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ORIGINAL ARTICLE

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Hatching asynchrony reduces the duration, not the magnitude, of peak load in breeding green-rumped parrotlets (*Forpus passerinus*)

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Abstract The peak load reduction hypothesis suggests that hatching asynchrony in altricial birds is adaptive because it reduces parental workload during the most energetically costly time in brood rearing. By staggering the ages of their offspring, parents may ensure that all nestlings do not reach maximum energy demand simultaneously. To test the hypothesis, we used the doubly labeled water technique to measure the energy expenditure of green-rumped parrotlets (*Forpus passerinus*) that reared experimentally manipulated synchronous and asynchronous broods. Peak metabolic rates of the two experimental groups did not differ, but parents of asynchronous broods metabolized significantly less energy than did parents of synchronous broods throughout the first half of the brood-rearing period. Our results suggest that hatching asynchrony in parrotlets substantially shortens the temporal duration of high brood energy demand, but does not reduce the magnitude of peak energy demand.

Key words Asynchronous hatching · Peak load · *Forpus passerinus* · Green-rumped parrotlets · Doubly labeled water

Introduction

Hatching asynchrony is widespread among altricial birds, occurring across a diversity of groups including parrots, raptors, herons, and passerines. Numerous explanations of the proximate causes and adaptive value of asynchronous hatching have been proposed, including 17 distinct hypotheses, many of which may operate in concert with one another (Clark and Wilson 1981; Magrath 1990; Stoleson and Beissinger 1995). The peak load reduction hypothesis (Hussell 1972) suggests that parents may lessen their workload at the most energetically demanding time in brood rearing by staggering the ages of their young, so that all nestlings do not reach maximum energy demand at the same time.

Mathematical simulations have tested the peak load reduction hypothesis without actually creating or observing synchronous broods. Bryant and Gardiner (1979) predicted synchronous hatching would increase peak brood energy demand by 7–8% in house martins (*Delichon urbica*), but Lessells and Avery (1989) calculated that synchronous hatching in European bee-eaters (*Merops apiaster*) would increase parents' provisioning rate by only 1%. Mock and Shwagmeyer (1990) modeled the effects of synchronous and asynchronous hatching on parental effort under a variety of clutch sizes and hatching intervals. They concluded that peak load reduction seldom approaches 5% under natural scenarios and is unlikely to provide substantial selection pressure for asynchronous hatching.

Experimental studies have only sometimes demonstrated increased indicators of nestling food demand in synchronous compared to asynchronous broods. Synchronous hatching increased nestling food consumption throughout the brood-rearing period in American kestrels (*Falco sparverius*) and cattle egrets (*Bubulcus ibis*), apparently due to increased sibling competition (Fujioka 1985; Mock and Ploger 1987; Wiebe and Bortoletti 1994). In other species, synchronous hatching affected neither parental mass loss during the breeding season (Amundsen and Slagsvold 1991) nor provisioning rate (Hébert and Barclay 1986; Slagsvold 1997; Stoleson and Beissinger 1997).

Green-rumped parrotlets (*Forpus passerinus*) are among the most likely of species to reduce peak load

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energy demands through asynchronous hatching because broods are large and hatch unusually asynchronously over periods of up to 2 weeks (Beissinger and Waltman 1991; Mock and Schwagmeyer 1990). Yet experimentally induced synchronous hatching in parrotlets increased nestling survival without affecting nest provisioning rate (Stoleson and Beissinger 1997), suggesting that hatching asynchrony does not reduce peak load.

Similar provisioning rates or mass changes in parents rearing synchronous and asynchronous broods may not be strong enough evidence to refute the peak load reduction hypothesis. Provisioning rate and mass change are only indices of parental effort, not direct measures (Siegel et al., in press). Provisioning rate may not be sensitive enough to detect subtle but nonetheless important differences in parental effort, particularly if the quantity of food delivered varies substantially between nest visits, or if the energy expenditure necessary to gather a constant quantity of food varies considerably over time. Parental mass change is an even less reliable index of parental effort, as mass change and daily energy expenditure correlate positively in some species studied, but negatively or not at all in others (Bryant 1988).

In contrast with provisioning rate and mass change, the doubly labeled water technique (DLW) measures directly the energy expenditure of free-living animals (Lifson and McClintock 1966). In this study, we used DLW to test directly for the first time whether asynchronous hatching reduces peak parental energy expenditure. We measured energy expenditure of green-rumped parrotlets rearing experimentally manipulated synchronous and asynchronous broods early, midway through, and late in the brood-rearing period. We first measured parents' energy expenditure 5 days after their first chick hatched, when synchronous broods were fully hatched but only about half of the chicks in asynchronous broods had hatched. We measured energy expenditure again 11 days later, after all chicks in both experimental treatments had hatched, and then a third time on day 27, just before the first-hatched chick fledged. We predicted that synchronous broods would have greater energy demands than asynchronous broods on each sampling day, and parents rearing synchronous broods would consequently expend more energy than parents rearing asynchronous broods. We expected that energy expenditure of parents, regardless of experimental treatment, would be greatest around day 27, but that parents rearing asynchronous broods would have substantially lower peak energy expenditures.

Methods

Study area and species

In 1995 and 1996, we studied color-banded green-rumped parrotlets breeding in PVC-pipe nestboxes at Hato Masaguaral, an active cattle ranch in the state of Guárico in the Venezuelan llanos (8°31′N, 67°35′W). The ranch, characterized by seasonally flooded grassland and scattered clumps of small trees and palms, is described in detail by Troth (1979) and O'Connell (1989). Nestboxes are described in Beissinger and Bucher (1992).

Green-rumped parrotlets are small (24–36 g), mostly granivorous parrots native to grasslands and forest edges of northern South America (Forshaw 1989). Clutch size averages seven eggs, which is unusually large for a tropical bird (Beissinger and Waltman 1991). Females generally lay eggs at 1- to 2-day intervals and begin incubation after laying the first egg. The resulting hatching spread of up to 2 weeks is among the largest of any species studied and leads to dramatic size disparities among nestmates (Beissinger and Waltman 1991; Stoleson and Beissinger 1997). First-hatched chicks may complete nearly half their 4- to 5-week period in the nest before their youngest sibling hatches.

Females are fed by their mates while they incubate their eggs and brood young nestlings, but they switch from primarily brooding to primarily foraging and provisioning nestlings 1–2 weeks after the first chick hatches. Chicks fledge 28–35 days after hatching, and post-fledging parental care appears to be minimal (Waltman and Beissinger 1992; Stoleson and Beissinger 1997).

Measuring parent field metabolic rate (FMR)

We checked nestboxes daily to ascertain laying dates of all eggs. After females stopped laying, but before eggs hatched, we transferred eggs among nests to create clutches of eight eggs. Clutches either hatched asynchronously, mimicking the natural hatching pattern (10–12 days between the first and last egg), or synchronously (within 3 days). We chose a clutch size slightly larger than the modal clutch size, hypothesizing that any elevation of parental workload due to synchronous hatching would be greatest (and most likely to be measurable) in large broods. Perfect synchrony could not be achieved because incubation periods of individual eggs varied slightly. All manipulated clutches received eggs from multiple donor nests, and procedures for moving eggs followed those used by Stoleson and Beissinger (1997).

Daily checks of nestboxes when hatching became imminent assured certainty of hatching dates. To maintain broods of eight nestlings, we replaced eggs that failed to hatch, and nestlings that died due to predation or other causes, with similar-aged eggs or nestlings from other nests. Partial brood loss occurred in about one-fourth of nests, and chicks were usually less than 5 days old when they died. Parents readily accepted and fed substitute nestlings. We excluded broods from the remainder of the experiment if they were missing more than one nestling and appropriately aged replacement nestlings were unavailable.

We used the single-sample DLW protocol to measure the FMR of parents at 5, 16 and 27 days after their first chick hatched. The single-sample protocol is less invasive than the more frequently used double-sample method, and has been shown to yield acceptable accuracy; Webster and Weathers (1989) provide a detailed exploration of potential errors associated with the single-sample method. Parent birds were mist-netted or captured inside their nestbox, injected intramuscularly with isotopically labeled water and released in their nestbox. Prior to release, we held 16 of the birds for 1 h for isotope equilibration and subsequent blood sampling to estimate total body water. We attempted to recapture all birds approximately 24 or 48 h after release, and collect blood from the brachial vein. Actual intervals between injection and bleeding (± SD) averaged 23.6 ± 3.5 h for birds recaptured 1 day after injection, and 49.1 ± 7.8 h for birds recaptured after 2 days. Blood samples were refrigerated and then distilled to obtain pure water (Nagy 1983; Wood et al. 1975). Water samples were assayed for tritium activity (Searle model Mark III liquid scintillation counter, toluene-Triton X100-PPO scintillation cocktail) and for oxgen-18 content by cyclotron-generated proton activation of oxygen-18 to fluorine-18 with subsequent counting of the positron-emitting flourine-18 in a Packard Gamma-Rotomatic counting system (Wood et al. 1975). Body water volumes and rates of carbon dioxide production were calculated using the equations of Nagy (1980, 1983).

Data were analyzed using SYSTAT (Wilkinson 1990) and SAS (1988). We confirmed homogeneity of variance of FMR measurements (Bartlett's test: $B = 1.2$, $P = 0.30$) and used analysis of variance (ANOVA) to assess the effects of sex, brood age, and synchrony treatment on parent FMR. We used one-tailed *t*-tests to assess the prediction that asynchronous hatching would reduce parent energy expenditure on each sampling day.

Results

We successfully measured FMR of at least one parent on at least one sampling day at 25 synchronous nests and 22 asynchronous nests. At many nests, we measured parent FMR on multiple sampling days. To account for any resulting pseudoreplication, we included 'individual,' nested within sex, as an effect in the ANOVA. Sex and number of days since the first chick hatched significantly affected parent FMR, and the overall effect of synchrony treatment was nearly significant (Table 1).

Energy savings due to hatching asynchrony were apparent for both males and females on each sampling day (Fig. 1), though not all differences were statistically significant. By day 5, all eight eggs in synchronous clutches had already hatched, whereas only two to four eggs had hatched in asynchronous nests. As a result day 5 FMRs of both males and females tending asynchronous broods averaged about 17% lower than rates of their counterparts rearing completely hatched synchronous broods. Females' FMRs were lower because they generally spent day 5 brooding chicks and incubating remaining eggs, while males were foraging and delivering food to their nestlings and mates. Hatching asynchrony significantly reduced FMR on day 5 among both males and females (Table 2). By day 16, all eight eggs in both synchronous and asynchronous clutches had hatched. FMRs of parents rearing asynchronous broods averaged 13% lower than those of their counterparts rearing synchronous broods. Despite relatively small sample sizes, this reduction in FMR due to hatching asynchrony was significant for females and was nearly significant for males (Table 2). FMRs of parents rearing synchronous and asynchronous broods did not significantly differ on day 27, but our sample sizes were small (Table 2). Day-27 FMRs did not differ significantly by sex (*t*-tests: $t=0.7$, $df=11$, $P=0.47$ for synchronous parents; $t=1.1$. $df=8$, $P=0.30$ for asynchronous

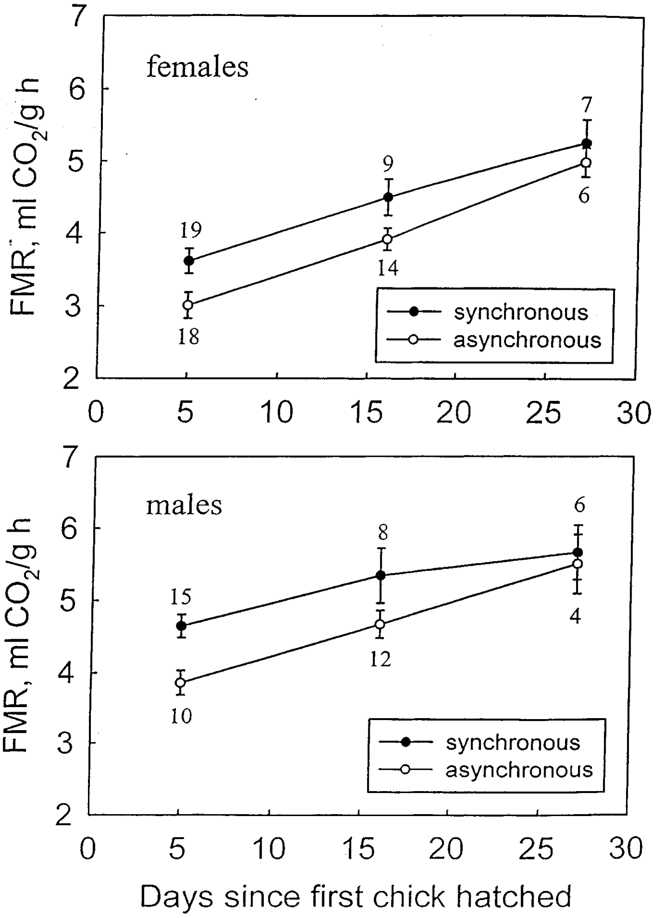

Fig. 1 Average field metabolic rate (FMR) of female (**a**) and male (**b**) green-rumped parrotlets tending experimentally created synchronous and asynchronous broods of eight nestlings. Shown are means ± 1 SE, with number of parents tending synchronous broods indicated above the curves, and number of parents tending asynchronous broods indicated below the curves

Table 1 ANOVA testing effects of days since the first chick hatched (5, 16 or 27), sex, and synchrony treatment (synchronous or asynchronous) on field metabolic rate measurements of breeding green-rumped parrotlets

Effect	df	*F*	*P*
Days since first chick hatched	2	13.4	< 0.001
Sex	1	19.0	< 0.001
Synchrony treatment	1	3.9	0.06
Days × sex	2	1.2	0.32
Days × synchrony treatment	2	1.0	0.37
Sex × synchrony treatment	1	0.0	0.93
Sex × days × treatment	2	0.6	0.54
Individual (sex)	80	0.8	0.79
Error	36		

Table 2 Percentage decrease in average field metabolic rates of green-rumped parrotlets tending synchronous versus asynchronous broods 5, 16, and 27 days after their first chick hatched (*t*-tests are one-tailed)

Day	Percent decrease	*t*	*df*	*P*
Males				
5	17.0	3.4	23	< 0.01
16	12.5	1.6	18	0.06
27	2.8	0.2	8	0.41
Females				
5	16.9	2.4	35	< 0.05
16	12.9	2.0	21	< 0.05
27	5.1	0.6	11	0.27

parents), so we pooled values from both sexes to provide greater statistical power. With the sexes pooled, FMRs of parents rearing asynchronous brood were still not significantly lower than FMRs of parents rearing synchronous broods ($t = 1.1$, $df = 21$, $P = 0.27$). By day 27, FMRs of parents rearing synchronous and asynchronous broods had converged for both males and females, at the time when energetic demands of the brood were likely greatest.

Discussion

Hatching asynchrony did not significantly reduce parents' peak energy expenditure. We expected the total energy demand of natural broods to peak around day 27, because first-hatched nestlings begin fledging at day 28. On day 27, male and female parents of asynchronous broods metabolized only 2.8% and 5.1% less energy, respectively, than did their synchronous counterparts. Such modest reductions in peak load are consistent with the predictions of the model of Mock and Schwagmeyer (1990). They suggest that even species with unusually large clutches and long laying intervals, such as parrotlets, would be unlikely to reduce peak energy demands substantially through asynchronous hatching.

Parents rearing asynchronous broods achieved greater energy savings earlier in the brood-rearing period (Table 2), as we predicted. Relative energy savings were greatest at day 5, when many of the asynchronous chicks had not hatched but parents at synchronous nests tended fully hatched broods. In absolute terms, parents at this early stage of brood rearing were working well below the highest observed rate of energy expenditure (Fig. 1), whether their broods were synchronous or asynchronous. At day 16, energy savings due to hatching asynchrony were substantial (statistically significant for females, and very nearly so for males), and parents, especially of synchronous broods, were working much closer to apparent peak load levels. Males and females rearing asynchronous broods metabolized, 85% and 79%, respectively, as much energy on day 16 as on day 27, compared with 94% and 86% in males and females rearing synchronous broods. Asynchronous hatching thus reduced the temporal duration of high parental energy expenditure, rather than the magnitude of the energy expenditure on a single day of peak parental effort.

The energy expenditure of parents likely reflects the food requirements of their broods. However, even large changes in parental effort may result in only minor changes in parent FMR, because parent FMR includes not just energy expended on parental care, but also non-reproductive components of the energy budget. We estimated the energy demand of synchronous and asynchronous broods throughout the nestling period to see if the consequences of asynchronous hatching on brood energy demand could explain the shortened period of high parental energy expenditure.

Stoleson and Beissinger (1997; unpublished data) monitored fledging interval (the time from hatching to fledging) and growth of 337 green-rumped parrotlet chicks reared in synchronous or asynchronous broods, and described growth rate using the logistic equation. They found that fledging interval and growth rate both varied with hatching order and synchrony treatment (Stoleson and Beissinger 1997). We used their average growth rates and fledging intervals, partitioned by hatching order and synchrony treatment, to generate growth curves for each nestling in a hypothetical asynchronous brood of eight nestlings hatching over 11 days and a hypothetical synchronous brood of eight nestlings hatching over 3 days. We estimated resting metabolic rates (kJ/day) of growing nestlings throughout the nestling period from nestling mass, using Eq. 7 of Weathers and Siegel (1995), which provides a phylogenetically robust estimate of the resting metabolism of altricial nestlings.

Summing nestling energy demands yielded estimates of the energy required for resting metabolism in synchronous and asynchronous broods on each day from first hatching to last fledging (Fig. 2a). Cumulative

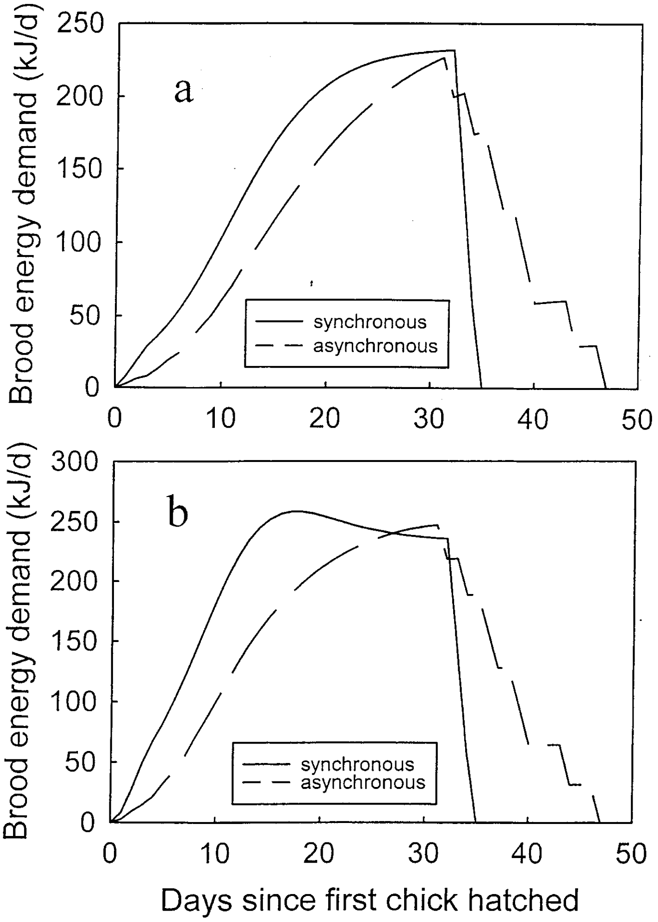

Fig. 2 Estimated energy required by synchronous and asynchronous broods of eight nestlings for resting metabolism (**a**) and resting metabolism plus growth (**b**)

resting metabolism requirements for synchronous and asynchronous broods were nearly identical (5137 kJ for synchronous broods, 5252 kJ for asynchronous broods). Hatching asynchrony reduced brood maximum daily energy requirement for resting metabolism by only 2%, which could explain why asynchrony had no significant effect on peak parent FMR. Such a minor reduction in peak energy requirement is unlikely to provide selection pressure for asynchronous hatching.

The overall shapes of the two brood energy demand curves in Fig. 2a differ much more than do their maxima. The energy demand of the asynchronous brood increases slowly at first and then rises steeply to a peak of 227 kJ/day on day 31. In contrast, the resting energy requirement of the synchronous brood increases rapidly early in brood rearing, and then plateaus near the peak load of 232 kJ/day. Parents of asynchronous broods must supply their nestlings with enough food to meet a resting requirement of 227 kJ/day on a single peak load day, whereas parents of synchronous broods must supply at least that much energy for 7 days to meet the energy demand of their chicks. Similarly, the asynchronous brood requires 204 kJ/day, or 90% of its peak energy demand for resting metabolism, for 6 consecutive days, whereas the synchronous brood requires at least that much energy for 14 days.

Our estimates of energy demand for brood resting metabolism suggest that temporal variation in brood energy demand explains why asynchronous hatching shortens the duration of high parent FMR without substantially reducing the magnitude of peak FMR. However, resting metabolism constitutes only around half of total chick energy demand (Drent et al. 1992). To produce a more complete approximation of brood energy demand, we added estimates of the energy content of accumulated tissue (RE, estimated by Eq. 13.10 of Weathers 1996) to our estimates of nestling resting metabolism. Although incorporating RE into the models substantially altered the shape of the synchronous-brood energy demand curve (Fig. 2b), hatching asynchrony still considerably reduced the duration of high brood energy demand. Brood energy requirements for resting metabolism plus RE peaked at 258 kJ/day in the synchronous brood and at 248 kJ/day in the asynchronous brood, yielding a peak load reduction of about 4%. While the asynchronous brood requires 248 kJ/day on a single day of peak demand, the synchronous brood requires at least that much energy for 8 consecutive days. Similarly, the asynchronous brood requires 223 kJ/day, or 90% of its peak demand, for 10 days, whereas the synchronous brood needs at least that much energy for 20 consecutive days.

The energy demand of the asynchronous brood (Fig. 2b) remained maximal at day 31, but the energy demand of the synchronous brood peaked much earlier in the season, at day 17. This result is inconsistent with parent FMRs, which were higher on day 27 than on day 16, irrespective of synchrony treatment.

The brood energy demand models in Fig. 2b account for resting metabolism and growth, but they do not include energy necessary for thermoregulation or activity, which together may account for as much as one-third of cumulative metabolizable energy in growing nestlings (Drent et al. 1992). If cumulative thermoregulatory and activity costs of nestling parrotlets are concentrated late in the nestling phase, a reasonable supposition, then total brood energy requirements, even for synchronous broods, could still peak around day 30. The discrepancy between the shape of the synchronous-brood energy demand curve in Fig. 2b and the empirical FMR measurements, however, suggests that activity and thermoregulatory costs may differ between synchronous and asynchronous broods.

Energy demand curves for nestling thermoregulation and activity are difficult to predict, but there are numerous reasons why they could differ markedly between synchronous and asynchronous broods. If synchronous hatching alters female brooding behavior, nest thermal environments could differ substantially, resulting in different thermoregulatory costs for chicks in synchronous and asynchronous broods. Even without differences in brooding behavior, detailed studies of nestbox microclimate are needed to determine if the presence of many similar-aged large nestlings substantially warms the nest, and perhaps alters thermoregulatory costs. Activity costs may also differ between synchronous and asynchronous broods. Asynchronous hatching may avoid extra energy expenditure due to competition for food, either by imposing a stable dominance hierarchy on the brood (Hahn 1981), or by enabling parents to preferentially feed younger nestlings, and thereby discourage an escalation of energetically costly begging (Stamps et al. 1985). Such energy savings seem unlikely in green-rumped parrotlets because nestlings do not engage in fights and parents have difficulty successfully seeking out and feeding youngest chicks in asynchronous broods (Stoleson and Beissinger 1997). Furthermore, recent evidence suggests that begging may only account for a trivial portion of nestling energy budgets (Chappell and Bachman, in press; McCarty 1996).

Although our brood energy demand estimates have limited predictive power because of their incompleteness, they demonstrate the potential for asynchronous hatching to change the distribution of parental effort required throughout the brood-rearing period. With or without accounting for RE, our energy demand estimates suggest that asynchronous hatching substantially reduces the duration of high brood energy demand, without markedly affecting the magnitude of peak energy demand. Models or empirical tests of the peak load reduction hypothesis that narrowly focus on a single day of peak energy demand will fail to discern such differences. Our results also highlight the potential limitations of relying on provisioning rate as an index of parental effort, rather than constructing more complete time budgets, or directly measuring FMR. Provisioning rate in parrotlets does not vary with synchrony treatment

(Stoleson and Beissinger 1997), yet our FMR data show that asynchronous hatching alters the temporal distribution of parental energy expenditure.

Reduced FMRs of parents rearing asynchronous broods on day 16 suggest that asynchronous hatching substantially shortens the duration of high parental energy expenditure in parrotlets. Nevertheless, a link between such a reduction and reduced reproductive costs still remains to be established. Stoleson and Beissinger (1997) were unable to detect differences in survival or future reproductive efforts of parents raising synchronous versus asynchronous broods, but they cautioned that sample sizes were relatively small and statistical power to detect differences was fairly low. One possibility inviting further study is that reduced parental energy expenditure and/or reproductive costs due to a shortened peak load may be offset by costs associated with a longer overall period of parental care (Fig. 2). Alternatively, green-rumped parrotlets have unusually low ratios of FMR to basal metabolic rate, even during the days of peak brood energy demand (R.B. Siegel, W.W. Weathers, S.R. Beissinger, unpublished data), suggesting that reproductive output in this species may not be energy limited at all. If breeding parrotlets work well below physiological capacity throughout the reproductive cycle, then the subtle changes in patterns of energy expenditure caused by hatching asynchrony may not have any fitness consequences. Further work is needed to test the link between short-term energy costs and long-term reproductive success, and to explore the mechanisms that may relate the two.

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