_{y \times s}, p)$	9	79.39	97.39	Constant p	
2. $(\phi_{y \times s}, p_s)$	10	79.39	99.39	Synchrony-specific variation in p	Synchrony treatment effect on p, model 1 vs. 2: $\chi^2_1 = 0.00$, $P > 0.99$
3. $(\phi_{y \times s}, p_y)$	11	79.39	101.39	Year-specific variation in p	Year effect on p, model 1 vs. 3: $\chi^2_2 = 0.00$, $P > 0.99$
Modeling survival rates (ϕ)					
4. (ϕ, p)	2	90.84	**94.84**‡	Constant ϕ, constant p	
5. (ϕ_s, p)	3	90.66	96.66	Synchrony-specific variation on ϕ	Synchrony treatment effect on ϕ, model 4 vs. 5: $\chi^2_1 = 0.18$, $P = 0.67$
6. (ϕ_y, p)	5	87.93	97.93	Year-specific variation in ϕ	Year effect on ϕ, model 4 vs. 6: $\chi^2_3 = 2.91$, $P = 0.41$

Note: For each model we present the number of estimable parameters (np), the deviance (DEV), and Akaike's Information Criterion (AIC). Effects of year (y) and synchrony treatment (s) were tested by comparing neighboring models using likelihood ratio tests. Based on resightings of marked birds 1990–1993. Notation is as in Table 7.

† Model 4 was the best model based on the lowest AIC value among all models examined. Likelihood ratio tests between alternate models illustrate critical tests of effects. See *Methods: Analyses: Fledgling survival and recruitment* for details of model selection strategy.

‡ The boldface number is the lowest AIC value among all models examined.

TABLE 11. Potential models† for estimating resighting (p) and survival (φ) rates of male parent Green-rumped Parrotlets from experimental SYNC (n = 15 birds) and ASYNC (n = 16 birds) nests.

Model	np	DEV	AIC	Model effects	Comparisons between models
Modeling resighting rates (p)					
1. $(\phi_{y \times s}, p_s)$	10	105.81	125.81	Synchrony-specific variation in p	
2. $(\phi_{y \times s}, p)$	9	118.08	136.08	Constant p	Synchrony treatment effect on p, model 1 vs. 2: $\chi^2_1 = 12.27, P < 0.001$
3. $(\phi_{y \times s}, p_{y \times s})$	14	100.08	128.08	Year × synchrony interaction on p	Year effect on p, model 1 vs. 3: $\chi^2_4 = 5.73, P = 0.22$
Modeling survival rates (φ)					
4. (ϕ_y, p_s)	6	107.74	**119.74**‡	Year-specific variation in φ	Synchrony treatment effect on φ, model 1 vs. 4: $\chi^2_4 = 1.93, P = 0.75$
5. (ϕ, p_s)	3	116.76	122.76	Constant φ	Year effect on φ, model 4 vs. 5: $\chi^2_3 = 9.02, P = 0.03$

Note: For each model we present the number of estimable parameters (np), the deviance (DEV), and Akaike's Information Criterion (AIC). Effects of year (y) and synchrony treatment (s) were tested by comparing neighboring models using likelihood ratio tests. The table is based on resightings from 1990 to 1993. Notation is as in Table 7.

† Model 4 was best, based on the lowest AIC value among all models examined. Likelihood ratio tests between alternate models illustrate critical tests of effects. See *Methods: Analyses: Fledgling survival and recruitment* for details of model selection strategy.

‡ The boldface number is the lowest AIC value among all models examined.

of earlier hatched chicks (90%; Fisher's exact test, P = 0.02). Later hatched nestlings that fledged from fed nests reached significantly higher (Mann-Whitney U Test, U = 74.0, P = 0.045) asymptotic masses ($\overline{X}$ = 29.4 ± 1.8 g, n = 12) than later hatched nestlings that fledged from control nests ($\overline{X}$ = 27.6 ± 1.9 g, n = 8). Growth constants and inflection points did not differ significantly between treatments.

Checking crop contents three times daily revealed that food was not distributed evenly within broods (Fig. 8). All fifth-hatched chicks in control nests were fed at least once per day. However, seventh-hatched chicks had an 8% probability of not being fed for an entire day, and one-quarter of the eighth-hatched chicks did not receive food for an entire day. Thus, the distribution of food among chicks in large broods was highly inequitable ($\chi^2 = 40.7$, df = 2, P < 0.001).

Predictability of food resources for parrotlets

The amount of food available to parrotlets varied between wet and dry sites, and across years. Within a habitat, however, seed densities were significantly correlated for time lags up to 50 d (wet) and 60 d (dry) (Fig. 9). In wet sites, seed density showed a significant positive correlation with date in two of three years (both r > 0.89, n = 15, 12, P < 0.001; Fig. 9), indicating that food availability increased during the breeding season, and no significant change over time in the other year (r = 0.80, n = 7, P = 0.80). Seed density in dry sites was not significantly correlated with date in two years (P > 0.70), but showed a significant seasonal decline in one year (r = −0.83, n = 19, P < 0.001; Fig. 9).

Seed density was significantly correlated with rainfall, although the relationship differed between habitat types. Seed density in dry sites was positively correlated (r = 0.52, n = 42, P < 0.001) with the total rainfall of the preceding 10 d. In wet sites, seed density was negatively correlated with rainfall (r = −0.50, n = 34, P = 0.003).

DISCUSSION

Does hatching asynchrony increase reproductive success in parrotlets?

Experimentally synchronized broods of the Green-rumped Parrotlet fledged as many or more young than broods with a normal degree of asynchrony (Fig. 1), contrary to predictions of adaptive hatching pattern hypotheses. According to the Brood Reduction Hypothesis, asynchrony must show greater reproductive success than synchrony only when food is limited (Pijanowski 1992, Forbes 1994), but our results were similar in a both a dry and a wet year. The only differences between treatments occurred in the largest broods, where food limitations should have been greatest. In large ASYNC broods, the penultimate and last-hatched chicks frequently died (Fig. 2). In contrast, experimental SYNC broods commonly fledged all of their young. Similarly, 31 of 34 other experimental tests of hatching asynchrony have reported equal or greater fledging success from synchronized broods (Amundsen and Slagsvold 1991b, Stoleson and Beissinger 1995).

Some authors have suggested that asynchronous hatching may function to maximize the quality rather than the quantity of fledglings (e.g., Magrath 1989, Seddon and van Heezik 1991b). Such a trade-off is a common theme in life history theory (e.g., Smith and Fretwell 1974, Lloyd 1987, Winkler and Wallin 1987). Nestling growth rates have frequently been considered a measure of both food supply and nestling condition (e.g., Braun and Hunt 1983, Haydock and Ligon 1986, Quinney et al. 1986, Skagen 1988, Smith et al. 1989, Magrath 1991). High-quality chicks may be expected to grow faster and fledge at a younger age than low-quality chicks (but see Ross and McLaren 1981). Par-

TABLE 12. Effects of experimental synchrony treatment on subsequent reproductive effort by female parrotlet parents. Data for different brood sizes have been pooled.

Measure	Treatment of first brood		Test	P
	SYNC	ASYNC		
Probability of second clutch†	0.85 (13)	0.75 (12)	Fisher's exact	0.65
Interval between broods (days)‡	30.4 (11)	30.8 (8)	$t = 0.12$	0.90
Size of next clutch (eggs)	7.1 ± 1.1 (25)	7.2 ± 1.5 (23)	$t = 0.25$	0.80
Fledges from next brood§	5.5 ± 2.2 (18)	4.7 ± 2.2 (19)	$t = 1.1$	0.30
Timing of first clutch in following yr‖	2.0 (13)	5.1 (14)	$t = 0.30$	0.76

Note: Means ±1 SD are presented and sample sizes are indicated in parentheses.

† For females that raised experimental first broods only.

‡ For females that raised experimental first broods; interval is the number of days between last fledge of the first brood and laying of the first egg of the second brood; excludes broods with uncertain dates.

§ Excludes subsequent broods that were depredated.

‖ Mean number of days from average starting date for first clutches of year following experimental broods, for experimental nests that were second broods only.

rotlet nestlings from SYNC broods reached asymptotic masses averaging 1.5 g less than nestlings from ASYNC broods, suggesting that they were of lower quality. However, the patterns of growth differed between the two treatments (Figs. 4 and 5). Nestlings from SYNC broods tended to reach the inflection point of their growth curves earlier than ASYNC nestlings.

Fledging mass has also been considered an indicator of fledgling quality because it has been positively correlated with survivorship in some species (e.g., Perrins 1965, Nur 1984b, Krementz et al. 1989, Tinbergen and Boerlijst 1990, Magrath 1991). However, no such correlation was found in another parrot species, the Long-billed Corella (*Cacatua pastinator pastinator*; Smith 1991), or in several other bird species (Lack 1966, Woolfenden 1978, Ross and McLaren 1981, Stromborg et al. 1988, Sullivan 1989, Wiggins 1990). Parrotlet

chicks from SYNC broods fledged at masses averaging 0.8 g less than chicks from ASYNC broods. However, SYNC young in large broods fledged at an earlier age than ASYNC young, so these fledging masses may not be comparable. In other asynchrony studies, young from synchronous broods have generally fledged at lower masses than asynchronous young (Amundsen and Slagsvold 1991b, Stoleson and Beissinger 1995).

Postfledging survival is a better measure of fledgling quality than fledging mass. In this study, a chick's probability of ever being resighted after fledging was not significantly related to fledging mass or to synchrony treatment (Table 6). Estimated annual survival rates of parrotlets fledged from experimentally synchronous and asynchronous nests were not detectably different (Table 8). Model estimates are subject to potential biases, however. Most importantly, survival models do not differentiate between mortality and permanent emigration (Clobert et al. 1987, Pollock et al. 1990). If, for some reason, the two groups of offspring differed in their rates of emigration from the study site, the
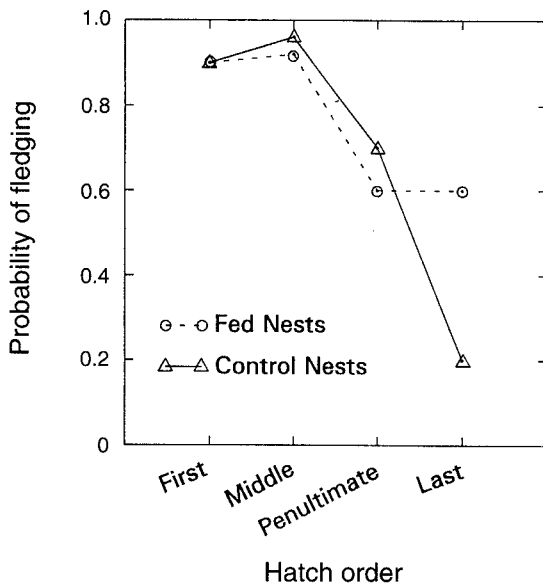

FIG. 7. The probability of young parrotlets fledging from experimental fed ($n = 10$) and control ($n = 10$) nests of eight young in relation to hatching sequence.
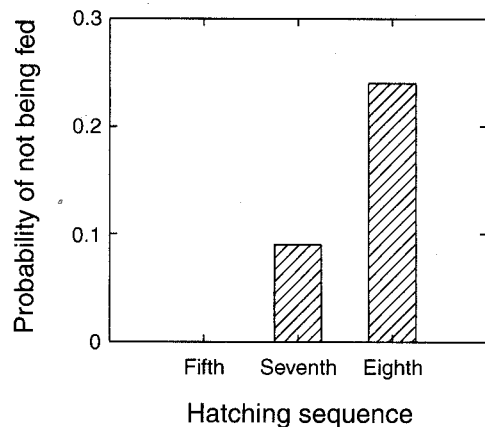

FIG. 8. The relationship between nestling hatching sequence and the probability of not receiving food from parents through an entire day for the first 2 wk after hatching of the last nestling. Results were based on three checks of crop contents per day in each of 10 nests for a total of 14 d.
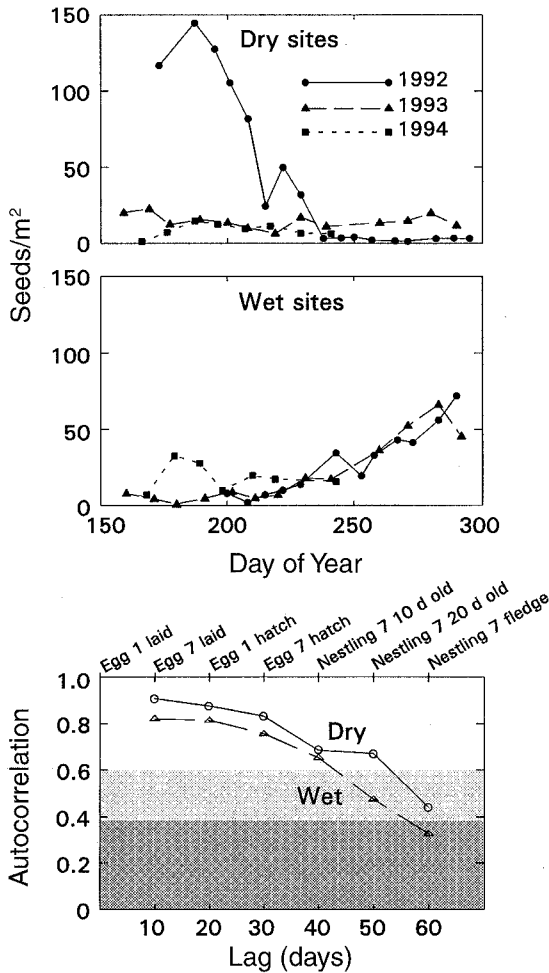
FIG. 9. Seed density over time at (top) wet and (middle) dry sites at Hato Masaguaral, Venezuela, for 1992–1994. (Bottom) Serial autocorrelation of seed density during the rainy season (May–November). Points are statistically significant within the lightly stippled area ($P < 0.05$) and above the stippled area ($P < 0.001$). The top axis shows the average timing of events in the nesting cycle of the Green-rumped Parrotlet for the modal clutch size of seven eggs.

survival estimates presented here may be unreliable (e.g., Buckland et al. 1983, Francis and Cooke 1992). We cannot clearly demonstrate heterogeneity of emigration rates. Although synchrony treatment did not affect the chance of ever being resighted again (Table 6), young from synchronous broods had a significantly lower probability of being resighted if alive and in the study area than did asynchronous young in any given year. The most likely explanation for the differences in resighting rates was irregular resightings of SYNC young: a greater proportion of SYNC young than ASYNC young were missed in their 1st yr of life but resighted in later years. Also, more SYNC than ASYNC young (5 vs. 1) were resighted outside the area searched systematically for banded birds and thus were resighted only sporadically. These observations are consistent with greater dispersal by SYNC young. An-

other possible cause of differences in resighting rates would be sex-biased dispersal (e.g., Krementz et al. 1989). Such a difference could have occurred if a greater proportion of males fledged from SYNC broods, because female parrotlets frequently breed in their 1st yr while males rarely do (S. H. Stoleson and S. R. Beissinger, *unpublished data*), and breeders are more easily resighted than nonbreeders. However, the sex ratio of young produced did not differ appreciably between treatments. Alternatively, because breeders are more readily resighted, resighting rates might have differed due to differences in recruitment.

Patterns of recruitment for parrotlet young produced from experimental nests differed by sex. We found no significant difference between treatments in the recruitment rates of males. But a greater proportion of ASYNC females than SYNC females were later found breeding within the study site. This observation may indicate a real difference between treatments in quality and recruitment of females. However, the possibility exists that recruitment of females into a breeding population may be less dependent on fledgling quality than for males (Trivers and Willard 1973). We have found that females are rapidly recruited into this breeding population and most breed in their 1st yr, probably due to the male-skewed adult sex ratio (S. H. Stoleson and S. R. Beissinger, *unpublished data*). An alternative explanation for differences in recruitment is that SYNC females may have dispersed out of our immediate study site more often than ASYNC females. Because we searched for breeders systematically only within the area delimited by nest boxes, females breeding outside this area would be less likely to be recorded as breeding. Males may not show a similar pattern of recruitment because female parrotlets tend to disperse greater distances than males (S. H. Stoleson and S. R. Beissinger, *unpublished data*), and so were less likely to be resighted at all (Table 6). Females from SYNC broods might disperse farther if they were of higher quality, and so better able to disperse than their ASYNC counterparts. Spanish Imperial Eagle (*Aquila adalberti*) fledglings of high quality were more likely to disperse out of their natal area than were low-quality young (Ferrer 1992). Alternatively, if SYNC females were of lower quality, they might have been less able to obtain nesting sites or mates within the study site. This seems unlikely since females are rapidly recruited into the study population. Further studies of dispersal are needed to reliably demonstrate differences in female quality or recruitment.

The effects of synchrony manipulations on offspring survival or recruitment are poorly known. In good food years, Blackbird (*Turdus merula*) chicks from experimentally synchronized broods had slightly higher survivorship to 4 wk after fledging than chicks from asynchronous broods. In bad food years, asynchronous chicks had higher survivorship (Magrath 1989). Harper et al. (1992) found that synchrony treatment had no

effect on survival or recruitment of House Wrens (*Troglodytes aedon*) for up to 2 yr after fledging. No previous asynchrony study has assessed differences in resighting probabilities to control for biases in survival estimates.

Does food availability limit fledging success?

An important premise of the Brood Reduction, Peak Load Reduction, and Hurry-up hypotheses is that parents are limited in their ability to provide their broods with food. Starvation may be expected to be a major cause of mortality for nestlings if food is limiting, especially in large brood sizes and in synchronously hatched broods. If dying with an empty crop indicated starvation, then starvation was a major cause of mortality for parrotlet nestlings. A high proportion of later hatched chicks in large ASYNC broods died with empty crops. Nestlings that died of any cause tended to weigh less than same-aged nestlings that fledged (Fig. 5). Also, last-hatched chicks provided with supplemental food showed an increased probability of surviving (Fig. 7). Thus, starvation appeared to be a common cause of death in asynchronous broods.

Although some nestlings died of apparent starvation, evidence suggests that parents were not limited in their ability to provide food. Parent parrotlets were frequently able to provide sufficient food to rear eight young successfully in SYNC nests, where food demands should have been greatest. In control nests for the food supplement experiment, later hatched chicks sometimes did not receive food for an entire day, but earlier hatched chicks were always fed (Fig. 8). Thus, the starvation of later hatched chicks in ASYNC broods appeared to be due to the inequitable distribution of food among broodmates, rather than to the inability of parents to provide enough food.

It is unclear whether parents control the distribution of food within a nest or whether the inequitable distribution of food is a direct result of size disparities, and therefore competitiveness (sibling despotism, Forbes 1994) among nestlings (McRae et al. 1993). Parent birds generally provide food in response to the average begging level of a brood, and often feed the most visible nestlings first (Bengtsson and Rydén 1983, Smith and Montgomerie 1991, Redondo and Castro 1992). In asynchronous broods, smallest chicks are frequently the most hungry and often beg the most intensively, but the largest chicks are fed most frequently, presumably because they are the most visible (Rydén and Bengtsson 1980, Bengtsson and Rydén 1983). Thus, size disparities appear to handicap smallest nestlings. Parents can compensate for this competitive disadvantage by preferentially feeding younger nestlings in some species (Ferguson and Sealy 1983, Stamps et al. 1985, Gottlander 1987). In such cases, it is difficult to reconcile the concept of an adaptive loss of small nestlings with parental investments that function to increase their survival. The distribution of food by par-

ents among nestling Green-rumped Parrotlets (Fig. 8) indicates that parents often do not or are not able to employ a similar strategy.

The inequitable allocation of food among broodmates was not the only cause of nestling mortality in asynchronous broods of parrotlets. Some chicks died with food in their crops. Although providing supplemental food to last-hatched chicks in large ASYNC broods increased their probability of survival, they still experienced significantly higher mortality than early-hatched chicks (Fig. 7). Providing supplemental food to penultimately hatched chicks did not improve their probability of survival. Rather than starvation, it appears that the size disparity among nestling parrotlets may itself lead to the death of the smallest chicks. Death of youngest nestlings has been related to size disparity rather than food abundance in species with variable degrees of hatching asynchrony, including Red-winged Blackbirds (*Agelaius phoeniceus*; Strehl 1978), Starlings (*Sturnus vulgaris*; Stouffer and Power 1990), Jackass Penguins (*Spheniscus demersus*; Seddon and van Heezik 1991*b*), and Acorn Woodpeckers (*Melanerpes formicivorus*; Stanback 1991). Thus, the size hierarchy among nestlings that results from hatching asynchrony frequently appears to bear a cost in the form of high mortality of smaller young. Partial brood loss could still be adaptive if the cost inherent in the incidental mortality of small nestlings is offset by benefits derived from the improved quality or increased survival of surviving nestlings, reduced costs of reproduction to parents, or both.

Does brood reduction benefit older chicks?

An important prediction of the hypotheses based on adaptive brood reduction (Brood Reduction and Insurance) is that surviving nestlings should benefit from the death of their smaller nestmates through a reduction in competition for nonshareable forms of parental care, especially food resources (Lack 1954, Mock and Parker 1986). For example, growth rates of surviving nestlings in broods of Great Tits (*Parus major*) and Curve-billed Thrashers (*Toxostoma curvirostre*) increased after the death of their younger siblings (Gibb 1950, Ricklefs 1965). This prediction was not upheld in this study, however. Growth parameters for surviving nestlings from reduced broods were similar to those for nestlings from broods that did not experience brood reduction. However, a lower proportion of older chicks fledged from reduced broods than from unreduced broods (Table 2). Thus, rather than benefiting from the alleviation of food stress, older chicks continued to be at risk even after brood reduction. Similarly, early brood reduction did not improve the survival or condition of surviving nestlings in Starlings (Stouffer and Power 1991) or Pied Flycatchers (*Ficedula hypoleuca*; Hillström and Olsson 1994).

It might be argued that brood reduction occurred in nests where parents delivered less food, and therefore

surviving nestlings should be expected to grow more slowly or be less likely to fledge than in unreduced broods. However, we found that not all mortality resulted from insufficient food. More importantly, it is critical to differentiate between adaptive brood reduction and partial brood loss (sensu Mock 1994). The fundamental purpose of adaptive brood reduction is to adjust a brood to a size that parents can provision successfully. If food limitation is alleviated via brood reduction, then surviving chicks should grow and fledge at rates similar to (or greater than, if growth is negatively correlated with brood size, as we found with the parrotlet) those of chicks in unreduced broods, where food presumably was not limited (O'Connor 1978, Mock and Parker 1986, Anderson 1989). Our finding that parrotlet chicks that survived brood reduction were still less likely to fledge than chicks from unreduced broods is inconsistent with the concept of adaptive brood reduction.

If the function of hatching asynchrony is to give priority to earlier hatched nestlings, then later hatched nestlings that survive may be expected to be of relatively lower quality. Later hatched nestlings that survived in ASYNC broods did grow more slowly and fledged at a later age than earlier hatched nestmates. However, later hatched nestlings generally were heavier at fledging than their nestmates. A flexible growth rate and consequently a variable nestling period may be adaptations to enable nestlings to survive temporary food shortages (Emlen et al. 1991, Negro et al. 1994) without requiring the more costly strategy of brood reduction. Variable growth patterns have been observed in a number of altricial species that hatch their eggs asynchronously, including Barn Owls (*Tyto alba*; White and Brisbin 1980), Monk Parakeets (*Myiopsitta monachus*; Navarro and Bucher 1990), House Martins (*Delichon urbica*; Bryant 1978), White-fronted Bee-eaters (*Merops bullockoides*; Emlen et al. 1991), and Black Kites (*Milvus migrans*; Viñuela and Bustamante 1993).

Does hatching asynchrony reduce costs of reproduction for parents?

Hypotheses based on adaptive hatching patterns suggest that asynchronous hatching may benefit parents by reducing the cost of reproduction (Stoleson and Beissinger 1995). Reductions in costs may be manifested as decreased effort in raising the current brood, improved survival, or increased future reproduction. Because of its large clutch sizes and extreme degree of asynchrony, the Green-rumped Parrotlet is one of the few species that may derive significant energy savings through hatching asynchronously by reducing peak work loads of parents (Mock and Schwagmeyer 1990). No evidence was found to support the Peak Load Reduction Hypothesis. Parents attending SYNC broods did not provision their broods at significantly higher rates than parents of ASYNC broods (Fig. 6). In Amer-

ican Kestrels (*Falco sparverius*), synchronous hatching increased the total nestling energy demands, rather than concentrating peak demands (Wiebe and Bortolotti 1994). Only five other experimental tests of asynchrony have monitored parental effort: parents at experimentally synchronized broods of Cattle Egrets (*Bubulcus ibis*) fed at higher rates than parents at asynchronous broods (Fujioka 1985, Mock and Ploger 1987), but no significant differences were found in other species (Hébert and Barclay 1986, Amundsen and Slagsvold 1991a, Bowman 1992).

Asynchrony may be selected if raising a synchronized brood adversely impacts parental survival. Avian parents with enlarged broods may suffer reduced survival (e.g., Askenmo 1979, Bryant 1979, Nur 1984a, Pugesek 1987, Gustafsson and Sutherland 1988), although support for costs of reproduction is far from universal (e.g., Smith 1981, Finke et al. 1987). Variation in parental quality may mask the expected negative relationship between reproductive effort and survival (Högstedt 1981, Stearns 1989).

We detected no significant negative effect of raising a synchronous brood on adult survival in parrotlets (Table 9). Males that raised SYNC broods were less likely to be resighted than males that raised ASYNC broods (Table 11). Rather than a consequence of raising SYNC broods, the lower resighting rates of SYNC fathers was probably a spurious result, due to several SYNC males repeatedly removing their plastic bands and the fact that males are more difficult to recapture than females. For females, model estimates suggested resighting probabilities did not differ significantly from 100% (Table 9). For neither sex could we reject the null hypothesis of no difference in survival rates between treatments. Small sample sizes contributed to high variance in both survival and resighting parameter estimates, resulting in low statistical power in tests for differences (Pollock et al. 1990), although sample sizes were sufficient to detect differences in male resighting probabilities. While the results presented for parental survival should be considered inconclusive, they do not suggest a particular advantage for asynchrony. Interestingly, a higher proportion of female Blue Tits (*Parus caeruleus*) that raised experimentally synchronized broods survived to the following year than females at asynchronous control broods, while males showed the opposite relationship (Slagsvold et al. 1994), suggesting a reduction in effort for females raising synchronous broods.

For species that have multiple broods within a year, an increase in parental effort may decrease the probability of having a second brood (Hegner and Wingfield 1987, Tinbergen 1987, Gustafsson and Sutherland 1988, de Laet and Dhondt 1989). An increased level of effort to raise first broods may increase the amount of time between clutches so that females can regain breeding condition, or decrease the number of eggs produced or young fledged from second broods (e.g.,

Roskaft 1985, Hegner and Wingfield 1987, Rohwer and Heusmann 1991, Ten Cate and Hilbers 1991). We detected no significant differences in future reproductive efforts of parents that raised experimental ASYNC and SYNC broods. Although sample sizes were relatively small, most of the nonsignificant trends observed were opposite that predicted by the hypotheses. In Starlings, the degree of asynchrony of first broods had no effect on the size or success of second broods (Stouffer 1991).

Predictability and seasonal trends of food resources

Results of seed sampling suggested that the Brood Reduction Hypothesis may not apply to the parrotlet. An important premise of the hypothesis is that future food resources are unpredictable at the time of egg-laying (Lack 1947, 1968). Such a premise might apply to species that prey on ephemeral animal prey such as schooling fish or aerial insect swarms. However, parrotlets fed on seeds and fruits, which did not vary spatially or temporally on a daily basis. Seed sampling demonstrated that the density of seeds of known food plants was relatively predictable over time spans that were biologically relevant to parrotlets (Fig. 9). Similarly, seed densities generally increased or showed no trend through the breeding season, in opposition to the basic premise of the Hurry-up Hypothesis (Fig. 9).

To the best of our knowledge, no previous study has tested the premise that food resources vary unpredictably from the time of egg-laying. Such a test is critical to determine if the Brood Reduction Hypothesis applies to any species. Thus, most field experiments of hatching asynchrony that ostensibly tested the Brood Reduction Hypothesis failed to establish whether the premise of the hypothesis was applicable. It is insufficient to demonstrate variability, or the existence of good vs. bad food years, because environmental variation can occur in a highly predictable manner (Colwell 1974, Stearns 1980, Beissinger and Gibbs 1993). Unfortunately, most theoretical models of brood reduction also fail to make explicit the distinction between variable and unpredictable food resources (e.g., Pijanowski 1992, Konarzewski 1993, Forbes 1994), and none has explored how much unpredictability is required to favor a strategy of brood reduction over other strategies, such as laying a smaller clutch or delaying egg-laying until conditions improve. Does a correlation explaining ≈50–90% of the variability in seed resources over a 30–50 d period, when the food demands of chicks are at their peak, indicate food is predictable enough that a brood reduction strategy is unwarranted? Very likely so in this case, especially considering that nestling parrotlets are able to survive several days without food (Fig. 8) and are quite flexible in their growth trajectories (Fig. 4). Flexibility and individual variability in growth patterns are not uncommon in birds (Brisbin et al. 1987), and physiological condition of nestlings provides a buffer against some degree of unpredictability of food. Nonetheless, the question of how much and

what kinds of environmental unpredictability will select for brood reduction is not trivial and remains to be tackled.

If resources are variable yet predictable, as appears to be true for the parrotlet, parents may adjust their clutch size to anticipated resource availability (Lack 1954), rendering a costly brood reduction mechanism redundant and unnecessary. Such a facultative adjustment of clutch size may occur in the parrotlet. Female parrotlets may routinely adjust clutch size to food availability during egg-laying, as the rates at which males provisioned laying females were significantly correlated with final clutch size (Waltman and Beissinger 1992). Parrotlets respond to seed unavailability at the time of laying, caused by extreme drought or flooding, by simply delaying egg-laying, sometimes for several months. The protracted breeding season that extends up to 5 mo facilitates this strategy.

Conclusions

Relative to synchronous hatching, the net costs incurred by hatching eggs asynchronously appeared to exceed benefits in the Green-rumped Parrotlet. Asynchronous hatching appeared to bear a distinct cost in the mortality of smallest young in large broods. Because of this mortality, large SYNC broods fledged more young than ASYNC broods. Asynchrony appeared to affect the distribution of food within broods in favor of larger chicks. In addition, some mortality of smallest chicks clearly was not due to starvation, but rather due to the size disparities among broodmates. Our results suggested the possibility of an additional cost to asynchronous hatching: chicks in large ASYNC broods generally took longer to fledge than their SYNC counterparts. Rapid fledging may be beneficial if chicks are subject to a greater risk of predation while in the nest (Hussell 1972).

On the other hand, we found no clear benefit to asynchronous hatching. Only one general prediction of the hypotheses based on adaptive hatching patterns was clearly upheld in this study. Nestlings from SYNC broods fledged at lower masses than nestlings from ASYNC broods. However, mass differences did not affect the probability of resighting after fledging, or translate into reduced survival of SYNC fledglings. More female offspring fledged from ASYNC nests than from SYNC nests were recruited into the study population, although we could not exclude the possibility that this observation resulted from greater dispersal by SYNC females. Nestlings that died in ASYNC broods tended to do so at an earlier age than nestlings in SYNC broods. This is a premise of the Brood Reduction Hypothesis. It does not mean that ASYNC parents benefited by not investing as much in these chicks as SYNC parents, however, because many fewer young died in SYNC broods.

Other predictions corresponding to particular hypotheses were not upheld in these experiments. Food

did not appear to be limited for parrotlets during this study. While some offspring mortality in asynchronous broods appeared to be due to starvation, it is likely that the distribution of food within a brood rather than insufficient food was the cause. Older nestlings did not appear to benefit from the death of their younger nestmates. This contradicts predictions of hypotheses based on adaptive brood reduction.

Parent parrotlets may still potentially derive benefits of brood reduction or insurance under conditions not encountered or detected in these experiments. However, they seem unlikely to be important functions of hatching asynchrony, nor do they adequately explain the extreme degree of asynchrony found in this species. Complete asynchrony is unnecessary to facilitate the loss of one or two chicks from a brood of seven or more young. The probability of fledging did not differ significantly among the first five nestlings in large broods, and in smaller broods, smaller nestlings do not seem to suffer disproportionate mortality (Beissinger and Stoleson 1991). Thus, the Brood Reduction Hypothesis and other hypotheses based on adaptive hatching patterns appear to be insufficient to explain extreme asynchrony observed in the parrotlet.

Our results are congruent with those of most other experimental tests of hatching asynchrony (Amundsen and Slagsvold 1991*b*, Stoleson and Beissinger 1995). Furthermore, our results are more conclusive than those of most other studies because we assessed not only short-term measures of reproductive success, such as the number and size of fledglings produced by broods with differing degrees of synchrony, but long-term measures of costs and benefits as well. We also tested the premise that food resources varied unpredictably or declined seasonally. Although a few of the analyses presented here had relatively low statistical power to detect differences between treatments, our sample sizes were larger than the median value of 21 nests per treatment that have been used in other studies ($n = 35$ studies; Stoleson and Beissinger 1995).

Although asynchronous hatching in parrotlets entailed a distinct cost, and synchronous hatching appeared to offer parents the benefit of greater fledging success without incurring additional costs, hatching is completely asynchronous in this species. Asynchronous hatching patterns are generally produced by initiating incubation before all eggs have been laid (Drent 1975, Clark and Wilson 1981). The methodology employed in these experiments contrasted hatching patterns only, and ignored the potential costs and benefits of the early onset of incubation. Asynchronous hatching may be selected if the benefits derived from early incubation outweigh the costs associated with a staggered hatching pattern (Clark and Wilson 1981). Several hypotheses have proposed that the early onset of incubation may itself have an adaptive function: protecting eggs from predators (Bollinger et al. 1990) or brood parasites (Kendra et al. 1988), defending scarce

nest sites (Beissinger and Waltman 1991), maintaining the viability of eggs under unfavorable ambient conditions (Hussell 1972, Veiga 1992), or accelerating the fledging of the first chicks (Clark and Wilson 1981, Hussell 1985). According to these hypotheses, the size hierarchy imposed on nestlings by asynchronous hatching is merely an epiphenomenon and does not necessarily have an adaptive value (Clark and Wilson 1981, Stoleson and Beissinger 1995). Results presented here suggest that complete asynchrony in the Green-rumped Parrotlet cannot be explained by benefits gained from an asynchronous hatching pattern. Future studies should examine if asynchrony in this species is likely to result from selection for or constraints on the early onset of incubation.

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