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Laying date and laying sequence influence the sex ratio of crimson rosella broods

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Abstract We examine the patterns of sex allocation in crimson rosellas *Platycercus elegans*, a socially monogamous Australian parrot. Overall, 41.8% of nestlings were male, a significant female bias. However underlying this population-level bias were non-random patterns of sex allocation within broods. Broods produced early in the season were female-biased, but the proportion of males in a brood increased as the breeding season progressed. Female rosellas may obtain greater fitness benefits from early-fledging daughters than sons because daughters can breed as 1-year-olds whereas sons do not breed until they are at least 2 years old. Laying date and laying sequence also interacted to influence the sex ratio of eggs. The sex of early-laid eggs strongly followed the brood level pattern, whereas the sex of middle- and late-laid eggs did not change significantly as the season progressed. Nevertheless, late-laid eggs were very unlikely to be male at the end of the season. We argue these differing seasonal patterns reflect the relative costs and benefits to producing early-hatched males and females at different times of the season. Female rosellas appear to maximise the probability that daughters are able to breed early but to minimise competitive asymmetries within the brood. In particular, late-hatched male chicks are disadvantaged if their oldest sibling is male, explaining the dearth of broods containing late-hatched males at the end of the breeding season.

Keywords Hatch order · Parrots · Seasonal patterns · Sex allocation · Sibling competition

Introduction

Biased sex ratios will be favoured in species where the reproductive costs or fitness benefits of sons and daughters differ and where selective pressures are sufficient to overcome the constraints imposed by the Mendelian segregation of sex chromosomes (Fisher 1930; Trivers and Willard 1973; Williams 1979; Charnov 1982). Although the mechanism remains obscure (see Krakow 1999) many recent studies on birds have demonstrated sex ratio biases at either hatching or fledging (see Hardy 1997; Sheldon 1998 for reviews). In some sexually dimorphic species, shifts in sex ratio toward the smaller sex are observed when food is limited (e.g. blue-footed boobies *Sula nebouxii*, Torres and Drummond 1999a), or maternal condition is poor (e.g. lesser black-backed gulls *Larus fuscus*, Nager et al. 1999; great skuas *Catharacta skua*, Kalmbach et al. 2001). Facultative shifts in sex ratios are also observed when the fitness benefits of offspring vary with resource availability (e.g. Appleby et al. 1997), territory quality (e.g. Komdeur et al. 1997), maternal condition (e.g. Nager et al. 2000), or male attractiveness (e.g. Burley 1981; Ellegren et al. 1996; Sheldon et al. 1999). In some cases facultative sex ratio adjustment can be extreme (e.g. Seychelles warblers *Acrocephalus sechellensis*, Komdeur et al. 1997; eclectus parrots *Eclectus roratus*, Heinsohn et al. 1997; laughing kookaburras *Dacelo novaeguineae*, Legge et al. 2001).

The benefits of producing males and females will also differ if the opportunities for breeding vary. For example in many raptors, the probability of early breeding by one sex is influenced by fledging date, leading to seasonal changes in sex ratios (Daan et al. 1996; Pen et al. 1999). Dijkstra et al. (1990) showed that female European kestrels *Falco tinnunculus* produce male-biased broods early in the season and female-biased broods late in the season. This pattern appears to increase female fitness be-

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cause early fledging sons, but not daughters, are more likely to breed as yearlings (Dijkstra et al. 1990).

Sex ratio biases are not only observed at the brood level; in many species the sex ratio of eggs changes predictably with laying sequence (e.g. common grackles *Quiscalus quiscula*, Howe 1977; bald eagles *Haliaeetus leucocephalus*, Bortolotti 1986; zebra finches *Taenio pygia guttata*, Kilner 1998; Montagu's harriers *Circus pygargus*, Leroux and Bretagnolle 1996; Harris' hawks *Parabuteo unicinctus*, Bednarz and Hayden 1991; laughing kookaburras, Legge et al. 2001). In species characterised by a high degree of sexual dimorphism or hatching asynchrony, the order with which each sex is produced within the brood will determine competitive disparities and the intensity of sibling competition (Bortolotti 1986; Edwards and Collopy 1983). Producing the larger sex first may facilitate brood reduction whereas producing the larger sex later in the laying sequence will minimise competitive asymmetries between chicks but may increase sibling competition.

We examine the patterns of sex ratio variation in a socially monogamous Australian parrot, the crimson rosella *Platycercus elegans*. Rosellas have a number of life-history traits that may influence individual strategies of sex allocation. First, the costs of raising sons is likely to be higher than daughters since adult males are 15% heavier than females, and the growth curves of chicks diverge about halfway through the nestling phase (Marchant and Higgins 1990; Krebs 1999). If sons are more costly to raise, a breeding female should produce a female-biased brood when her current condition or access to resources is poor (Gomendio et al. 1990; Wiebe and Bortolotti 1992; Nager et al. 1999). Second, some female rosellas breed as 1-year-olds, whereas males are only observed to breed as 2-year-olds (Marchant and Higgins 1990; Krebs 1998). If as a result fledging date has a greater influence on the probability of early breeding of females than males, the fitness benefits of producing female offspring are expected to decrease over the breeding season (see Daan et al. 1996 for a model). Rosella broods would then be predicted to be most female-biased early in the breeding season. Third, within rosella broods first-hatched male chicks are fed more than all other chicks (Krebs et al. 1999). This appears to occur because fathers feed the largest and most competitive chick, unlike mothers who distribute food equally to all chicks (Krebs et al. 1999; Krebs and Magrath 2000). If mothers benefit by reducing the competitive advantage of the larger sex, they may alter the hatching order of sons or daughters within the brood to minimise the competitive disparities between growing chicks. Since males are larger than females, size asymmetries within the brood will be smallest if females predominate in early-laid eggs.

Methods

Species and study methods

Crimson rosellas are a locally abundant broad-tailed parrot that breeds in eastern Australia. The sexes have similar plumage, but males are about 15% heavier than females and have slightly broader bills (Krebs 1999). Adults acquire their crimson and blue approximately 16 months after hatching, and 1-year-old rosellas are easily identified by their mottled green plumage (Forshaw 1981; Krebs, unpublished data). Young remain with their parents for approximately 1 month after fledging and then join flocks composed of juveniles and non-breeders (Forshaw 1981; Marchant and Higgins 1990). Although little is known about post-fledging movements of rosellas, Krebs (1998) observed that females dispersed further from their natal territory than males.

Rosellas breed in long-term monogamous pairs (Forshaw 1981) with very low rates of extra-pair paternity (Krebs, unpublished data). Pairs share a large home range with other individuals throughout the year, defending a small area containing several nesting hollows in the breeding season (ca. September–December; Forshaw 1981; Marchant and Higgins 1990). Crimson rosellas are typically single-brooded and lay from 3 to 8 eggs (mean \pm SD=5.1 \pm 0.1, $n=64$; Krebs 1998). Females usually lay eggs at 2-day intervals and initiate incubation in the middle of the laying sequence so that broods hatch asynchronously over 1.5–7 days (mean \pm SE=3.5 \pm 0.5; Krebs 1998). The female incubates the eggs and broods small nestlings. Males feed incubating and brooding females until the brood is approximately 5 days old, at which point both parents feed the young directly. Male nestlings grow faster than females and are 10% larger at fledging (Krebs 1999).

In 1993 and 1994, we placed a total of 46 nestboxes in the dry sclerophyll eucalypt forest (mainly *Eucalyptus rossi*, *E. macrohyncha*) of Black Mountain Nature Reserve. Nestboxes were spaced 50 m apart in a grid system and mounted approximately 4 m above the ground. Nestboxes were inspected at least weekly during the laying period to determine the date that clutches were initiated. Eggs could be identified as 'newly laid' within 24 h of laying by the presence of translucent patches and their pristine condition. We revisited nestboxes where laying had commenced every 48 h and marked all new eggs with indelible ink to allow laying and hatching sequences to be matched.

Nestboxes were inspected daily towards the end of incubation to determine the precise sequence of hatching. Hatchlings were marked initially by trimming the down on different parts of the body, and then with a single coloured leg band when approximately 10 days old. Where the order of hatching was observed directly we assigned a hatching rank to each chick (first, second, etc.) and a hatching time to the nearest 0.5 day, based on the dryness of a chick and its crop contents. Where more than one chick hatched on the same day, hatch time was assigned based on a combination of wing chord and dryness of the down. In a brood where several chicks had already hatched, chicks were assigned ranks retrospectively using a regression of wing chord on age for all chicks of known hatching times. The oldest chick in these broods was never more than 4 days old, and we never noted rank reversals early in the nestling period. All nestlings that survived until 4 weeks of age were banded with numbered Australian Bird and Bat Banding Scheme bands. At banding, a small blood sample was taken from the brachial vein of nestlings during 1993–1995.

Sexing nestlings

Nestlings were sexed either using DNA extracted from the blood samples collected from nestlings produced in 1993–1995 ($n=129$) or on the basis of their bill width immediately prior to fledging in 1996. We used a PCR-based sex-specific genetic marker to molecularly sex all bled young (see Griffiths et al. 1998 for details of the method). This technique was tested using blood samples collected from 36 adults (17 male, 19 female) all of whom were sexed correctly using this procedure. Morphological measures showed that

there was little overlap in the bill width of male and female nestlings sexed using the molecular technique (culmen width: males=13.3±0.45SD, $n=46$; females=12.0±0.35SD, $n=49$). We therefore assumed that nestlings were male if they had a bill width greater than 12.7 mm and female if they had a bill width of less than 12.4. These morphological criteria would have correctly sexed 45/46 male nestlings and 44/49 female nestlings whose sex had been determined from their DNA. Two female nestlings would have been sexed incorrectly. The sex of one male nestling and three female nestlings would have been ambiguous (i.e. they had bill widths between 12.4 and 12.7 mm). All 1996 nestlings could be sexed unambiguously using these criteria.

Statistical analysis

We examined the overall population sex ratio (proportion males) using the binomial test (Zar 1984).

At the brood level, we examined the factors influencing brood sex ratio by fitting a generalised linear model with a binomial error distribution and a logit link using Genstat 5.4.1 for Windows (Genstat Committee 1997). In this analysis the response variable was number of males in a brood over brood size (x/y) and each brood was treated as independent because the majority of females (32/33) were represented once. Explanatory variables of interest included: (1) year, (2) clutch initiation date ('laying date'), (3) clutch size (4) female age (sub-adult/adult), (5) female tarsus length, (6) male tarsus length and (7) whether hatching failure or early mortality had occurred (entire clutch sexed/entire clutch not sexed). To evaluate the potential influence of hatching asynchrony on the brood sex ratio, we used a measure of average hatching interval between eggs ('relative hatching asynchrony'). This removes any changes in hatching asynchrony associated with brood size. We calculated relative hatching asynchrony as $[\text{First} - \text{Last hatching interval} / (\text{brood size} - 1)]$.

We initially fitted a full model containing all explanatory variables and two-way interaction terms. A final model was selected by progressively eliminating non-significant interaction terms ($P > 0.1$) and then non-significant main effects. The significance of terms was assessed by the change-in-deviance (which approximates a chi-square distribution) associated with dropping that term from a fuller model. The brood level analysis consisted of data from 34 broods (145 nestlings). Broods were excluded if we did not sex at least three nestlings or if nestlings from more than 2 eggs were not sexed. In addition we assessed brood level effects using 11 complete clutches (50 nestlings) where all eggs were sexed.

To examine whether the sex ratio varied with the laying sequence within broods we categorised nestlings as coming from early-, middle- or late-laid eggs. We chose to categorise eggs rather than use the laying sequence directly (i.e. 1, 2, 3, 4, etc; cf. Kilner 1998) because in asynchronously hatching species, relative laying order determines the competitive asymmetries in the brood. For example, being laid fourth has very different consequences posthatching for chicks in four-egg clutches compared to chicks in seven-egg clutches. We fitted a generalised linear mixed model using the GLMM procedure in Genstat 5.4.1 for Windows (Genstat Committee 1997). In this model "brood" was specified as a random term, since the data was structured with each brood contributing data on the sex of nestlings hatching at the start, middle, or end of the laying sequence. Within a brood, we attempted to assign equal number of chicks to each category, but if that was not possible more eggs were assigned to early or middle categories. Since incubation begins mid-laying and hatching intervals increase with later-laid eggs (Krebs 1998) this categorisation reflects the relative hatching spreads within a brood. For example in 5-egg clutches the first two eggs were categorised as early, the third and fourth as middle, and the fifth egg as late. We tested the following explanatory variables: (1) year, (2) clutch initiation date, (3) clutch size, (4) relative hatching asynchrony, (5) female age (sub-adult/adult), and (6) laying order (early, middle, late). We initially fitted a full model and progressively eliminated non-significant in-

teraction terms and then non-significant main effects until only significant terms remained. The significance of terms was assessed using the Wald statistic (which again approximates a χ^2 distribution) calculated when the term of interest was fitted last in the model (see Genstat Committee 1997 for rationale). The laying sequence analysis included data both from clutches where eggs had been marked ($n=25$) and where all eggs hatched ($n=11$) since hatch order typically reflected laying order in this study (see Results). In total 58 early-laid, 49 middle-laid and 29 late-laid eggs were sexed. Clutches where eggs were not marked and eggs failed to hatch ($n=7$) were excluded from the analysis since hatching failure was independent of laying sequence (Krebs, unpublished data).

To assess whether the effect of laying date on the post-fledging prospects of female and/or male chicks was dependent on hatching rank, we examined how fledging mass changed over the breeding season. Fledging mass was taken as the mean mass of nestlings after their growth had reached an asymptote ('mean maximum mass', see Krebs 1999 for details). This measure minimises any variation associated with large, infrequent feeding visits. We fitted two mixed models using female and male fledging mass as the response variable and laying date, brood size and year as explanatory variables. These models were fitted using the REML procedure in Genstat. Brood was specified as a random factor in both models. In total, 50 early-hatched, 48 middle-hatched and 31 late-hatched sexed chicks are included in the analyses. Note that the number of chicks in each hatching category differs somewhat from the number of eggs in each laying category, because hatching order is assigned based on the relative position within the brood.

We ensured that our data conformed to the distributional assumptions (i.e. deviations from normality or over-dispersion) of the statistical models. Sex ratios throughout this paper refer to the proportion of nestlings that were male.

Results

Population sex ratio

Overall, the crimson rosella nestlings in our study population were female-biased. The sex ratio of 158 eggs from 42 clutches, including some clutches where all eggs were not sexed, was 41.8% male (binomial test, $P=0.05$). Nestlings were also female-biased when the sample was restricted to clutches where all eggs were sexed (34% male, 11 clutches, 50 nestlings; binomial test, $P=0.05$).

Laying sequence and hatch order

Hatch order reflected laying order in the majority of clutches (21 of 24 cases). The three cases where hatch order differed from lay order included one case where the second egg hatched third, one case where the fifth egg hatched sixth, and one case where the sixth egg hatched third.

Sex ratios of broods

The proportion of male chicks within a rosella brood increased through the breeding season (Table 1, Fig. 1). Thus, broods were highly female-biased early in the breeding season and became less female-biased as the

Table 1 Summary of GLMM model examining the factors influencing brood sex ratio in crimson rosellas *Platycercus elegans*. The significance reported is the change-in-deviance when the term of interest is dropped from the final model. (Deviance of final model $\chi^2=34.4$, $df=32$; see Methods for variable definitions)

| Final model=laying date | | | |
|-----------------------------------|----------|------|------------|
| Variable dropped from final model | χ^2 | df | P -value |
| Laying date | 4.50 | 1 | 0.03 |
| Year | 1.84 | 3 | 0.61 |
| Clutch size | 1.54 | 1 | 0.21 |
| Hatching asynchrony | 0.74 | 1 | 0.39 |
| Female age | 1.13 | 1 | 0.29 |
| Female tarsus length | 1.17 | 1 | 0.28 |
| Male tarsus length | 0.12 | 1 | 0.73 |
| Full/partial clutch | 2.42 | 1 | 0.12 |

season progressed (Table 1, Fig. 1). This seasonal pattern was consistent across all four years of the study (year \times laying date interaction: $\chi^2_3=6.1$, $P>0.1$). The increasing sex ratio was not driven by seasonal changes in mortality between laying and sexing mid-way through the nestling period. Late-laid eggs were less likely to produce chicks that survived until sexing than early- or middle-laid eggs, but this pattern did not change over the breeding season (GLMM model: laying order: $\chi^2_2=6.0$, $P=0.05$; laying date: $\chi^2_1=0.01$, $P=0.75$; laying order \times laying date interaction: $\chi^2_2=3.5$, $P=0.17$). Brood sex ratios also increased as the season progressed in broods where all eggs laid were sexed, although the seasonal effect on brood sex ratio was not significant in this restricted data set ($n=11$ broods; laying date: $\chi^2_1=1.46$, $P=0.23$; Fig. 1).

Brood sex ratios did not vary significantly between years (1993= $0.50\pm 0.28SD$, $n=7$; 1994= 0.37 ± 0.30 , $n=10$; 1995= 0.48 ± 0.21 , $n=13$; 1996= 0.38 ± 0.08 , $n=4$) and were not affected by parental phenotypes (female age, female tarsus length or male tarsus length), clutch size, relative hatching asynchrony, or post-laying mortality (Table 1).

Sex ratios of early-, middle- and late-laid eggs

The sex ratio of eggs tended to vary seasonally with laying order in rosella broods. The proportion of males in early-laid eggs increased with laying date, whereas the proportion of males in late-laid eggs decreased seasonally (laying order \times laying date interaction: Table 1, Fig. 2). In contrast, the sex ratio of eggs laid in the middle of the laying sequence was not influenced by laying date (Fig. 2).

To examine this complicated interaction in more detail, we fitted separate models for the sex ratio of early-, middle- and late-laid eggs. As the previous model suggested, the proportion of males in first-laid eggs increased strongly with laying date ($\chi^2_1=4.68$, $P=0.03$) while the sex of middle-laid eggs did not vary seasonally ($\chi^2_1=0.15$, $P=0.70$). The proportion of males in late-laid eggs appeared to decline with laying date but this rela-

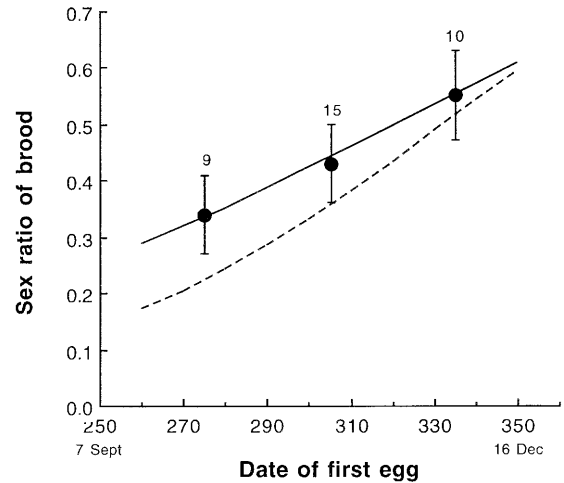


Fig. 1 Relationship between brood sex ratio and laying date in crimson rosella *Platycercus elegans* broods. Solid line shows predicted values from the GLMM model using the entire data set. Points show the means ($\pm SE$) for clutches initiated at 30-day intervals commencing at day 260 (17 September). The number of broods sampled is indicated over each point. Dashed line shows predicted values from the GLMM model using only clutches where all eggs were sexed

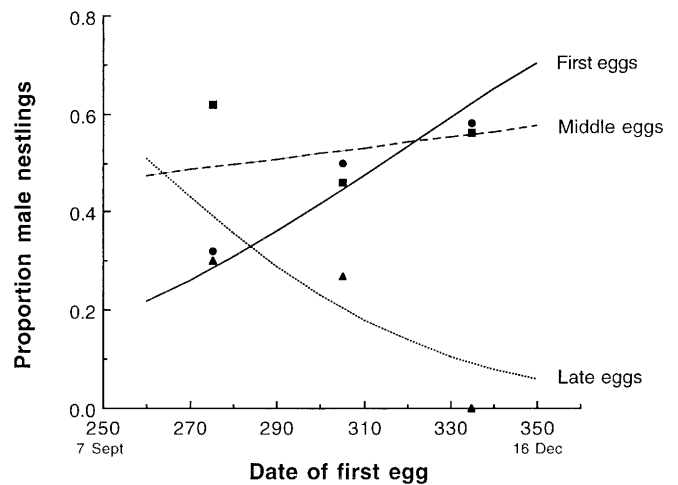


Fig. 2 Relationship between laying sequence and sex ratio over the breeding season in crimson rosella broods. The relationship for early-laid (circles, solid line), middle-laid (squares, dashed line) and late-laid (triangles, dotted line) eggs are presented separately. Lines show the predicted relationship from the GLMM model. Points show the means for clutches initiated at 30 day intervals commencing at day 260 (17 September). The number of broods used to calculate the means were: early-laid eggs (11, 12, and 9); middle-laid eggs (10, 12, and 8); and late-laid eggs (10, 11, and 4)

tionship was not statistically significant ($\chi^2_1=2.05$, $P=0.15$).

There was no evidence that the year of the study, clutch size, or relative hatching asynchrony had any effect on the sex ratio of early-, middle- and late-laid eggs (Table 2).

Female fledging mass varied with year and declined with brood size and laying date, but was not influenced

Table 2 Summary of the mixed model examining the factors influencing egg sex ratio. Brood was included as a random factor in the analysis. The significance reported is the Wald statistic calculated when the term of interest was fitted last in a model that contains all significant terms

| Final model = lay date + lay order + lay date \times lay order | | | |
|--|----------|-----------|-----------------|
| Term dropped from final model | χ^2 | <i>df</i> | <i>P</i> -value |
| Laying order \times laying date | 5.3 | 2 | 0.07 |
| Laying order \times laying date \times year | 2.3 | 6 | 0.89 |
| Laying order \times year | 7.4 | 6 | 0.29 |
| Laying order \times clutch size | 0.6 | 2 | 0.74 |
| Laying order \times hatching asynchrony | 4.0 | 2 | 0.14 |
| Clutch size | 0.8 | 1 | 0.37 |
| Hatching asynchrony | 0.5 | 1 | 0.48 |
| Year | 4.5 | 3 | 0.21 |

Table 3 Summary of mixed model examining the effect of sex and hatching rank on fledging mass of female chicks ($n=75$). Brood was included as a random factor in the analysis. The significance reported is the change-in-deviance when the term of interest is dropped from the final model

| Final model = year + lay date + brood size | | | |
|--|----------|-----------|-----------------|
| Term dropped from final model | χ^2 | <i>df</i> | <i>P</i> -value |
| Year | 12.63 | 3 | 0.006 |
| Laying date | 9.01 | 1 | 0.003 |
| Brood size | 6.16 | 1 | 0.01 |
| Hatching rank | 0.65 | 2 | 0.42 |
| Laying date \times hatching rank | 2.06 | 2 | 0.36 |

Table 4 Summary of mixed model examining the effect of sex and hatching rank on fledging mass of male chicks ($n=54$). Brood was included as a random factor in the analyses. The significance reported is the change-in-deviance when the term of interest is dropped from the final model

| Final model = year + lay date + hatching rank + lay date \times hatching rank | | | |
|---|----------|-----------|-----------------|
| Term dropped from final model | χ^2 | <i>df</i> | <i>P</i> -value |
| Year | 7.35 | 3 | 0.06 |
| Laying date \times hatching rank | 5.98 | 2 | 0.05 |
| Brood size | 1.97 | 1 | 0.16 |

by hatching rank (Table 3, Fig. 3a). In contrast, male fledging mass was influenced by an interaction between laying date and hatching rank and tended to vary with year (Table 4). In males, the fledging mass of first-hatched chicks decreased slightly over the breeding season, whereas the mass of last-hatched chicks decreased strongly over the breeding season (Fig. 3b).

Discussion

We found the population sex ratio of crimson rosella nestlings was consistently female-biased across the four

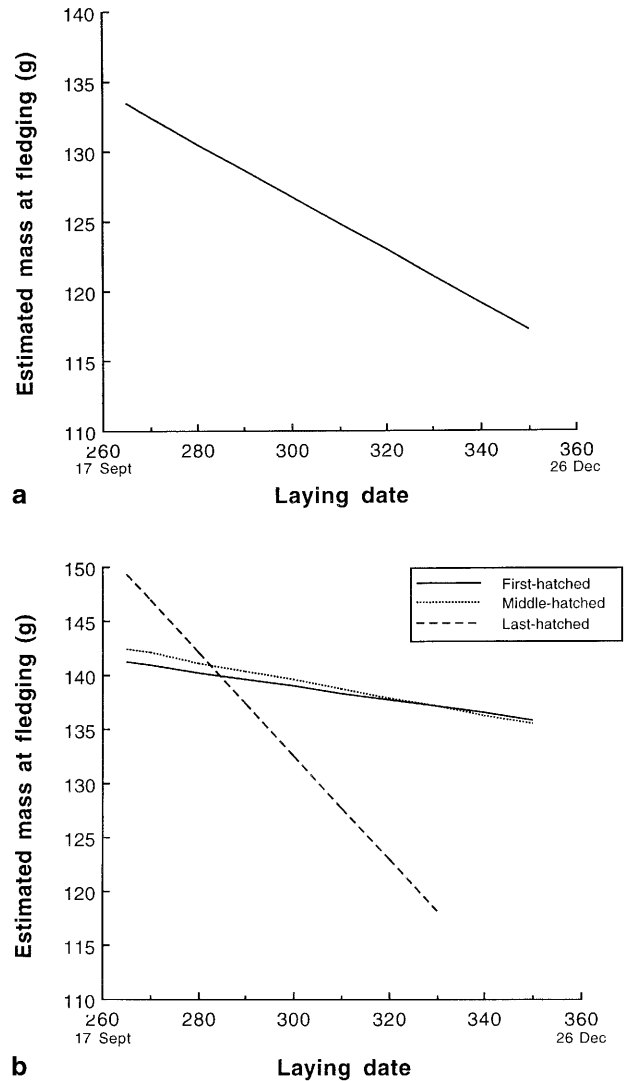


Fig. 3 The predicted relationship between fledging mass and laying date for **a** female nestlings ($n=75$), controlling for year and brood size and **b** male nestlings, plotted separately for each hatching rank (first-hatched $n=25$, middle-hatched $n=17$, last-hatched=12), and controlling for year

years of the study. However underlying this population-level bias were non-random patterns of sex allocation within broods. Rosella broods were highly female-biased early in the breeding season and the proportion of males in a brood increased over the season. In addition, laying order influenced the sex ratio of eggs within the brood. Early-laid eggs strongly followed the brood level pattern and the sex ratio increased over the breeding season. There were no statistically significant changes in the sex ratio of middle and late-laid eggs over the season, although the proportion of males in late-laid eggs fell from 0.3 to 0.0, suggesting a decrease might be detected with a larger sample. Thus, sex allocation in crimson rosellas was influenced by both clutch initiation date and laying sequence.

The female bias we observed in the study population is consistent with equal parental investment in male and

female offspring (Fisher 1930). Adult male rosellas are 15% larger in mass than females, and male chicks grow at a higher rate than females over the nestling period (Krebs 1999). Although we do not have direct data on the relative costs of male and female offspring, parents provision first-hatched male chicks more than first-hatched female chicks (Krebs et al. 1999). Thus it is likely that male chicks are more costly for parents to raise. In other species the larger sex also appears to be more costly for parents to raise because they typically have greater energetic requirements over the entire nestling period (reviewed by Anderson et al. 1993; Krijgsveld et al. 1998; but see Torres and Drummond 1999b for a counter example). Nevertheless apparent differences in parental costs have not led to consistent sex ratio biases in sexually dimorphic birds (Olsen and Cockburn 1991; Krackow 1993). However, population level biases would not be expected if other selective pressures, such as local resource competition or local resource enhancement, simultaneously favour production of the more costly sex (Cockburn et al., in press).

Since we determined the sex of nestlings approximately halfway through the nestling period our results may not reflect changes in primary sex ratio of young produced, but some pattern of systematic mortality within the brood. Although late-laid eggs were less likely to produce chicks that survived until sexing than early- or middle-laid eggs, we have no evidence that mortality changed over the breeding season as would be required to produce the observed seasonal pattern. In addition the seasonal increase in brood sex ratio was also apparent in clutches where all eggs were sexed, although the seasonal effect was not statistically significant in the smaller restricted data set. If differential mortality of eggs or young was driving the sex ratios we were observing, the seasonal increase of males in broods should have been most pronounced in late-laid eggs, which had higher overall mortality. However, this was not the case, if anything late-laid eggs were less likely to be male as the season progressed. Thus the overall changes in sex ratio observed within rosella broods are difficult to explain by any patterns of differential mortality of nestlings, and are consistent with changes in the underlying patterns of sex allocation.

It is not clear whether female rosellas adjust the sex ratio of the brood relative to the costs of reproduction. We found no evidence that brood sex ratios were influenced by maternal size or age, although our measure of female age was very crude (yearling vs 2+). If sons and daughters differ in size, females are predicted to produce less of the more costly sex if their condition prior to egg-laying is low (Wiebe and Bortolotti 1992; Gomendio et al. 1990). Female rosellas would thus be expected to produce males when in good condition and females when in poor condition. We were unable to collect data on the condition of females, however if females were in worse condition when food availability was low, inter-annual patterns of sex ratios support the idea that brood sex ratios were adjusted in a way that reduces the costs of chick rearing. In 1994, rainfall was extremely low, pre-

sumably reducing food availability (see Krebs 1998 for details). Although the sex ratios of broods did not vary significantly between years, it is noteworthy that the fewest males were produced in this year, as would be expected if females minimise the costs of reproduction by raising fewer sons.

Why does laying date influence sex ratios in rosella broods?

Seasonal changes in brood sex ratio are also commonly observed in raptors (e.g. Dijkstra et al 1990; Daan et al. 1996). For example, brood sex ratios become increasingly male-biased over the breeding season in marsh harriers *Circus aeruginosus* (Zijlstra et al. 1992), sparrowhawks *Accipiter nisus* and goshawks *A. gentilis* (Daan et al. 1996). Within raptors, the direction of seasonal changes in sex allocation across species can be explained by the differential effects of fledging date on the probability of early breeding for each sex. In marsh harriers and goshawks differences in plumage maturation suggest that the probability of breeding as a 1-year-old is higher for early fledged females, whereas in sparrowhawks, fledging date appears to influence the probability of female, but not male recruitment (Daan et al. 1996).

Differences in maturation times are likely to generate strong differences in maternal fitness. Using estimates of age-dependent mortality and mean clutch sizes for yearling and older birds, Dijkstra et al. (1990) estimated that in European kestrels, first year breeders would produce 30% more eggs over their lifetime in comparison to individuals who start to breed in their second year. Thus females obtain substantial increases in fitness through differential sex allocation when maturation times differ for each sex.

The data from crimson rosellas suggest that the seasonal patterns of sex allocation reflect the relative benefits a female obtains from early fledging. Crimson rosellas spend the first 16 months of their life in a mottled green subadult plumage, which allows 1-year-old birds to be readily identified (Forshaw 1981; Marchant and Higgins 1990; Krebs, unpublished). Female rosellas are frequently observed to breed in subadult plumage, whereas males are not. In our study population, 14% ($n=72$) of breeding pairs contained a subadult female, whereas none contained a young male. Thus, it is clear that female crimson rosellas have a much higher probability of breeding in their first year compared to males. We have no data on the influence of fledging date on the probability of becoming a first year breeder since female fledglings disperse further from their natal territory than males and were very rarely resighted (Krebs 1999). However, fledging earlier in the breeding season maximises the length of time a fledgling has to develop foraging skills, obtain a mate, and find a suitable breeding site, so it would be surprising if there was no influence of fledging date on sex ratio in species where one sex can breed in their first year. Data on captive budgerigars

suggest that fledging date, and possibly fledgling age, influence the subsequent reproductive success of 1-year-old captive budgerigars (Stamps et al. 1987), implying that early fledging may be advantageous to females in parrot societies.

Why does season and laying order influence the sex ratio of rosella eggs?

Sex-dependent hatching sequences are one of the most commonly observed patterns of sex allocation in birds (e.g. Bednarz and Hayden 1991; Dijkstra et al. 1990; Leroux and Bretagnolle 1996; Kilner 1998; Legge et al. 2001). Even when other factors, such as laying date, influence the sex ratio of broods, the effects tend to be particularly pronounced for early-laid chicks. For example in European kestrels, the percentage of males in early-laid eggs decreases over the breeding season from 67% to 34% whereas in the whole brood it drops from 57% down to 43% (Dijkstra et al. 1990).

Differing sex biases over the laying sequence occur in many species, but the reasons for these changes remain largely unexplained. Potentially, stronger sex ratio biases in early-laid eggs are simply a reflection of the costs and benefits of selective resorption of follicles, since early follicles of the undesirable sex can be reabsorbed without increasing inter-egg intervals (Krakow 1999). Alternatively, position in the laying sequence may have differing consequences for male and female chicks, leading to selection for differing patterns of sex allocation. Nager et al. (1999) demonstrated experimentally that female lesser black-backed gulls manipulated the sex of eggs in response to changes in maternal condition. When food was restricted egg size decreased over the laying sequence. Since male survival was more strongly reduced in smaller eggs, food restricted mothers, produced an increasing female bias in later-laid eggs.

In rosellas, laying sequence interacted with laying date to produce differences in the sex ratios of early-, middle- and late-laid eggs (Table 2). The seasonal increase in the proportion of males observed in a brood was mainly driven by a strong increase in early-laid eggs, and while middle-laid eggs might weakly support this pattern, late-laid eggs clearly opposed it (see Fig. 2). We found no seasonal changes in mortality that would explain the seasonal differences in the sex ratios of early- and late-laid eggs. Thus in rosellas, seasonal patterns of sex allocation appear to differ for early- and late-laid eggs. Opposite seasonal patterns of sex allocation for first- and last-laid eggs were also observed in European kestrels, although the reasons for this pattern were unexplored (Dijkstra et al. 1990).

In rosellas, seasonal changes in the fledging mass of male and female chicks suggest that the consequences of hatching rank differs for the sexes within broods. Overall, the mass at fledging of chicks did not change significantly over the breeding season (Krebs 1999), however laying date interacted with both chick sex and hatching

rank. The fledging mass of female chicks was unaffected by rank, but decreased over the breeding season. In contrast, the difference in fledging mass of early- and late-hatched male chicks diverged over the breeding season (cf. Fig. 3a, b). The mass of early- and middle-hatched males changed very little over the season whereas that of late-hatched males decreased strongly. This suggests that late-hatched males were at an increasing competitive disadvantage as the season progressed.

The disparity between early- and late-hatched male chicks may partly be the result of sibling competition. Previous work shows that early-hatched males are fed more than chicks of other hatching ranks, particularly by their fathers (Krebs et al. 1999). Thus, if early-hatched chicks are males, competitive asymmetries within the brood will be increased, a situation that appears to be especially disadvantageous for last-hatched male chicks. Our data support this interpretation, the fledging mass of male chicks decreases with date and hatching rank, whereas the mass of females of all hatching ranks decreases with date and brood size. Mothers thus appear to refrain from producing early-hatched males until late in the season, and minimise the consequences for the brood by simultaneously producing females in late-laid eggs. This suggests that the relative benefits of producing early-hatched females switches over the season in favour of producing early-hatched males, emphasising that mothers are likely to be weighing multiple selective pressure when allocating sex.

In conclusion, our analyses reveal complex patterns of sex allocation in crimson rosellas that appear to be associated with both future breeding opportunities of young and within-brood dynamics. This work highlights the need for detailed information on both the breeding biology and parental care, and the life history and demographics of a species before patterns of sex ratio variation can be adequately understood. Future work on rosellas should include experiments that evaluate the role of competitive asymmetries within broods and parental provisioning patterns in determining seasonal changes in fledging mass and date-dependent recruitment by male and female nestlings.

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