

Against the odds? Nestling sex ratio variation in green-rumped parrotlets

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We investigated nestling sex ratio variation in the green-rumped parrotlet (*Forpus passerinus*), a small neotropical parrot breeding in central Venezuela. There are strong theoretical reasons to predict a female-biased sex ratio in this system according to the local resource hypothesis; juvenile males are philopatric and there are high levels of competition between male siblings for access to breeding females. Data were collected from two breeding sites over a 14-year period incorporating 564 broods with a total of 2728 nestlings. The mean percentage of male nestlings across years was 51%. Despite extreme hatching asynchrony in this system and increased survival of earlier hatched offspring, there was no bias in sex allocation associated with egg sequence. Patterns in sex allocation were not associated with clutch size, age, or size of the breeding female or breeding site. The potential for selective resorption of eggs was considered; however, no significant relationship was found between extended laying intervals and the sex of subsequent eggs. Together, these results suggest that female parrotlets are unable to regulate the sex ratio of their clutch at laying or that facultative manipulation of nestling sex ratio may not confer a fitness benefit to breeders in these populations. *Key words:* *Forpus passerinus*, green-rumped parrotlet, laying interval, local resource competition, sex ratio. [*Behav Ecol* 15:607–613 (2004)]

When there are differences in the fitness returns of producing sons versus daughters, sex allocation theory predicts selection should favor investment in offspring of the higher reproductive value (Charnov, 1982; Frank, 1990). Population-level biases in offspring sex ratio have been predicted in response to local resource enhancement (e.g., increase in helper numbers), and sex ratio adjustment toward the nonphilopatric sex is expected in populations exhibiting high levels of dispersal (Clark, 1978; Frank, 1990). Conversely, the local resource competition hypothesis (Clark, 1978) states that under conditions of limited resources, there is a cost of overproduction of the nondispersing sex. If not engaged in helping behaviors, these retained offspring will compete for access to breeding sites, mates, and resources, thereby reducing parental fitness.

Interest in sex allocation by birds has escalated in recent years (for reviews, see Clutton-Brock, 1986; Frank, 1990; Hardy, 1997; Hasselquist and Kempenaers, 2002; Krackow, 2002; Sheldon, 1998), yet evidence for the adaptive regulation of avian sex ratio is equivocal. Few studies of population-level variation in offspring sex ratio have demonstrated a significant bias (Koenig and Dickinson, 1996; Koenig et al., 2001; Radford and Blakey, 2000; South and Wright, 2002; but see Krebs et al., 2002), and it has been argued that broad-scale investigations of population-level sex ratio variation are unsuitable in the absence of detailed knowledge of fitness functions (Sheldon, 1998). Furthermore, investigations at this level may mask individual adaptation (West and Sheldon, 2002). Sheldon (1998) and West and Sheldon (2002) suggest that research should focus on questions relating to facultative adjustment of sex ratio by individuals, combining experimental manipulations with sex-specific responses.

Such individual level sex ratio adjustment is expected in response to a number of factors, including male quality (see Ellegren et al., 1996; Sheldon et al., 1999; Svensson and Nilsson, 1996), female condition (see Nager et al., 1999),

resource availability (see Appleby et al., 1997; Kilner, 1998; but see Wilson and Hardy, 2002), and helper presence (Komdeur, 1996; Komdeur et al., 1997), and there is stronger evidence for sex ratio adjustment at this level. However, individual level studies can also fail to demonstrate biases in offspring sex ratio (Bradbury et al., 1997; Leech et al., 2001; Questiau et al., 2000; Saino et al., 1999), and Palmer (2000) highlights the possibility that these significant findings represent a small fraction of a pool of nonbiased studies, a situation he attributes to quasireplication and selective reporting. To determine whether sex ratio biases are consistently in the predicted direction across groups, West and Sheldon (2002) performed a meta-analysis on the effect sizes from a subset of studies. By using only those studies testing either the mate attractiveness hypothesis or helper presence hypothesis (termed helper status), West and Sheldon (2002) demonstrated consistent facultative adjustment of offspring sex ratio in the predicted direction. The investigators also present “fail-safe” numbers (the number of unpublished studies averaging zero effect size that would yield the meta-analysis nonsignificant) and conclude that a publication bias would not affect the overall result. However, in the analysis of avian data, these fail-safe numbers are not robust under the criterion presented (West and Sheldon, 2002).

The mechanism of avian sex ratio adjustment is little understood (Oddie, 1998). Birds undergo chromosomal sex determination (females are the heterogametic sex), which may act as a constraint on sex ratio adjustment through random segregation during meiosis (Williams, 1979). However, Krackow (1995) has suggested that differential rates in the development of follicles may result in the nonrandom production of males and females and that this mechanism could explain variation in sex ratio and egg sequence effects (see Clotfelter, 1996; Kilner, 1998; Krebs et al., 2002; Nager et al., 1999). West and Sheldon (2002) also argue that, although the mechanism of sex determination may be important, it may not always be a constraint and therefore other factors must be considered when interpreting sex ratio data.

In the absence of a definitive explanation for the mechanism of primary sex ratio adjustment during meiosis, an alternative is to consider the adjustment of sex ratio through selective resorption (or dump laying) of offspring,

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which would result in a gap in laying (Emlen, 1997). Assuming random meiotic division, a female would have to skip 2 days between laying consecutive eggs to obtain an 87% probability of producing the desired sex (Emlen, 1997). This process would likely prolong exposure of the earlier laid eggs to potentially lethal ambient conditions, increase the length of exposure of the nest to nest predators, and increase the degree of hatching asynchrony (Stoleson and Beissinger, 1995, 1999). Alternatively, the onset of laying may be deferred until after production of the favored sex without incurring such costs, with the sex of remaining eggs determined by chance (Emlen, 1997). This represents a potential mechanism for the extreme sex ratio variation observed in the Seychelles warbler, in which females lay only a single egg (Komdeur, 1996; Komdeur et al., 1997), and may also explain biases in the sex of the first laid egg (Badyaev et al., 2002; Ryder, 1983) or when there is a large interval between eggs (see Heinsohn et al., 1997). However, further work on a separate population of Seychelles warblers found that both first and second laid eggs were female biased in two egg clutches, providing strong evidence of preovulation control of sex ratio (Komdeur et al., 2002).

We studied sex ratio allocation in the green-rumped parrotlet (*Forpus passerinus*), characterizing the sex of 2728 young produced over 14 years. This small (25–34 g) granivorous parrot is native to grasslands and forest edges of northern South America, is sexually monomorphic in size but dimorphic in plumage (even as nestlings), and is both socially and genetically monogamous (Forshaw, 1989; Meland, 2000). Dispersal among juvenile females in the study population is high; local survival of juvenile females averaged 0.141 compared with 0.465 for juvenile males (Sandercock and Beissinger, 2002). This population has a male-biased adult sex ratio (1.7:1), and approximately 50% of males in the population are nonbreeders in comparison with approximately 25% of females (Sandercock et al., 2000). Skewed adult sex ratio does not necessarily favor biased offspring sex ratio if it is attributable to sex-biased mortality after the period of parental care (Fiala, 1981; Leigh, 1970; Shaw and Mohler, 1953). Nevertheless, there are conditions under which a bias might be predicted to occur (Bensch et al., 1999; Harmsen and Cooke, 1983). More importantly, sex-biased philopatry can result in intense sibling competition for access to resources. In parrotlets, nonbreeding males do not contribute by helping breeding pairs, will compete in lengthy (1–3 day) and intense fights with up to a dozen other males over females that lose their mates while nesting, and can destroy unguarded eggs or young (Beissinger et al., 1998; Beissinger SR, personal observation). Examination of 104 conflict events associated with either a mate loss or a takeover event revealed that 12 events (11.5%) involved sibling males, in comparison with zero events involving sibling females. Furthermore, the proportion of interactions involving male siblings is 62% higher than expected by chance (7.1%), when calculated by generating a random sample of 1000 conflict events using a population of 210 males from years 2000–2001 (the mean number of males alive annually during the 14 years of this study). Although marginally nonsignificant ($\chi^2 = 2.94$, $df = 1$, $p = .09$), this trend demonstrates the potential for intense competitive interactions between male relatives. Given the high levels of competition arising from male philopatry, and the apparent reproductive advantage of females, this species is well suited to investigation of population-level sex ratio variation in response to the local resource competition, and we tested the prediction that the population offspring sex ratio would be female biased.

We also investigated a potential mechanism of sex allocation. Green-rumped parrotlet eggs hatch extremely asynchronously (Beissinger and Waltman, 1991). Clutch size

averages seven eggs (range = 4–12), with consecutive eggs typically laid at intervals of 1–3 days. Incubation is initiated on the first egg, resulting in a spread of up to 17 days between the first and last hatched nestlings. This leads to dramatic size disparity among young within the nest and to reduced survival of penultimate and last hatched nestlings (Stoleson and Beissinger, 1997). Should females in this population be able to selectively allocate sex according to laying sequence, we would predict a female bias in early laid eggs. Furthermore, although eggs are often laid on consecutive days, intervals of two or more days are common. Given the potential for sex-specific resorption of embryos (or dump laying), we predicted that eggs laid after an increased interval would be female biased (following Emlen, 1997). In addition, evidence of individual-level variation in sex ratio allocation was examined by incorporating age and size of the breeding female, clutch size, and laying date (season) into the model.

Finally, we investigated the potential for female parrotlets to reduce competitive asymmetries between same sex offspring in asynchronous broods by clustering eggs of the same sex. Hatching asynchrony results in body size variation within broods and can play an important role in sibling competition, with relatively larger nestlings gaining a competitive advantage (see Cotton et al., 1999; Kilner, 1995; Malacarne, 1994). Furthermore, male and female offspring of some species can demonstrate different competitive behaviors within the nest (see Price and Ydenberg, 1995; Teather, 1992), with males out-competing females for resources. In this population in which hatching synchrony is advantageous in large broods (Stoleson and Beissinger, 1997) but is constrained by nest failure (Beissinger et al., 1998; Stoleson and Beissinger, 2001) or through reduced egg viability (Stoleson and Beissinger, 1999), we predicted that females would be selected to cluster the sex of eggs in order to decrease the size disparity and therefore competitive asymmetry between same sex offspring.

METHODS

Study site

Data were collected between 1988 and 2001 from a banded population of green-rumped parrotlets, breeding at two sites within the Hato Masagual 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–December; Waltman and Beissinger, 1992). Approximately 100 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.

Data collection

Nest-boxes were checked daily to establish the breeding pair and to determine laying dates, egg sequence, and hatching and fledging dates. Eggs and nestlings were individually marked upon laying and hatching, respectively. Unique colored-band combinations identified adult and fledging birds. Nestlings were sexed at approximately 2 weeks of age; females have green wings and yellow foreheads, whereas males have blue underwing coverts, green foreheads, and a green cheek patch and are typically brighter on the rump. Nestling mortality can occur before the emergence of sex-specific plumage, and therefore, the data we present are analyses of secondary sex ratios.

Table 1
GLMM effect sizes explaining variation in fledging success and sex allocation broods of green-rumped parrotlets

Effect	Fledging success		Sex allocation	
	Estimate	SE	Estimate	SE
Intercept	-1.09	0.30	0.07	0.40
Egg 1	2.26	0.31	0.00	0.41
Egg 2	2.32	0.31	-0.24	0.41
Egg 3	2.18	0.31	0.06	0.41
Egg 4	2.18	0.31	-0.16	0.41
Egg 5	1.94	0.31	-0.06	0.41
Egg 6	1.49	0.31	-0.19	0.42
Egg 7	1.42	0.32	-0.19	0.42
Egg 8	0.86	0.34	-0.37	0.45
Egg 9+	0.00	—	0.00	—

Broods of parrotlets were manipulated as part of several experiments during the 14 years of this study, including manipulation of clutch size and hatching asynchrony (see Curlee and Beissinger, 1995; Siegel et al., 1999; Stoleson and Beissinger, 1997, 1999). Therefore, we included only data from nests that were not subject to invasive experimental procedures and excluded those nests abandoned before clutch completion. Nests with nine or more eggs were pooled for clutch size comparisons, and eggs laid after number eight were grouped for comparisons of egg sequence.

In our analyses of offspring survival and sex ratio at the individual egg level, we used generalized linear mixed models (GLMMs) with brood identity as a random effect to correct for overdispersion (Krackow and Tkadlec, 2001; Krackow et al., 2002; Wilson and Hardy, 2002) and egg number treated as a categorical variable. Analyses of sex ratio data at the brood level included each individual female as a random factor. To test for population-level differences in offspring sex ratio, we ran a GLMM including year and breeding site as categorical variables within the model. To identify sources of individual level variation, we ran a GLMM analysis including female identity and clutch size as categorical variables, and Julian date of first egg and female wing length (a surrogate for body size) as continuous variables. Sample sizes vary owing to missing data points in some analyses (e.g., unknown females, no data on female wing length). GLMMs were performed in SAS, version 8.02, using the glimmix macro developed by SAS (<http://ftp.sas.com/techsup/download/stat/glimm800.html>). All other analyses (except the simulation detailed below) were run in SPSS, version 11.0 (SPSS, 2002).

To verify our prediction that unequal offspring survival underlies sequential sex ratio allocation, we first determined the effect of egg sequence on the probability of an egg surviving to fledge. We included only nests that had fledged at least one young, as we were interested in differential mortality within broods and not brood mortality owing to predation or abandonment. A GLMM demonstrated a significant effect of egg sequence on survival to fledging ($F = 19.50$, $df = 8,3045$, $p < .01$) (Table 1) with later laid eggs less likely to fledge (Figure 1). However, a Z test of the random factor brood identity revealed strong variation in survival among broods (covariance estimate = 1.05, SE = 0.12, $Z = 9.04$, $p < .01$).

Examination of same sex clustering among offspring within a brood was performed by using a randomization analysis. We generated a series of distributions of offspring sex by using within brood counts of male and female offspring from the data set. In this way, the analysis resulted in randomized broods that had *exactly* the same sex ratio (both within and across broods) as the original data, which eliminated the

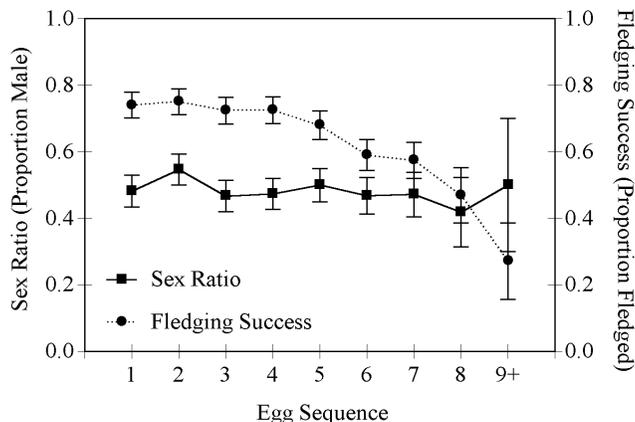


Figure 1
 Influence of egg laying order on the probability of fledging and sex ratio of green-rumped parrotlets. Data presented as proportions across all clutch sizes with 95% confidence intervals.

possibility that effects other than laying order could have inadvertently led to significant results.

RESULTS

Population-level variation in offspring sex ratio

Offspring sex ratio approached parity, with 51% males in our sample of 2728 sexed nestlings from 564 broods. There was no effect of year on brood sex ratio ($F = 0.73$, $df = 13,503$, $p = .74$) (Table 2 and Figure 2), and there was no correlation between variation in brood sex ratio and annual rainfall (Spearman $R = 0.01$, $p = .97$) (Figure 2). There was also no significant effect of breeding site on brood sex ratio ($F = 0.30$, $df = 1,231$, $p = .58$) (Table 2).

Individual-level variation among females?

We examined variation among females by including Julian date of first egg, clutch size female wing length, and female

Table 2
GLMM effect sizes investigating population-level variation in green-rumped parrotlet brood sex ratios

Effect	Estimate	SE
Intercept	0.09	0.14
Year		
1988	0.00	0.22
1989	-0.15	0.22
1990	-0.01	0.19
1991	-0.08	0.18
1992	-0.05	0.26
1993	-0.29	0.46
1994	0.42	0.30
1995	-0.03	0.21
1996	-0.08	0.18
1997	-0.03	0.17
1998	-0.04	0.19
1999	-0.42	0.23
2000	-0.25	0.20
2001	0.00	—
Breeding site		
Lowland	0.05	0.09
Upland	0.00	—

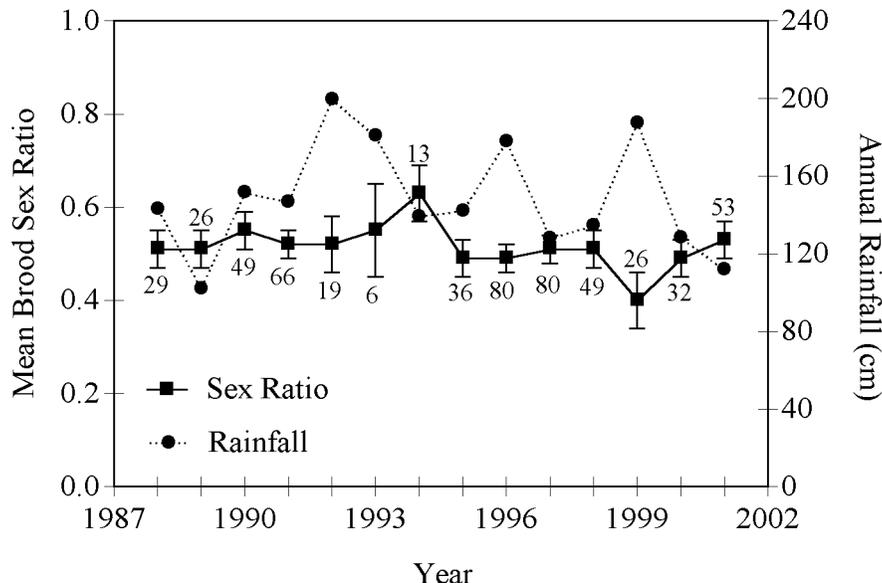


Figure 2

Annual variation in brood sex ratio of green-rumped parrotlets in relation to annual total rainfall. Sex ratio data presented as mean \pm 1 SE.

age as variables within the model. There was no significant effect of clutch size ($F = 1.13$, $df = 5,472$, $p = .34$) or lay date ($F = 0.09$, $df = 1,209$, $p = .76$) on brood sex ratio (Table 3). We also investigated the interaction between laying date and breeding site, as the sites are known to differ in seed densities (Stoleson and Beissinger, 1997), but there was no effect ($F = 0.06$, $df = 1,199$, $p = .82$) (Table 3). There was also no effect of female wing length ($F = 0.63$, $df = 1,136$, $p = 0.43$) or female age ($F = 0.33$, $df = 1,248$, $p = .57$) (Table 3) on brood sex ratio when we included all breeding females, treating females banded as adults as 1 year of age at banding. The analysis was repeated by using a subset of data in which female age was certain (banded as nestlings; $n = 223$ broods), and again, there was no significant effect of female age on brood sex ratio ($F = 0.45$, $df = 1,131$, $p = .51$). However, in this instance, a test of the random factor female identity revealed individual variation between breeding females (all data covariance estimate = 0.03, SE = 0.05, $Z = 0.75$, $p = .23$; subset covariance estimate = 0.41, SE = 0.24, $Z = 1.68$,

$p = .05$), which may partly be attributable to the smaller sample size.

Are there egg sequence effects?

Despite evidence of sequence-related mortality, a GLMM found no significant effect of egg sequence on the sex of an egg ($F = 1.21$, $df = 8,2630$, $p = .29$) (Table 1 and Figure 1). A Z test of brood identity as a random effect revealed no significant variation in the proportion of males between clutches (covariance estimate = 0.015, SE = 0.05, $Z = 0.29$, $p = .38$).

Is there evidence for selective resorption?

Given the temporal constraint of sex-specific resorption or dump laying of an egg, we might expect to see a bias in the sex of the first egg, as this would not interfere with a laying sequence. A two-tailed binomial test of the first laid egg in each clutch found no evidence of a sex bias (proportion male = 0.52, $n = 444$, $p = .37$). Alternatively, intervals of more than a day within the laying sequence may represent periods of sex discrimination by the female. We examined the sex of eggs produced after an interval of either 1, 2, or 3 days in a subset of the data for which laying dates were certain. GLMM demonstrated no effect of laying interval on egg sex ($F = 1.52$, $df = 2,1197$, $p = .22$; mean effect estimate = -0.08 ± 0.19 SE).

Does sex ratio vary with competitive asymmetries?

We performed a randomization analysis using data from 805 broods across 1000 iterations and found no evidence that eggs were clustered with respect to sex. The randomization model revealed that in 51% of the iterations the simulated broods had fewer runs of two same sex offspring than the actual data set. In the case of three same-sexed offspring, 81% of the iterations had broods with fewer same sex clusters than did the original data, and when examining clusters of four same sex offspring, the randomization generated broods with less clusters in 84% of the iterations. Thus, the two-tailed probability of same sex clusters within broods occurring more

Table 3

GLMM effect sizes investigating individual-level variation in green-rumped parrotlet brood sex ratios

Effect	Estimate	SE
Intercept	1.58	1.68
Clutch size		
4	-0.09	0.41
5	0.14	0.23
6	-0.25	0.15
7	-0.10	0.14
8	-0.03	0.15
9+	0	—
First egg date	0.00	0.00
Site \times first egg date		
Lowland	0.00	0.00
Upland	0	—
Female age	-0.03	0.04
Female wing length	-0.01	0.02

than expected by chance is $p = .98$ for clusters of two same sex offspring, $p = .39$ for three same sex offspring together, and $p = .32$ for clusters of four same sex offspring.

DISCUSSION

There are good theoretical reasons to predict a population-level sex ratio bias in green-rumped parrotlets according to the local resource competition hypothesis. Juvenile females disperse much farther than do males (Sandercock and Beissinger, 2002), and there is a high proportion of non-breeding males in the population (Sandercock et al., 2000) and a high incidence of competition between male siblings for access to breeding opportunities. Nevertheless, we found no evidence for a bias in offspring sex ratio despite a large sample of sexed nestlings. Similar results were found in another parrot exhibiting female dispersal (South and Wright, 2002) and in other long-term studies testing the local resource competition hypothesis (Koenig and Dickinson, 1996; Koenig et al., 2001; but for a review of sex ratio variation specific to local resource competition, see Gowaty, 1993).

There was no female bias in the sex ratio of earlier laid eggs despite strong evidence that earlier laid eggs have an increased probability of fledging. Even with the potential constraint imposed by chromosomal sex determination (Williams, 1979; see also Kraak and Pen, 2002; West and Sheldon, 2002), there is the opportunity for females to selectively reabsorb or dump lay eggs of the wrong sex. Biased sex allocation of only the first egg would result in species that lay smaller clutches exhibiting larger biases in sex ratio (Emlen, 1997). Given the large clutch size of green-rumped parrotlets, it is possible that the equitable sex ratio we found is attributable to random allocation of sex after adjustment of the first egg. There was, however, no evidence for a sex bias in first laid parrotlet eggs. Furthermore, despite relatively large intervals between the laying of consecutive eggs, the sex ratio of eggs did not differ from parity by prior laying interval.

Sex ratio is also predicted to vary in relation to environmental variability (see Appleby et al., 1997; Sheldon, 1998) and parental quality (see Nager et al., 1999; Sheldon et al., 1999). We studied parrotlets at two breeding sites that differed in food (seed) density, which is highly correlated with rainfall (Stoleson and Beissinger, 1997). We found no population-level variation in brood sex ratio that could be attributed to differences between breeding sites, nor was there any apparent pattern in the annual variation observed despite variation in rainfall. Furthermore, seed density often increases during the breeding season (Stoleson and Beissinger, 1997), and so, we might predict individual-level variation in sex ratio by laying date. Yet, we found no support for females adjusting the sex ratio of their brood according to laying date across the population as a whole or within individual breeding sites. In addition, individual-level variation in brood sex ratio could not be explained by female age (akin to breeding experience) or clutch size, and using female wing length as a surrogate for body size did not explain any additional variation. In the reduced data set of known age birds, there was evidence of individual variation between females. Although this result may be attributable to the smaller sample size, we have not been able to examine all parameters of individual variation, and future research evaluating female condition and mate quality may be beneficial.

Rather than demonstrate facultative primary sex ratio manipulation, adjustments to brood sex ratio may occur through differential investment after hatching (see Gowaty and Droge, 1991; Westneat et al., 1995; but see Lessels et al.,

1998), resulting in sex-biased mortality and a bias in secondary sex ratio (Kilner, 1998; Price, 1998; Price et al., 1996; Teather, 1992). A relationship between laying order and sex would result in sex-biased mortality in parrotlets owing to the loss of later hatched eggs (Beissinger and Waltman, 1991; Stoleson and Beissinger 1997), but there was no effect of laying order on the sex of offspring in parrotlets. Grouping same sex offspring to reduce competitive asymmetries across clusters of males and females may facilitate increased survival of female young (particularly if females were placed early in the clutch), but again, there was no evidence of clustering same sex parrotlet offspring. Indeed, other studies of begging in parrots have shown that female offspring beg more intensely than do male offspring (Krebs, 2002; Stamps et al., 1989), so any separation of the sexes may favor male nestlings rather than females in this system. Although secondary sex ratio adjustment may be operational in green-rumped parrotlets, it is not possible to predict benefits of offspring clustering, or the potential for parents to manipulate secondary sex ratio without accurate information on the begging and parental provisioning behaviors within the nest.

Our results strongly suggest that, against the odds, female parrotlets do not adjust offspring sex ratio in relation to the social, environmental, and parental variables reported here. However, the question remains why such an adjustment does not occur (Krackow, 2002). Females may be unable to manipulate the outcome of chromosomal sex determination in this species, despite evidence of primary sex ratio adjustment in another parrot species (Heinsohn et al., 1997). In addition, although the local resource competition hypothesis predicts a female bias, it would be necessary to first derive the exact fitness effects of male competition and female dispersal to quantify the expected brood sex ratio. Such data are difficult to obtain, and although trends in sex ratio variation are sometimes consistent with predictions of local resource competition, Gowaty (1993) argues that correlates of local resource competition (such as male philopatry) provide little information about the mechanism of competition, which will differ among species. It is imperative that more studies with large sample sizes test predictions generated by sex ratio theory to develop a broader perspective of the incidence of offspring sex ratio manipulation and the conditions under which it occurs.

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