Current Biology *21*, 1744–1747, October 25, 2011 ©2011 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2011.08.064

Report

Adaptive Secondary Sex Ratio Adjustments via Sex-Specific Infanticide in a Bird

Robert Heinsohn,[1],* Naomi E. Langmore,[2]
Andrew Cockburn,[2] and Hanna Kokko[2]
[1]Fenner School of Environment and Society
[2]Research School of Biology
Australian National University, Canberra, ACT 0200, Australia

Summary

Infanticide is easiest to understand when it involves killing the offspring of others [1], but a parent may also kill its own offspring if the sacrifice of currently dependent young leads to higher survival of brood mates [2] or an improvement in the parent's likely future reproduction [3]. However, sex-specific infanticide by parents of their own offspring, although occurring in some human societies [4], is rare across species. Its rarity may be because killing one sex combines wasted parental effort with consequent biases in population sex ratios that are detrimental for the fitness of the overproduced sex [5–7]. We show that killing male offspring can be advantageous to *Eclectus* parrot (*Eclectus roratus*) mothers even though frequency-dependent selection then elevates the reproductive value of sons above that of daughters. In poorer-quality nest hollows, broods with a single female nestling had higher reproductive value than broods in which the female had a younger brother. Our data demonstrate frequent targeted removal of male nestlings within 3 days of hatching in these specific brood types and nesting conditions. The ability of *Eclectus* parrots to perceive the sex of their offspring relatively early may favor decisions to kill one sex before further investment in parental care.

Results and Discussion

We found several lines of evidence of adaptive posthatching sex-specific infanticide over our 8 year study of wild *Eclectus* parrots (*Eclectus roratus*). This follows previous evidence that captive *Eclectus* parrots have strong control over the primary sex ratio of their offspring and often produce long unbroken runs of one sex (e.g., 30 males in a row) [8]. Further sex-specific infanticide may be facilitated in this species, because in contrast to the sexually monomorphic nestlings found in most birds [9], nestling *Eclectus* parrots develop sex-specific down colors and then molt directly into their dramatically sexually dichromatic adult plumage [10]. Their gender is obvious at a very early age and potentially allows for secondary corrections of initial sex ratios at an early enough stage to be cost effective [7, 11] should these prove suboptimal for any reason (see Supplemental Experimental Procedures available online).

The sex ratio in the wild was close to parity among nests in which both chicks were reared (proportion male = 0.51, n = 87 clutches). However, parents frequently reared just a single chick, despite always laying two eggs and hatching both of them if they are fertile. Brood reduction occurred in two distinct phases with 38% of nestling deaths occurring within 3 days of hatching and the remainder of deaths occurring more gradually over the 11–12 week nestling period (Figure 1A).

Early phase brood reduction was male-biased and was influenced by nest hollow quality; male offspring up to 3 days old tended to disappear from nests that were prone to flooding in heavy rain (generalized linear mixed model [GLMM], χ^2_1 = 4.41, p = 0.011, Figure 1B). Heavy rain during the breeding season can harm eggs and drown nestlings hatched in nest hollows that do not drain adequately. Females with hollows less prone to flooding enjoy longer periods of nest availability to rear their offspring and are also attended by more males [12]. Male numbers are important because females defend hollows to the exclusion of all other activities and rely entirely on males for their own food and that of their offspring. Although there is little size dimorphism in this species either as nestlings or as adults, female chicks fledge about 7 days sooner than males (Supplemental Experimental Procedures), suggesting that breeding females with flood-prone hollows should favor female offspring.

Importantly, the early disappearance of male nestlings in flood-prone hollows occurred before any of the hollows flooded. Instead, four lines of evidence suggest that their disappearance was due to adaptive infanticide. First, at seven of the nests suffering early brood reduction we found the corpse of the dead chick. All were male (confirmed using molecular sexing [13]) and were found either at the edge of the nest hollow or at the base of the tree, and most (4/7) had bruising consistent with peck marks from adult birds. Chicks of this age are altricial, neither sex has a size advantage or special weaponry that would have allowed siblicide [14, 15], and no overt aggression between nestlings was observed in over 100 hr of observation at the nest (Supplemental Experimental Procedures). There was neither evidence (e.g., emaciation) that the young chicks were being discarded because they had already died, nor that males grow more quickly than females and are therefore more likely to succumb in harsher conditions [16] (Supplemental Experimental Procedures). Adult males were unlikely to be involved in brood reduction. The breeding female never leaves the nest and prevents male access [17] and is therefore the sole candidate for killing of the chicks.

Second, although females that were using a nest for the first time produced a balanced sex ratio regardless of hollow quality, females who were reusing a flood-prone nest, and hence had previous experience that their nest was vulnerable to flooding, were more likely to lose sons from the nest (GLMM, χ^2_1 = 7.38, p = 0.007, Figure 1C).

Third, we confirmed experimentally a causative effect of hollow quality by erecting protective covers over cavities. This improved hollow dryness and caused females in previously wet hollows to have fewer reduced broods (6/13 broods in flood-prone hollows were reduced to one nestling compared with 1/11 after experimental improvement of hollows) and a higher proportion of sons (GLMM, χ^2_1 = 5.61, p = 0.012, Figure 1D). This effect was only apparent after 2 years, suggesting that females needed time to respond to the hollow

---

*Correspondence: robert.heinsohn@anu.edu.au

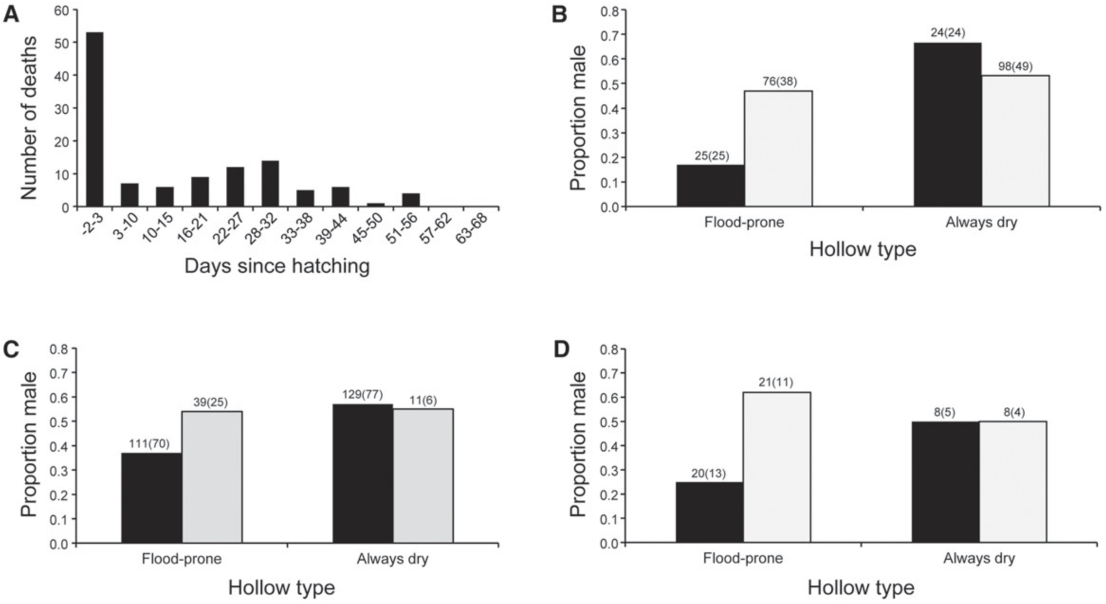

Figure 1. Sex-Specific Mortality of Nestlings

(A) Number of nestling deaths versus days since hatching (n = 154 broods).

(B) Proportion of male nestlings in one-nestling broods (black bars) versus two-nestling broods (gray bars).

(C) Sex ratio of nestlings of experienced (black bars) and inexperienced (gray bars) breeding females.

(D) Sex ratio of broods before (black bars) and after (gray bars) experimental improvement of dryness of nest hollows. “Always dry” refers to hollows that are available for nesting for the whole breeding season, and “flood-prone” refers to hollows that may flood during the breeding season. Sample sizes of nestlings (broods) are shown above bars.

changes. Our long-term data further substantiate this experimental result by showing that ten females that changed nest hollows naturally adjusted their nestling sex ratios according to hollow wetness, independently of other factors such as female age or weather patterns (Wilcoxon signed-ranks test, two-tailed: T = 3.50, p = 0.014; [12]).

Finally, because not all missing chicks were found and sexed, we constructed statistical models that are able to account for censored data (Supplemental Experimental Procedures). These show that the observed patterns of sex bias among living chicks 3 days after hatching are best explained by models that specifically incorporate a higher probability of death for the second-hatched male chicks in nests where they had an older sister and where the nest was prone to flooding. Simpler models that did not target the vulnerability of these particular males only, for example, by elevating the vulnerability of all male nestlings or all second-hatched male nestlings, failed to reproduce the observed data, which indicates that the disappearance of male chicks happens in a much more targeted fashion than a simple sex difference in mortality would predict. The models rule out, for example, any possibility that male nestlings are generally more susceptible to disease in wet hollows. Models that rely on primary sex ratio biases alone similarly failed to account for the observed distribution of live chicks, although one likely model incorporates both primary and secondary sex ratio adjustments (for details see Supplemental Experimental Procedures and Figures S2 and S3).

We have uncovered a compelling adaptive reason to explain why *Eclectus* parrot mothers in flood-prone nests are likely to kill their male offspring. In these nests, there were some broods in which the younger brother of the female nestling was not killed. These broods (referred to as FM for female hatched first, male second) were significantly less productive than broods with only a single female nestling (restricted maximum likelihood [REML] $\chi^2_5 = 36.3$, $p < 0.001$). Importantly, this advantage to raising just a single female in these circumstances survives incorporation of the enhanced reproductive value of males from their relative scarcity at fledging (29% above that of females based on the population-wide fledging sex ratio of 43.7% male, see Experimental Procedures, Figure 2). Overall, broods containing two nestlings were less productive in wet hollows (Figure 2), because these nests have fewer males on average to feed nestlings [12] and because of the deaths caused by flooding. Male nestlings had higher mortality than females, and second-hatched nestlings had higher mortality than first-hatched nestlings with the combined effect that broods with a male hatched second (FM or MM) had the lowest success. This was especially true in flood-prone nests where broods with males hatched second suffered higher losses from flooding (Supplemental Experimental Procedures). However, only FM broods in flood-prone hollows presented the breeding female with the opportunity to increase her productivity by eliminating male nestlings and raising a single, faster-fledging female (Figure 2).

Our data provide strong support for adaptive sex-specific infanticide in this species. They explain why sex-specific infanticide is not maladaptive despite the wasted reproductive effort and the elimination of the sex that becomes more valuable because killing makes it the scarce sex. Our argument remains valid when productivity is weighted with the higher reproductive value that the male might have enjoyed had it survived, which according to simple interpretations of frequency-dependent selection should make parents favor (rather than kill) sons [5, 7]. Population sex ratios do not self-evidently evolve toward unity, however [7], and our case

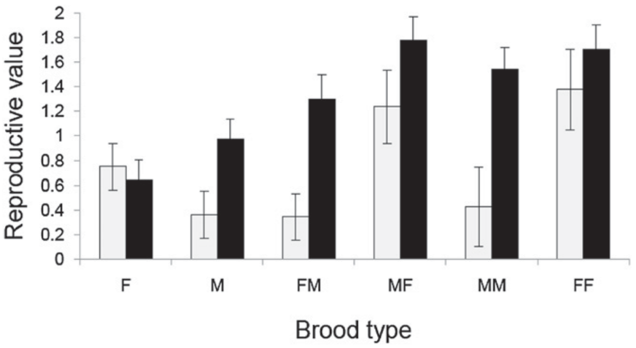

Figure 2. Predicted Reproductive Value of Broods

Predicted reproductive value (n female fledglings + 1.29×n male fledglings) ± standard error of broods of varying sex composition in flood-prone (gray bars) and always dry nests (black bars). The following abbreviations are used: M, male only; F, female only; FM, female hatched first, male second; MF, male, female; MM, male, male; FF, female, female. Reproductive value accounts for the relative scarcity of males at fledging. Full restricted maximum likelihood model: brood composition $\chi^2_5 = 36.3$, $p < 0.001$; hollow dryness $\chi^2_1 = 5.1$, $p = 0.032$; year of study $\chi^2_7 = 15.9$, $p = 0.033$.

shows that limited and targeted sex-specific infanticide, based on the birds' ability to perceive the sex of their offspring at an early age and past experience with ecological conditions, can be adaptive by preventing wasteful investment in parental care.

Experimental Procedures

Field Data

This research was conducted under license from the Australian National University Animal Ethics Committee (permit No: C.R.E.35.04). See Supplemental Information for a description of the study site and early sexual dimorphism of nestlings. Two hundred eighty-one nestlings (178 broods at 42 nest hollows) were sexed, and their survival was documented weekly over the 11–12 week nestling period over 8 years. One hundred thirty-seven of these nestlings (48.8%) were male. Seventy-six out of 174 fledglings (43.7%) were male. Most analyses presented here were carried out on broods from experienced females, defined as those who had already occupied their breeding hollows for one season or more (240 nestlings from 147 broods). All clutches in this sample were initially of two eggs, the usual clutch size for *Eclectus* parrots. These were examined for fertility and developmental stage (by "candling" the egg with a light) when first encountered and again approximately 3 days before hatching. Eleven out of 147 broods from experienced females had one infertile egg. Forty-nine broods were further reduced to just one egg or nestling within ± 3 days of hatching. In all cases, this occurred after the last examination of eggs and before nestlings reached 3 days old. The hollow was always dry at the time of these deaths, confirming that these deaths did not occur as a result of flooding of the nest hollow or damp conditions. Eighty-seven clutches resulted in broods of two nestlings that survived for longer. We refer to broods that were reduced to one nestling by 3 days posthatching as "one-nestling broods" and those that kept two nestlings for longer as "two-nestling broods."

Nest Hollow Quality and Experimental Improvement

Breeding females occupy and defend the same hollow exclusively over multiple years [12, 17, 18]. Whether the hollow was flooded (contained free-standing water) or dry enough to be used as a nest was recorded on each climb; we used one value for each month between July and February (eight values) each breeding season to estimate the proportion of time the hollow was dry enough to be used for nesting. One measure per month is sufficient to estimate a hollow's availability for nesting because free-standing water in a hollow usually takes weeks to dry. A "damp" hollow without free-standing water was considered potentially usable for nesting. We used the proportion of time a nest hollow was observed to be dry over the entire study as a continuous variable in analyses and the following categories for visual presentation of data in Figures 1B, 1C, and 1D: always dry = available for nesting for whole breeding season, flood-prone = hollows that were observed to flood at least once during the study (range = 60%–95% availability for nesting).

We improved the dryness of 11 natural nest hollows (eight flood-prone, three always dry) by attaching waterproof aluminum roofs (approximately 0.16 m^2) to the tree trunk 0.5 m above the hollow entrance. Nine of these hollows (seven flood-prone, two always dry) continued to be used for at least 2 years following modification (two modified hollows were lost as a result of natural collapse of the hollow floor). All nine nests remained completely dry for the remainder of the study. We compared the sex ratios of 57 nestlings hatched to the same nine females (verified via their leg bands or DNA; [18]) for the 2 years before the hollow improvements (n = 28) and 2 years after (n = 29).

Data Analysis

We used generalized (nonnormal error) and linear mixed models (normal error) utilizing the GLMM and REML procedures in Genstat 12.2 (VSN International Ltd) for all analyses concerning sex ratios (proportion of males, Figures 1B, 1C, and 1D) and survival of nestlings and reproductive value of brood types (Figure 2; see Supplemental Experimental Procedures).

We used randomization techniques accounting for censored data to evaluate the underlying process responsible for early loss of nestlings. The data comprise 42 cases with censored (missing) data where only one nestling could be sexed and 87 cases with data for two-nestling broods. The models were aimed at determining the type of process that can account for (1) the higher proportion of male nestlings in drier hollows (logistic regression $\chi^2_1 = 3.94$, $p = 0.047$, Figure S2) in one-nestling broods and (2) a similar pattern for the second-hatched nestlings only (logistic regression $\chi^2_1 = 3.98$, $p = 0.046$, Figure S2) in two-nestling broods. Modeling each process meant distributing the 42 deaths among the 129 broods. In the null model, the deaths are distributed randomly, whereas in all other models the 42 deaths were more likely to target some nestlings than others. Importantly, the models allow for single chick broods to be created via random deaths as well as through targeted infanticide and for some broods that might be more productive with infanticide to retain their two nestlings. *Eclectus* parrots are also known to be able to bias the primary sex ratio [8], and we therefore investigated, via a tailor-made hybrid approach that combines randomization tests with a model selection procedure, whether primary sex ratio variation alone, infanticide alone, or both together could produce values similar to those observed in the real data. For full details of model development see Supplemental Experimental Procedures and Figures S2 and S3.

Supplemental Information

Supplemental Information includes three figures and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2011.08.064.

Acknowledgments

We thank M. Hall, S. Murphy, A. Nathan, D. Wilson, and especially C. Blackman and S. Legge for assistance with field work; P. Huybers and E. Huybers for logistical support; and R. Cunningham, C. Field, M. Magrath, and A. Welsh for discussion of statistical analyses. This study was funded by the Australian Research Council, National Geographic Society, and Winifred Violet Scott Foundation.

Received: May 12, 2011
Revised: August 12, 2011
Accepted: August 30, 2011

References

1. Hrdy, S.B. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. Ethol. Sociobiol. *1*, 13–40.
2. Klug, H., Lindström, K., and St Mary, C.M. (2006). Parents benefit from eating offspring: density-dependent egg survivorship compensates for filial cannibalism. Evolution *60*, 2087–2095.
3. Klug, H., and Lindström, K. (2008). Hurry-up and hatch: selective filial cannibalism of slower developing eggs. Biol. Lett. *4*, 160–162.

4. Hesketh, T., and Xing, Z.W. (2006). Abnormal sex ratios in human populations: causes and consequences. Proc. Natl. Acad. Sci. USA *103*, 13271–13275.
5. Fisher, R.A. (1930). The Genetical Theory of Natural Selection (Oxford: Oxford University press).
6. Frank, S.A. (1990). Sex allocation theory for birds and mammals. Annu. Rev. Ecol. Syst. *21*, 13–55.
7. West, S.A. (2009). Sex Allocation (Princeton: Princeton University Press).
8. Heinsohn, R., Legge, S., and Barry, S. (1997). Extreme bias in sex allocation in Eclectus parrots. Proc. R. Soc. Lond. B Biol. Sci. *264*, 1325–1329.
9. Butcher, G.S., and Rohwer, S. (1989). The evolution of conspicuous and distinctive coloration for communication in birds. In Current Ornithology, *Volume 6*, D.M. Power, ed. (New York: Plenum).
10. Heinsohn, R., Legge, S., and Endler, J.A. (2005). Extreme reversed sexual dichromatism in a bird without sex role reversal. Science *309*, 617–619.
11. Maynard Smith, J. (1980). A new theory of sexual investment. Behav. Ecol. Sociobiol. *7*, 247–251.
12. Heinsohn, R. (2008). The ecological basis of unusual sex roles in reverse-dichromatic eclectus parrots. Anim. Behav. *76*, 97–103.
13. Griffiths, R., Double, M.C., Orr, K., and Dawson, R.J.G. (1998). A DNA test to sex most birds. Mol. Ecol. *7*, 1071–1075.
14. Bortolotti, G.R. (1986). Influence of sibling competition on nestling sex-ratios of sexually dimorphic birds. Am. Nat. *127*, 495–507.
15. Mock, D.W., and Parker, G.A. (1997). The Evolution of Sibling Rivalry (Oxford: Oxford University press).
16. Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. (1985). Parental investment and sex differences in juvenile birds and mammals. Nature *313*, 131–133.
17. Heinsohn, R., and Legge, S. (2003). Breeding biology of the reverse-dichromatic, co-operative parrot Eclectus roratus. J. Zool. *259*, 197–208.
18. Heinsohn, R., Ebert, D., Legge, S., and Peakall, R. (2007). Genetic evidence for cooperative polyandry in reverse dichromatic Eclectus parrots. Anim. Behav. *74*, 1047–1054.