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Brood Sex Ratio of the Lilac-crowned Parrot (*Amazona finschi*)

Shannon M. Pease,¹ Alejandro Salinas-Melgoza,¹ Katherine Renton,²
Patricia Escalante,³ and Timothy F. Wright^{1,4}

ABSTRACT.—Evolutionary theory predicts birds should adjust the sex ratio of their broods in response to external factors that differentially affect the reproductive value of each sex. We examined the brood sex ratio in the Lilac-crowned Parrot (*Amazona finschi*) in relation to climate, hatching date, and hatching order. We used polymerase chain reaction amplifications to identify the gender of 66 nestlings from 32 clutches spanning 7 years. There was a tendency to produce more female offspring in years of high nestling survival following high rainfall with a slight female-bias in third-hatched nestlings. We found no significant associations between brood sex ratio and rainfall, hatching date, or hatching order within clutches. Our results suggest the examined factors provide insufficient differential costs or benefits of offspring gender to promote sex ratio bias in this monomorphic species. Received 17 August 2011. Accepted 29 November 2011.

Animals that have the ability to alter the sex ratio of their offspring are predicted to do so as an adaptive response to external factors (Trivers and Willard 1973). Parents are expected to bias offspring sex ratio toward the gender that will yield the greatest fitness benefits (Trivers and Willard 1973, Addison et al. 2008; but see Fawcett et al. 2011). Factors shown to affect brood sex ratio in birds include resource availability (Budden and Beissinger 2004, Addison et al. 2008), date of hatching (Dijkstra et al. 1990, Radford and Blakey 2000), and sequence of hatching (Genovart et al. 2003).

Strong dimorphism and non-monomorphic mating systems are usually an indication of strong sexual selection, which may promote a bias in brood sex ratio at hatching (Heinsohn et al. 1997, Trewick 1997, Genovart et al. 2003), or second-

arily through differential mortality of young of a specific gender (Pike and Petrie 2003, Addison et al. 2008, Heinsohn et al. 2011). It remains less clear whether monogamous or monomorphic species should exhibit similar control over brood sex ratios.

Among parrots, the Eclectus Parrot (*Eclectus roratus*) and the Kakapo (*Strigops habroptila*) have shown extreme bias in brood sex ratio (Heinsohn et al. 1997, Trewick 1997, Heinsohn et al. 2011); both species are sexually dimorphic with non-monomorphic mating systems. In contrast, no sex ratio bias was found in the sexually monomorphic Yellow-naped Amazon (*Amazona auropalliata*) (South and Wright 2002).

We studied the Lilac-crowned Parrot (*Amazona finschi*), a socially monogamous and sexually monomorphic species endemic to the tropical dry forest of western Mexico. Clutches are usually small (mean = 2.6, range = 1–4 eggs), and eggs hatch asynchronously (Renton and Salinas-Melgoza 1999, 2004). There is no difference in nestling growth rate between first- and second-hatched chicks; third-hatched chicks demonstrate significantly slower growth and lower probabilities of survival, while fourth-hatched chicks occurred only in 1 year and all chicks died within a few days of hatching (Renton 2002, Renton and Salinas-Melgoza 2004). Previous work has shown marked inter-annual variation in reproductive success with fluctuations in rainfall resulting from the El Niño-La Niña cycle of the Southern Oscillation (Renton and Salinas-Melgoza 2004). Thus, there is potential for inter-annual fluctuations in rainfall and resulting differential parental investment to affect brood sex ratio in this species.

We measured nestling sex ratio to test three hypotheses that predict an association between external factors and sex ratio. (1) We used annual rainfall to test the local resource hypothesis, which predicts a brood sex ratio bias in years of relative resource abundance (Trewick 1997, Sasvári and Nishiumi 2005). (2) We examined distribution of males and females across the breeding season for

¹Department of Biology, Mail Stop Code 3AF, New Mexico State University, Las Cruces, NM 88003, USA.

²Estación de Biología Chamela, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 21, San Patricio, Jalisco, Código Postal 48980, México.

³Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, México D.F.

⁴Corresponding author; e-mail: wright@nmsu.edu

TABLE 1. Lilac-crowned Parrot productivity and sex ratios from 2001 to 2009.

Breeding season	Number of clutches	Nestlings examined	Nestling survival (fledglings/hatchlings)	Proportion of males
2001	5	11	0.583	0.55
2002	7	17	0.778	0.59
2003	5	9	0.313	0.56
2004	5	10	0.909	0.40
2006	2	4	0.50	0.50
2007	4	8	0.50	0.50
2009	4	7	0.813	0.29
Overall	32	66	0.619	0.50

all years combined to test the date of hatching hypothesis (Dijkstra et al. 1990, Genovart et al. 2003), which predicts manipulation of brood sex ratio early in the season to allow more parental investment and ensure survival of the most fit young. (3) We examined the distribution of males and females with hatching order within a clutch to test the sequence of hatching hypothesis (Dijkstra et al. 1990, Genovart et al. 2003), which predicts a sex bias with order of hatching within clutches.

METHODS

The study population inhabits the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve along the Pacific Slope of Jalisco, Mexico. Rainfall is highly seasonal with 80% occurring in the rainy season from June to October (Bullock 1986). Lilac-crowned Parrots nest during the dry season from February to May (Renton and Salinas-Melgoza 1999), and fluctuations in rainfall influence subsequent availability of food resources (Renton 2001, 2002). We used the amount of rainfall from June to February, the period prior to egg laying, as a proxy for environmental quality. We monitored 32 nesting attempts between 2001 and 2009, and collected

blood samples from 66 nestlings; no samples were collected in 2005 or 2008. About 20 µL of blood was collected when nestlings were >1 month of age. Blood was stored in lysis buffer at -20 °C until analysis. Purified DNA was extracted using a Qiagen DNEasy kit. The primer multiplex of Han et al. (2009) (P0-P2-P8) was used for polymerase chain reaction (PCR) amplification (conditions available upon request). PCR products were examined on a 2% agarose gel to score sex by product size.

We calculated sex ratios for the entire data set and by year. A Chi-square goodness of fit test was applied to identify any deviation from a 0.5 proportion of males in the entire population of nestlings. We used linear regression on the yearly proportion of males with the amount of rainfall prior to egg-laying to evaluate whether sex ratio was related to environmental quality. The breeding season was divided, for analysis of hatch date, into three hatch periods of equal length between the earliest (26 Feb) and latest (1 Apr) recorded hatch date over the 7 years, and young were assigned to a period by hatch date. We used Chi-square contingency table analysis to examine whether offspring gender was associated with (1) hatching period, and (2) hatching order within a clutch (first, second or third-hatched). We used nominal logistic regression to examine the effects of rainfall prior to egg-laying, hatch date, and hatch order on gender of nestlings.

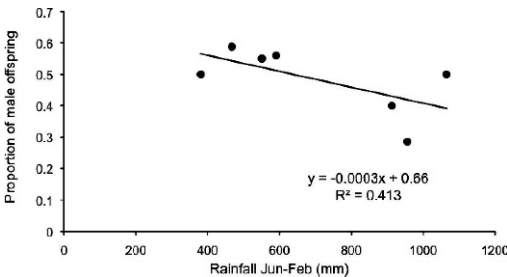


FIG. 1. Linear regression of the proportion of male Lilac-crowned Parrot offspring produced in the population on the amount of rainfall prior to egg-laying over seven breeding seasons.

TABLE 2. Frequency of male and female Lilac-crowned Parrot offspring by hatching order.

Hatching order	Males	Females
First hatched	15	14
Second hatched	15	13
Third hatched	3	6

Sex ratios are presented as mean \pm SD and significance was set at $P < 0.05$.

RESULTS

The overall sex ratio was 50% male with 33 males and 33 females of 66 nestlings (Table 1). The annual sex ratio was $48.3 \pm 10.6\%$ males, and ranged from 28.6% males in 2009 to 58.8% males in 2002 (Table 1). The number of males produced per year did not differ ($X^2_6 = 1.4$, $P > 0.05$) from the number of males expected assuming a 1:1 ratio (Table 1). There was a tendency to produce more females following periods of high rainfall (Fig. 1), particularly in 2004 and 2009, when nestling survival was high (Table 1). However, there was a 50:50 sex ratio in 2007 following the highest annual rainfall of 1,065 mm. Overall, the annual nestling sex ratio was not related ($R^2 = 0.413$; $F_{1,5} = 3.5$, $P = 0.12$) to environmental quality as indicated by rainfall (Fig. 1).

The frequency of offspring gender was not associated with date of hatching ($X^2_5 = 1.8$, $P = 0.88$). Twenty-two nestlings hatched in the early period of which 54.5% were male; 28 nestlings hatched in the middle period with 39.3% males, and 14 nestlings hatched in the late period with 57.1% males. There was no association of nestling sex ratio with hatching order ($X^2_2 = 0.68$, $P = 0.61$). However, 51.7% of first-hatched nestlings were males and 53.6% of second-hatched nestlings were males whereas third-hatched nestlings were only 33.3% males (Table 2). A nominal logistic regression showed no effect of rainfall prior to egg-laying, hatch date or hatch order on nestling sex (Whole Model $X^2_9 = 3.7$, $P = 0.92$).

DISCUSSION

We found no evidence of modification of brood sex ratio by the Lilac-crowned Parrot for the variables evaluated. Our results did not support the local resource hypothesis, although we observed a tendency to produce more females following periods of high rainfall when there was high nestling survival. The date of hatching hypothesis was also not supported by our results. However, Lilac-crowned Parrots exhibit high synchrony in nest initiation (Renton and Salinas-Melgoza 1999), which may limit the influence of hatching date on brood sex ratio. We found no significant association of sex ratio with hatching order, although our data indicate a slight female-bias in third-hatched nestlings. The sexually dimorphic Common Kestrel (*Falco tinnunculus*)

and Audouin's Gull (*Ichthyaetus audouinii*) both produce more males in early clutches and fewer males later in the season (Dijkstra et al. 1990, Genovart et al. 2003). There may be a tendency for Lilac-crowned Parrots to produce more female offspring in years of high nestling survival by producing larger clutches with a slight female-bias in third-hatched nestlings; a larger sample size may be required to detect significant associations.

One possible explanation for the lack of evidence in our study is that the factors evaluated do not affect the costs or benefits associated with rearing either males or females (Radford and Blakey 2000). The factors we evaluated have been associated with sex ratio manipulation in strongly dimorphic parrot species (Trewick 1997, Heinsohn et al. 2011), but they may not result in differential costs or benefits in monomorphic species like the Lilac-crowned Parrot or the Yellow-naped Amazon (South and Wright 2002). In addition, restrictions imposed by chromosomal sex-determination could prevent females from altering the primary sex ratio of their offspring (Pike and Petrie 2003; but see Heinsohn et al. 1997, Genovart et al. 2003). However, some studies suggest this constraint can be overcome, although the mechanisms are not well understood (West and Sheldon 2002, Korsten et al. 2006).

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