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## Egg mass in an asynchronously hatching parrot: does variation offset constraints imposed by laying order?

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**Abstract** Life history theory predicts phenotypic trade-offs between the number and quality of offspring produced. Intraspecific variation in egg mass is common in birds and increased egg size can have positive effects on offspring fitness. However, evidence of a trade-off with clutch size is limited. We analyzed variation in mass of 5,743 Green-rumped parrotlet (*Forpus passerinus*) eggs laid over 15 years to evaluate the potential for facultative adjustment of egg mass and factors governing variation. Heavier eggs had an increased probability of both hatching and fledging but egg mass did not affect post-fledging recruitment. Offspring egg mass differed between populations and the potential for seasonal adjustment to egg mass may be related to environmental factors such as seed density. Egg mass was moderately heritable ( $h^2=0.42$ ) which accounts for some of the individual variation detected, and these results are likely attributable to strong maternal effects. We found an effect of female age on egg mass, but no effects of previous reproductive experience. Finally, egg mass was strongly governed by position within the laying sequence, independent of clutch size, and such adjustment may facilitate brood reduction under some conditions in this highly asynchronous species.

**Keywords** Asynchrony · Brood-reduction · Heritability · Reproduction

### Introduction

Life history theory predicts a phenotypic trade-off between the number of offspring produced and the amount invested per offspring (Lack 1968). Larger offspring often have increased fitness compared to smaller individuals so offspring size, like fecundity, should be under strong selection. Given a fixed amount of resources available for reproductive effort, investment in offspring size could limit the number of young that can be produced. Therefore parents can increase overall investment either through the production of large brood sizes, or by increasing the size of individual offspring (Clutton-Brock 1991; Roff 1992), and the trade-off between these traits is critical for understanding the evolution of offspring size (Smith and Fretwell 1974; Parker and Begon 1986). Nevertheless, evidence of this trade-off in populations may be obscured by variation among females, because high quality females may produce both large offspring and large broods (van Noordwijk and de Jong 1986).

In birds, increases in egg size, mass or volume can have positive effects on offspring fitness, posthatching growth, development and survival of nestlings (Price 1998; Merilä and Sheldon 2001; Blomqvist et al. 1997; but see Bize et al. 2002). Yet, there is little evidence of a trade-off between egg size and clutch size, and intraspecific variation in offspring size is large (Christians 2002). Egg size is relatively consistent within individual females among breeding attempts and can be highly heritable across avian species (Christians 2002). Furthermore, measures of heritability and repeatability of egg size are higher than for other characters of female breeding performance, such as clutch size and timing of breeding (Christians 2002). High heritability may be attributable to genetic effects but also to cultural inheritance of environmental conditions, such as breeding sites or territory, although how egg size varies with environmental variation remains unclear. For example, food supplementation during the breeding season can

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increase egg size (Wiebe and Bortolotti 1995; Ramsey and Houston 1997; Reynolds et al. 2003), but examples of positive effects of supplemental feeding on egg size are few compared to studies finding no effects (Christians 2002). Egg size can also be affected by ambient temperature (Nager and van Noordwijk 1992; Saino et al. 2004) in addition to maternal age, size and reproductive experience, although these explain little variation present in avian systems (Christians 2002). Nonetheless, high levels of variation are apparent among individuals and flexibility in egg size production in relation to current environmental conditions should be favored if there is a fitness consequence of hatching from small eggs. Larger eggs hatch out larger young with greater nutrient reserves, which can increase the chances of survival within the first few days of life (Williams 1994). Although the benefits of increased egg size may be short-lived (Amundsen et al. 1996; Styrsky et al. 1999), offspring egg mass can positively affect survival through the chick rearing period (Blomqvist et al. 1997), possibly arising from increased competitive ability of larger nestlings (Kilner 1995; Krebs et al. 1999; Cotton et al. 1999), and it is common for last-laid eggs to be slightly smaller (mean = -4%) than earlier-laid eggs in altricial birds (Slagsvold et al. 1984). Sequential variation in egg size may confer fitness benefits in synchronously hatching broods. However, in asynchronously hatching species variation in egg size is likely to contribute less to variation in nestling size and survival than position within the laying sequence, although it may facilitate brood reduction (Slagsvold et al. 1984).

Here we present data on the variation in mass of 5,743 Green-rumped parrotlet (*Forpus passerinus*) eggs laid over 15 years within 874 broods. This small neotropical parrot lays large clutches that hatch and fledge highly asynchronously (Stoleson and Beissinger 1997). Mean clutch size is seven eggs (range 4–12) and females initiate incubation on the first egg (Beissinger and Waltman 1991; Grenier and Beissinger 1999). Clutches hatch over 6–17 days and this high level of hatching asynchrony leads to low survival of later hatched young (Stoleson and Beissinger 1997; Budden and Beissinger 2004). We examined variation in egg mass with year, laying sequence, clutch size, season and parental age. We also determined maternal effects, estimated heritability, and investigated paternal effects because male parrotlets feed females extensively prior to laying and clutch size is positively correlated with courtship feeding rates (Waltman and Beissinger 1992; Curlee and Beissinger 1995). We predicted that heavier eggs should have an increased probability of survival and that egg mass should decrease within the laying sequence, reinforcing the competitive advantage provided to older nestlings through asynchronous hatching. We also predicted that if food availability affected egg mass, then egg mass should be negatively related to population size and positively related to rainfall (a correlate of seed density, Stoleson and Beissinger 1997). Finally, we expected to

find a high degree of variation in mean egg mass per clutch among individuals based on other studies of avian egg size.

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## Methods

### Field studies

Data were collected between 1988 and 2002 from an individually color banded population of Green-rumped parrotlets, breeding at two sites within the Hato Masaguaral cattle ranch in the llanos of Venezuela, 45 km south of Calabozo (8°31'N, 67°35'W). This area is a seasonally flooded, brushy savannah (Troth 1979) and parrotlet nesting coincides with the rainy season (May to December; Waltman and Beissinger 1992). Approximately 106 nest boxes comprised of a 1-m deep polyvinyl chloride (PVC) tube lined with a hardware cloth (Beissinger and Bucher 1992) were available each year and an average of 77 boxes were used for at least one breeding attempt annually. Boxes are distributed at two sites that function as distinct breeding populations. They are separated by  $\geq 600$  m of inhospitable forest habitat devoid of nesting parrotlets, and differ in elevation by 1–2 m but not in rainfall or air temperature (Stoleson and Beissinger 1997).

Nest boxes were visited daily to establish the identity of the breeding pairs, to resight banded birds, and to determine laying dates, egg sequence, hatching and fledging dates. Eggs and nestlings were individually marked with permanent markers upon laying and hatching, respectively. Egg mass was measured on the day of laying to the nearest 0.1 g using Pesola spring balances. Nestlings were sexed by plumage dichromatism at approximately 2 weeks of age and were color banded at approximately 25 days when a final mass measurement was also taken. Fledging occurs at about 28 days (Stoleson and Beissinger 1997). Nesting adults and nonnesting parrotlets were captured near boxes with mist nets or in boxes, and given unique combinations of colored bands (Sandercock et al. 2000). As an index of annual population size, we used the total number of banded adults resighted from daily surveys during the 6-month breeding season. The relatively high and annually constant probabilities of detection, especially for breeding individuals (Sandercock et al. 2000; Sandercock and Beissinger 2002) make the number of banded birds a reasonable index of population size except for the first year of study when relatively few birds were banded.

Parrotlet broods were manipulated over the course of this study, including manipulations of clutch size and hatching asynchrony (see Curlee and Beissinger 1995; Stoleson and Beissinger 1997, 1999; Siegel et al. 1999). Only data from nests with complete clutches that were subject to noninvasive experimental procedures are presented here.

## Data analyses

Variation in individual egg mass was analyzed using general linear models (GLM), incorporating brood identity (a unique identifier assigned to each brood independent of parental identity or nest location) as a random factor. To investigate the importance of laying sequence, we included egg number and clutch size in the model. GLM was used to investigate the relationship between egg mass and pre fledging body mass (measured on the day of banding) by including age at banding as a covariate. Due to smaller sample sizes of very large clutches, nests with more than eight eggs were pooled for clutch size comparisons and eggs laid after number eight were grouped for comparisons of egg sequence.

Among clutch variation was analyzed for 874 broods using mean egg mass per clutch as the unit of analysis in a mixed model including female (or male) identity as a random factor to control individual variability. To examine the nature of variation among breeding females, we included female age, age squared to test for a curvilinear response, and the cumulative number of offspring fledged in previous seasons (as a measure of reproductive experience). As nearly all natal dispersal takes place during the first year of a parrotlet's life (Sandercock and Beissinger 2002) and site fidelity of breeding adults is very high (Sandercock et al. 2000), age was assumed to be 1 year in the case of females banded as adults (71% of cases). Unbanded or unidentified females were excluded from this analysis. We repeated this analysis using male age (55% were banded as adults) and male reproductive experience, this time using male identity as a random factor.

Survival consequences of egg mass variation were investigated using logistic regressions of egg mass, egg rank sequence and their interaction on hatching success, fledging success (of hatched eggs), and recruitment into the breeding population (of fledged young). Probability of detection for parrotlets that are recruited into the

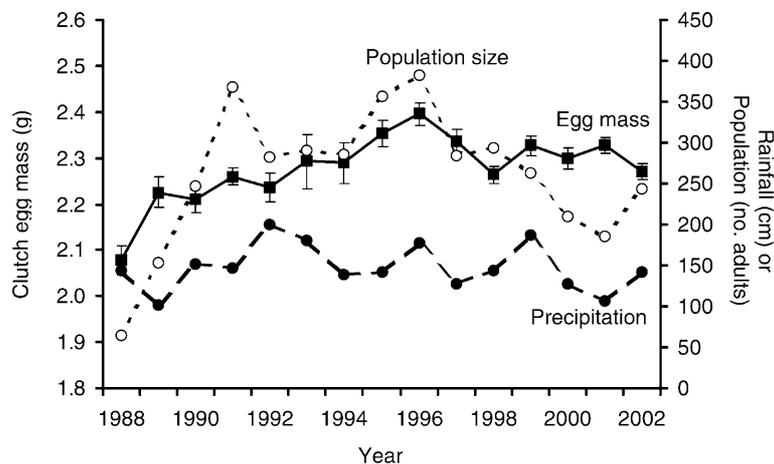
breeding population is 0.997, which makes logistic regression an appropriate and unbiased method for these analyses (Sandercock et al. 2000). Analyses of recruitment were separated by offspring sex because natal dispersal patterns differ (Sandercock et al. 2000). Sample sizes vary throughout the suite of analyses due to missing data (e.g. unidentified female or male parents) or use of reduced data sets (e.g. posthatching survival). All of the above analyses were performed using SAS version 8.02.

Heritability of egg mass was calculated from the regression of mean offspring egg mass on mother's egg mass and is equal to twice the regression coefficient (Falconer and Mackay 1996; Merilä and Sheldon 2001). For females with multiple clutches, offspring egg mass was included as a single mean across all clutches, so each mother and offspring pair appeared only once in the analysis. For 15 females that occurred in the data set both as an offspring and as a mother, the offspring data were excluded from analyses (remaining  $n=97$  female-offspring pairs). Similar analyses were also conducted using the father's egg mass ( $n=154$  male-offspring pairs), and for maternal and paternal grandmother-offspring relationships ( $n=16$  and  $n=15$  pairs, respectively).

## Results

### Annual variation in egg mass

Egg mass differed significantly among years ( $F=6.96$ ,  $df=14$ ,  $873$ ,  $p<0.001$ ; Fig. 1), appearing to increase between 1988 and 1996, and to decline thereafter. Annual variation was not correlated with annual rainfall ( $r_p=0.097$ ,  $p=0.731$ ,  $n=15$ ), which is a good predictor of food availability (Stoleson and Beissinger 1997), but was positively correlated with population size ( $r_p=0.705$ ,  $p=0.003$ ,  $n=15$ ; Fig. 1). Nevertheless, this



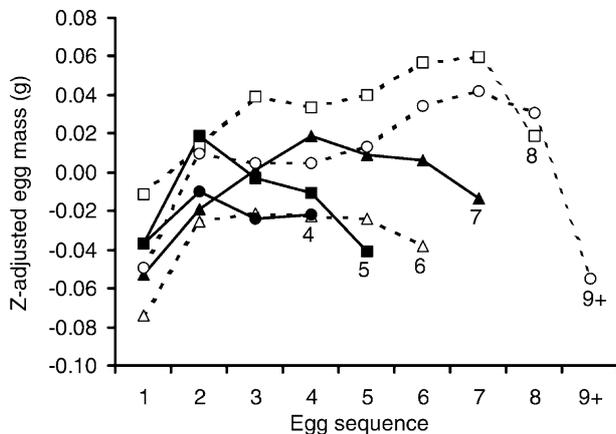
**Fig. 1** Variation in annual rainfall and clutch egg mass and population of Green-rumped parrotlet (*Forpus passerinus*) from 1988 to 2002. Data are presented as egg mass (mean  $\pm$  SE) (filled square), precipitation (cm) (filled circle) and number of adults (open circle)

relationship was not significant ( $r_p=0.439$ ,  $p=0.116$ ,  $n=14$ ) if we excluded 1988, the first year of the study when a smaller proportion of the population was banded and population size was underestimated. Annual variation was removed in all following analyses by using egg mass adjusted according to the annual mean ( $z=(x-\mu)/SD$ ).

### Sequential variation in egg mass

Egg mass varied significantly with laying sequence when analyzed in a GLM that included sequence and clutch size as fixed factors and brood identity as a random factor ( $F=11.95$ ,  $df=8$ , 4861,  $p<0.001$ ; Fig. 2). Tests of the least square means indicated that the differences lay predominantly with eggs 1 and 9, which had reduced egg mass compared with all others in the sequence ( $p<0.042$ ; Fig. 2), although last eggs tended to be smaller in all cases. Clutch size explained little additional variation in egg mass ( $F=1.97$ ,  $df=5$ , 4861,  $p=0.081$ ), but there was significant variation in egg mass among clutches ( $Z=18.96$ ,  $p<0.001$ ).

To investigate the relationship between clutch size and egg sequence, this analysis was repeated for laying sequence groups in a clutch (first egg, intermediate eggs, penultimate egg and last egg). There was a significant effect of sequence group on egg mass ( $F=17.35$ ,  $df=3$ , 4851,  $p<0.001$ ), but no significant effect of clutch size ( $F=1.80$ ,  $df=5$ , 4851,  $p=0.109$ ) nor an interaction between the two ( $F=0.76$ ,  $df=15$ , 4851,  $p=0.726$ ). A test of the least square means revealed no significant difference between intermediate and penultimate eggs ( $p=0.566$ ), but first and last eggs differed from all others ( $p<0.001$ ). First-laid eggs were the lightest followed by last-laid eggs (Fig. 2). As this rank order captured the observed variation in egg mass with laying sequence and controls for variation among clutches, all subsequent analyses used these sequence groups.



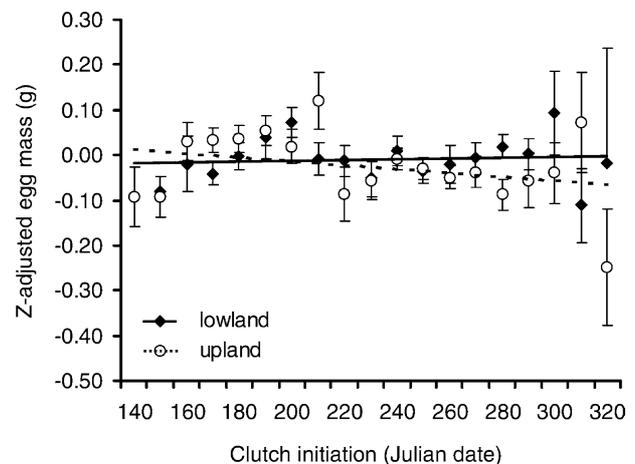
**Fig. 2** Influence of laying order (egg sequence) on mean egg mass in Green-rumped parrotlets. Data are separated by clutch size (values adjacent to data) and presented as mean annual z-adjusted egg mass. SE bars have been omitted for clarity

### Environmental and phenotypic effects on egg mass

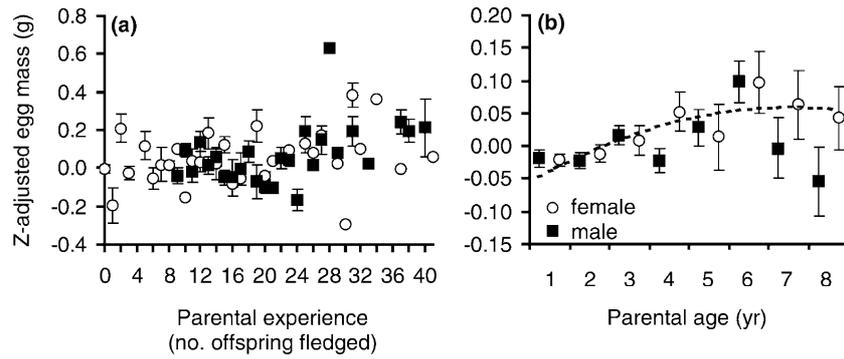
Mean egg mass per clutch did not change with laying date of the first egg (Fig. 3) when included in a mixed model with breeding site, clutch size, a quadratic Julian date term as fixed effects and female identity as a random factor ( $F=0.12$ ,  $df=1$ , 372,  $p=0.725$ ). However, mean egg mass per clutch differed significantly between birds nesting in the adjacent upland and lowland breeding sites ( $F=5.90$ ,  $df=1$ , 400,  $p=0.016$ ). A significant interaction between site and laying date ( $F=8.72$ ,  $df=1$ , 372,  $p=0.003$ ; Fig. 3) indicated upland birds laid heavier eggs earlier in the season and lighter eggs later in the season while lowland birds were consistent across season. Clutch size explained marginal additional variation in the data set ( $F=2.16$ ,  $df=5$ , 372,  $p=0.058$ ), although there was no pattern in the differences observed. However, there was a significant effect of the random factor, female identity (nested within population) on mean egg mass per clutch ( $Z=10.92$ ,  $p<0.001$ ).

Female reproductive experience (cumulative number of offspring fledged) did not explain any variation in the mean egg mass of clutches produced ( $F=0.53$ ,  $df=1$ , 388,  $p=0.469$ ; Fig. 4a) and female age was only marginally significant ( $F=3.64$ ,  $df=1$ , 388,  $p=0.082$ ). However, there was a significant quadratic effect of female age with younger and older females producing smaller eggs ( $F=7.79$ ,  $df=1$ , 388,  $p=0.005$ ; Fig. 4b). Female identity remained a significant factor in explaining variation in mean egg mass per clutch ( $Z=10.63$ ,  $p<0.001$ ).

We investigated the effect of male breeding experience using similar analyses. Neither male age nor male reproductive experience explained much variation in the data ( $F=0.42$ ,  $df=1$ , 392,  $p=0.518$ ; Fig. 4a and  $F=0.65$ ,  $df=1$ , 392,  $p=0.421$ ; Fig. 4b, respectively) and there was no quadratic effect of male age ( $F=0.15$ ,



**Fig. 3** Temporal effect of clutch initiation date on mean egg mass per clutch by breeding site [lowland (filled diamond) or upland (open circle)]. Data are presented as mean ( $\pm$ SE) annual z-adjusted clutch egg mass and lines represent linear trends (lowland  $y=0.0007x-0.0172$ ; upland  $y=-0.0044x+0.0172$ )



**Fig. 4** Effect of **a** parental reproductive experience (as measured by the number of offspring fledged) on mean egg mass per clutch and **b** parental age of female (*open circle*) and male (*filled square*) Green-

rumped parrotlets on mean egg mass per clutch. Data are presented as mean ( $\pm$ SE) z-adjusted clutch egg mass. *Line* represents a significant quadratic effect of female age

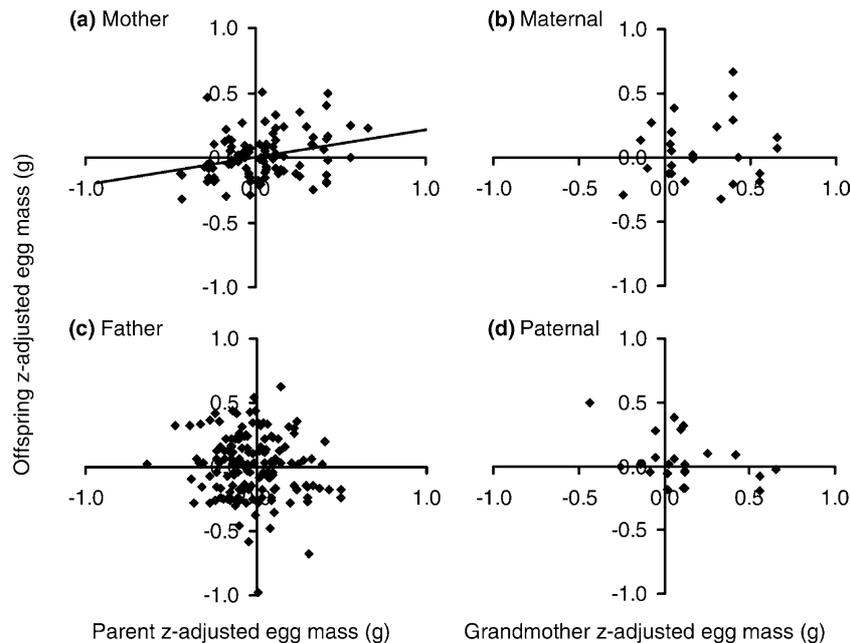
df=1, 392,  $p=0.701$ ). As with females, male identity explained a significant proportion of the variation in egg mass ( $Z=6.81$ ,  $p<0.001$ ).

We also investigated the dual impact of male and female quality on egg mass by examining the effect of pair bonds, including pair identity as a random factor. There was no significant effect ( $F=0.14$ , df=1, 262,  $p=0.713$ ) of pair bond duration (e.g. first year paired, second year etc.), but pair identity explained a significant proportion of the variation in egg mass ( $Z=10.72$ ,  $p<0.001$ ).

#### Heritability of egg mass

Offspring egg mass resembled that of their mothers (Fig. 5a) with heritability  $h^2=0.42$  ( $b=0.21$ , SE=0.15,  $p=0.008$ ,  $n=97$ , power=0.77). Heritability estimates

between nestlings and fathers were less than one and not significant ( $h^2=-0.28$ ,  $b=-0.14$ , SE=0.20,  $p=0.176$ ,  $n=154$ , power=0.27; Fig. 5c). There was no significant relationship between maternal grandmother egg mass and offspring egg mass ( $h^2=0.20$ ,  $b=0.05$ , SE=0.22,  $p=0.819$ ,  $n=16$ ; Fig. 5b), and no relationship between paternal grandmother and offspring egg mass ( $h^2=-1.28$ ,  $b=-0.32$ , SE=0.17,  $p=0.088$ ,  $n=15$ ; Fig. 5d). Power in this latter analysis was moderate (0.43) and a sample size of  $n=33$  would be sufficient to detect a difference with high power (0.80). This was not true for the heritability estimates between maternal grandmother egg mass and offspring egg mass which would require samples in excess of 2,000 with high power (0.80). Additionally, there was no significant relationship between offspring egg mass and maternal grandfather egg mass ( $h^2=-0.64$ ,  $b=-0.16$ , SE=0.14,  $p=0.255$ ,  $n=24$ ).



**Fig. 5** Regression of offspring egg mass on egg mass of parent (**a** mother; **c** father) and grandmother (**b** maternal; **d** paternal). Calculated heritability was 0.42, -0.28, 0.20 and -1.28 respectively. *Line* represents a significant relationship between offspring egg mass and mother egg mass. All other relationships were not significant

## Consequences of egg mass variation for offspring survival

Egg mass was a significant predictor of hatching and fledging success. Eggs that hatched were heavier than those that did not hatch ( $\chi^2=6.73$ ,  $df=1$ ,  $p=0.010$ ; Fig. 6). Rank sequence also predicted hatching success ( $\chi^2=45.52$ ,  $df=3$ ,  $p<0.001$ ), but there was no significant interaction ( $\chi^2=3.08$ ,  $df=3$ ,  $p=0.380$ ). Moreover, offspring survival from hatching to fledging was related to both egg mass ( $\chi^2=8.86$ ,  $df=1$ ,  $p=0.003$ ; Fig. 6) and egg rank sequence ( $\chi^2=41.65$ ,  $df=3$ ,  $p<0.001$ ), but not the interaction ( $\chi^2=0.06$ ,  $df=3$ ,  $p=0.996$ ). Neither initial egg mass ( $\chi^2=0.00$ ,  $df=1$ ,  $p=0.975$ ) nor by egg rank sequence ( $\chi^2=0.21$ ,  $df=3$ ,  $p=0.976$ ) influenced the probability of postfledging females recruiting into the breeding population. This was also true for philopatric males (Egg mass:  $\chi^2=0.01$ ,  $df=1$ ,  $p=0.914$ ; Egg rank sequence:  $\chi^2=2.15$ ,  $df=3$ ,  $p=0.541$ ). Male and female offspring did not differ in egg mass ( $F=0.20$ ,  $df=1$ , 2212,  $p=0.653$ ; GLM analysis including brood identity as a random factor).

Pre-fledging mass was marginally attributable to initial egg mass ( $F=2.89$ ,  $df=1$ , 1480,  $p=0.089$ ). Nestling age at measurement had a significant effect on pre-fledging mass ( $F=17.18$ ,  $df=1$ , 1480,  $p<0.001$ ), but the interaction between age and initial egg mass was not significant ( $F=2.23$ ,  $df=1$ , 1480,  $p=0.126$ ). There was a significant effect of the random factor, brood identity ( $Z=10.81$ ,  $p<0.001$ ).

## Discussion

Egg mass varied significantly during the 15 years of study. This pattern did not appear to be related to



**Fig. 6** Difference ( $\pm$ SE) in mean z-adjusted egg mass between individuals that survived (or returned) and those that did not. Data are grouped by life stage: survival to hatch, survival from hatching to fledging, postfledging recruitment for males and postfledging recruitment for females

rainfall, which affects food density (Stoleson and Beissinger 1997), nor was it related to population size upon removal of an outlying data point. We might predict that increased competition for food resources arising from higher population numbers would result in a negative relationship with mean egg mass. Given no such trend and no effect of rainfall on egg mass, it appears that food resources may not account for much annual variation in egg mass.

## Environmental effects and individual differences

A recent review has suggested that as much as 70% of variation in avian egg size is attributable to between clutch effects (Christians 2002). We found a significant effect of breeding population and an interaction between breeding population and laying date on mean egg mass per clutch. The sites used by the two parrotlet populations differ in vegetation structure and food availability; seed density increases during the breeding season at the lowland site, yet changes little or declines at the upland site (Stoleson and Beissinger 1997). In this study, egg mass decreased with laying date at the upland site but changed little at the lowland site. Although not a direct reflection, these patterns are consistent with changes in food availability and suggest that local variation in food availability, masked at the population level, can influence egg mass. Indeed, the direction of correlation between rainfall and seed density also differs between sites (Stoleson and Beissinger 1997). Other factors that vary seasonally could also affect egg size, such as ambient temperature (Magrath 1991; Nager and van Noordwijk 1992), which does not differ over the short distance between our two sites.

There was a significant quadratic effect of female age on egg mass, depicted by an increase in mean egg mass per clutch until age six followed by a plateau or slight decline (Fig. 4b). A reduction in egg size with increasing parental age is also apparent in the Western gull (*Larus occidentalis*) and Wandering albatross (*Diomedea exulans*) (Sydeman and Emslie 1992; Weimerskirch 1992). However, both species are long-lived compared to parrotlets (Sandercock et al. 2000) and egg size increases with female age in most other studies that found a difference (Christians 2002). Decreasing mass of parrotlet eggs with female age may indicate senescence in reproductive performance, or could be an artifact of selection where birds that produce smaller eggs were more likely to survive to older ages. Although, Sandercock et al. (2000) found that female survival increased with increasing reproductive effort (number of eggs laid). Previous reproductive experience (number of offspring fledged) did not explain any additional variation in egg mass. This measure integrates the quality of females, and indirect (hematological) measures of condition are relatively uninformative about reproductive success (Sheridan et al. 2004), although variation in female condition was not examined.

## Maternal effects and heritability of egg size

A significant proportion of variation in offspring egg mass was attributable to individual male and female parents and to pair identity. These results are likely driven by variation that exists among individuals. Egg mass was also demonstrated to be moderately heritable (0.42) in the maternal line. Although significant, this level of heritability is lower than values reported for other avian species (mean = 0.66; Christians 2002). Furthermore, our ability to separate maternal effects from heritability is limited, as we do not have accurate measures of female condition. An alternative approach is to examine the difference in heritability of egg mass between maternal grandmothers and offspring, and paternal grandmothers and offspring (Potti 1999). If egg mass was heritable and not subject to strong maternal effects, we would expect heritability coefficients from regressions of offspring egg mass on maternal and paternal grandmothers to be similar, and half that of the mother (Grant and Grant 1996). This was not the case. We found no significant relationships when analyzing heritability from the maternal and paternal grandmothers, and the coefficient of heritability was not 50% of that of the mother. Furthermore, there was no apparent heritability in the paternal line and no evidence of a 'grandfather effect', where a male can influence the trait of grand offspring through contribution to the mother's genome (Reznick 1981). Thus, despite moderate heritability of egg mass in parrotlets, variation in offspring egg mass is likely attributable to maternal effects. While low heritability estimates between fathers and offspring may reflect extra-pair fertilizations, occurrence of extra-pair paternity is not high in this system (7.7%; Melland 2000) and is unlikely to affect the nonsignificant result obtained. Interestingly, all coefficients of heritability generated from paternal analyses (father, paternal grandmother and paternal grandfather) were negative, suggesting a deviation in offspring egg mass opposite to that of the father/paternal grandparent. However, the likelihood of such results increases with a decrease in sample size (Palmer 2000) and where the sample between fathers and offspring was sufficient to generate confidence, the analysis had low power and a nonsignificant result was obtained.

## Survival consequences of egg mass variation

Egg size may correlate with offspring size soon after hatching (Amundsen 1995; Reed et al. 1999; Styrsky et al. 1999) and this effect can persist throughout the nestling phase (Amundsen et al. 1996; Styrsky et al. 1999). In addition, heavier eggs can increase survival of precocial and semialtricial birds (Blomqvist et al. 1997; Risch and Rohwer 2000). In parrotlets, initial egg mass influences both hatching and fledging success. Heavier parrotlet eggs were more likely to hatch than lighter eggs, regardless of position in the laying sequence.

Nestlings that hatched from heavier eggs were also more likely to survive to fledging indicating a surprisingly important effect of egg mass in this highly asynchronously hatching species, although position in the laying sequence is the most important factor affecting offspring survival. We found no effect of initial egg mass on pre-fledging mass, suggesting that egg size does not limit mass of nestlings and asynchronous fledging provides an opportunity for small nestlings to 'catch-up' in mass prior to leaving the nest. Indeed, most nestling mortality in parrotlets occurs within the first 12 days of a 30-day nestling phase and, despite deviations in growth rates, later-hatched nestlings that did survive fledged at a mass equal to or greater than earlier-hatched nestlings (Stoleson and Beissinger 1997).

Does parental manipulation of egg mass offset constraints imposed by laying order in an asynchronous parrot?

Given increased survival of heavier eggs, female parrotlets may be able to selectively advantage or disadvantage individual offspring within a brood through allocation of mass to eggs. For example, manipulating the size of the last-laid egg may facilitate brood reduction in asynchronously hatching species (Slagsvold et al. 1984). We found last-laid eggs of green-rumped parrotlets were significantly lighter than preceding eggs, and survival of later-laid eggs is significantly reduced in this highly asynchronously hatching species (Beissinger and Waltman 1991; Stoleson and Beissinger 1997; Budden and Beissinger 2004). Taken together, these findings might suggest that egg size manipulation facilitates brood reduction in this system. However, egg mass demonstrated a curvilinear relationship with position in the laying sequence, with the first egg significantly lighter than subsequent eggs (with the exception of last-laid eggs). When parents favor a 'brood-survival' as opposed to a 'brood reduction' strategy, egg size is predicted to increase with laying sequence to reduce the negative effects associated with asynchronous hatching (Clark and Wilson 1981). Whether the reduced egg mass of first-laid eggs in this system is an adaptive response to offset some costs of asynchronous hatching or a physiological constraint of egg production cannot be clearly evaluated. However, manipulations of hatching asynchrony have demonstrated that green-rumped parrotlets are capable of fledging as many, if not more offspring, from synchronous broods as from asynchronous broods (Stoleson and Beissinger 1997), suggesting a potential benefit of increasing egg (or nestling) size with laying sequence. Consequently, the 'brood-survival' and 'brood-reduction' hypotheses relating egg size and hatching asynchrony are not mutually exclusive, and parrotlets may selectively increase egg mass with sequence to a brood size optimum. Such a mixed strategy would allow parrotlets the flexibility to adjust their parental efforts in relation to maternal and environmental conditions,

investing less in final eggs and facilitating brood reduction of these last-hatched young in individuals that are incapable of feeding them.

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