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Hatchling sex ratio and female mating status in the great reed warbler, *Acrocephalus arundinaceus* (Aves, Passeriformes): further evidence for offspring sex ratio manipulation

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Abstract
Offspring sex in birds is maternally determined, thus females are expected to vary brood sex ratio adaptively in response to various environmental and/or genetic conditions preferring one sex to the other sex. However, recent studies provide controversial evidence showing mixed support for adaptive sex manipulation theory. One problem may lie in the fact that only sex ratios at fledging have been used in many of these studies, ignoring post-hatching sex-biased mortality. To validate these results, some authors call for replication of previous researches. Here we examined hatchling sex ratio variation in relation to female mating status in a local population of facultatively polygynous great reed warblers *Acrocephalus arundinaceus* in Central Europe. In agreement with results of previous works, we found that monogamous and primary females had a higher proportion of sons in their broods than secondary females. These results provide further evidence that great reed warbler females manipulate the sex ratio of their offspring in response to their social status.

Keywords: *Great reed warbler, sex ratio, social polygyny*

Introduction

In birds, where the sex of offspring is maternally determined, females are expected to adjust the primary sex ratio according to environmental and genetic conditions, which affect survival of males and females differently (Trivers & Willard 1973; Charnov 1982). The adaptive significance of this behaviour lies in differences in future reproductive value of nestlings of one sex relatively to nestlings of the other sex. In agreement with these expectations, many studies have shown that females may produce adjusted brood sex ratio as a response to their body condition, female mating status, timing of breeding and/or male attractiveness (see Hasselquist & Kempenaers 2002; Komdeur & Pen 2002 for previous reviews; Albrecht & Johnson 2002; Griggio et al. 2002; Velando 2002; Gwinner & Schwabl 2005; Husby et al. 2006, Freed et al. 2009; Du & Lu 2010; Philip et al. 2010). However, some other studies have failed to find such relationships in birds, even in the same species (Lessells et al. 1996; Hartley et al. 1999; Radford & Blakey 2000; South & Wright 2002; Ewen et al. 2004; Johnson et al. 2005; Maddox & Weatherhead 2009), questioning the adaptive brood sex ratio manipulation. One problem may lie in the fact that only sex ratios at fledging have been used in many of these studies, ignoring post-hatching sex-biased mortality which can be caused by differential provisioning of male and female offspring or sibling competition over food when sexual size differences are exhibited (Droge et al. 1991; Teather 1992; Clotfelter 1996; Hasselquist & Kempenaers 2002; Gonzáles-Solís et al. 2005; Verhulst et al. 2006). The rationale is that less favoured or smaller sex may be more exposed to starvation during food shortage periods leading to their death than the other sex (Westerdahl et al. 2000). On the other hand, larger sex can also

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be sensitive to starvation because it requires more food and energy to be raised (Teather & Wetherhead 1988; Anderson et al. 1993; Westerdahl et al. 2000; Maddox & Weatherhead 2009). As a consequence, many nestlings that died before they could be sexed did not have to be taken into account in studies in which only sex ratios at fledging were recorded. To validate these results, some authors call for replication of previous researches (Palmer 2000; Kelly 2006; Maddox & Weatherhead 2009).

Here we examined sex ratio variation in relation to female mating status in a local population of facultatively polygynous great reed warblers in Central Europe. Several previous studies have already provided some evidence that females of polygynous birds may be able to manipulate the sex ratio of their offspring in response to their mating status (Patterson et al. 1980; Nishiumi 1998; Westerdahl et al. 2000; Albrecht & Johnson 2002). They showed that higher ranking females (i.e. monogamous and primary females) had a higher proportion of sons in their broods than females of lower (secondary) harem status. The adaptive explanation for these male-biased sex ratios is that monogamous and primary females have more resources for nestling provisioning than secondary females because they receive normally more male feeding assistance than receive secondary females (Lifjeld & Slagsvold 1989; Sejberg et al. 2000; Westerdahl et al. 2000). As monogamous and primary females have better body condition and produce more fledglings than secondary females in some polygynous species (Johnson et al. 1993; Forstmeier et al. 2001; Griggio et al. 2003), an alternative explanation is that overproduction of sons in the monogamous and primary nests may be related to female intrinsic quality. However, because mainly fledging sex ratios have been analysed in these previous studies, proposed explanations may be still debatable. Therefore, to exclude possible effect of sex-biased chick mortality, we collected blood samples 1–2 days after all chicks in the brood have hatched (hatchling sex ratio). Due to high sensitivity of hatchlings, the study was conducted only in one breeding season. In accordance with the aforementioned studies we predicted that monogamous and primary females will have a higher proportion of sons in their broods than secondary females and that overproduction of sons in nests of monogamous and primary females will correlate with female body condition. Finally, as there is known direct relationship between offspring sex ratio, clutch size and timing of breeding in many species (i. e. Dyrcz & Cichoń 2009; Goodenough et al. 2009; Jones et al. 2010), and secondary females usually start breeding later than monogamous and primary females in polygynous species (Hansson et al. 1997; Griggio et al. 2003), we also predicted seasonal variations in clutch size and proportion of sons per brood in the great reed warbler.

Materials and methods

We conducted this study during breeding period 2009 on a local population of great reed warblers breeding at fishponds near Štúrovo, south-western Slovakia (47°51' N, 18°36' E, 115 m a. s. l.). This is a medium sized facultatively polygynous passerine that breeds in reed beds over much of the Palearctic temperate region (Cramp 1992). Males are larger than females, but female body condition did not differ between monogamous, primary and secondary females in the study population (Trnka & Prokop 2010; Trnka & Prokop 2011). The rate of polygyny in this species varies between 8–43% (Hasselquist 1998; Leisler & Wink 2000; Trnka et al. 2010). Socially polygynous males in our study area form pair bonds almost exclusively with two females only. The nestlings are sensitive to cold and shortage of food and many broods have failed during long cool weather periods in the study area (A. Trnka, unpublished).

Early in the breeding season (from the end of April to mid-May), we mist netted the majority of territorial males. Females were caught during early egg incubation stage, one or two days after clutch completion, not to disturb them during egg laying which could lead to nest desertion. Moreover, this procedure was necessery to avoid the possibility influencing sex ratios by handling the females before or during egg laying. All captured birds we marked with both aluminium and colour rings for identification, measured and weighed. We calculated the physical condition of each bird using residuals from the regression of body mass against length of right wing as a body size indicator (see also Trnka & Prokop 2010). To locate great reed warbler nests, we systematically searched the reed beds at 4–5 day intervals from May to late June. This resulted in detection of most (or at least 95%) of active nests in the study area. We determined the mating status of each male and female on the basis of captures of birds at their nests and direct observations of colour-ringed birds defending their nests or feeding young. We defined the status of females as status when they were laying or incubating eggs, i.e. at the time closest to female pre-laying and laying phases when they may manipulate sex ratio of their offspring and when we were capable to determine their actual social status. This also eliminated the effect of possible change of female nesting status during the season caused by predation of primary nest (see also Sejberg et al. 2000).

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Overall 14 nests from a total of 51 nests found in the study area in 2009 were depredated (two nests), abandoned (four nests) or successfully parasitized by the common cuckoo *Cuculus canorus* during the egg stage (eight nests). Of the remaining successfully hatched nests, 19 were monogamous, 8 primary and 10 nests secondary. The rate of natural cuckoo parasitism in the study area in 2009 reached 29.4% (Trnka, unpublished data).

The chicks were sampled for sexing when approximately 1–2 days old. A small drop of blood was collected from each nestling by means of foot-vein puncture and preserved in 96.5% ethanol. Neither chick has died or nest depredated during two days after blood sampling was realized. Of 164 eggs that survived the incubation period, 5.5% failed to hatch. Seven (4.3%) of them were sterile, thus we could not determine their sex. However, when we compared the proportion of sons in nests with and without unhatched eggs (0.609 ± 0.23, $n = 7$ nests and 0.488 ± 0.24, $n = 30$ nests, respectively), no difference was found between them (Mann-Whitney U-test: $U = 0.72$, $P = 0.2$). Three of 37 tested nests were unsuccessfully parasitized by the cuckoo (i.e. cuckoo egg was ejected from nest). As cuckoos typically remove one, sometimes two host eggs before depositing their own (Davies & Brooke 1989), at least in these cases this might bias our sex ratio estimates. No other egg losses we found in remaining nests. We are confident, therefore, that the sex ratio we measured should be close to the primary sex ratio. Hatchling sex ratio was calculated as a number of hatched males divided by the number of all hatched chicks in each brood.

DNA was isolated from blood samples using SV Genomic DNA Purification kit (Promega) or NucleoSpin Tissue (Macherey-Nagel) following the manufacturer's protocol. PCR-based technique, which applies sexual differences in CHD-Z and CHD-W genes (chromo-helicase-DNA-binding) located on the sex chromosomes, was used for DNA sexing. To amplify CHD genes we used P2 and P8 primers (Griffiths et al. 1998). PCR was performed in a total volume of 10 μL containing 1x BioTherm^{TM} buffer (Genecraft, Germany), 1.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.2 mM of each primer, 0.5 units of BioTherm^{TM} *Taq* DNA polymerase (Genecraft, Germany) and 2 μL of DNA. Amplification involved an initial cycle of denaturation at 95°C for 3 min, and 35 subsequent cycles of 94°C for 40 s, 49°C for 30 s and 72°C for 30 s, followed by a final extension step at 72°C for 5 min. PCR products were separated by electrophoresis on 2% agarose gel visualized with GoldView.

To compare differences between breeding variables and body condition of monogamous, primary and secondary females, one-way ANOVA was used. Data that were not normally distributed were $\log_{10}$ (x+1) transformed to achieve normality. Generalized Linear Mixed Model (GLMM) with binary error distribution and logit link function and the identity of the brood as a random effect was used to examine differences in sex ratios between monogamous great reed warbler nests and nests of primary and secondary status. The probability of becoming a particular sex was defined with dependent variable, social status was an independent categorical predictor, and female body condition and laying date were treated as covariates. Model selection was based on Akaike information criterion (AIC), corrected for low sample size following the recommendations of Burnham & Anderson (2002). Second-order Akaike information criterion (AIC_c) values were calculated using the package MuMIn implemented in R 2.12.0 (R Development Core Team 2010). Models were ranked from best to worst using ΔAIC_c. For the top candidate models that provided substantial support ($\Delta AIC_c \leq 2$), we applied model averaging (Burnham & Anderson 2002) to identify the relative importance of each model term in predicting the probability of becoming of a male and to estimate effect sizes of the predictors. The z-tests were used from the GLMM output. All statistical tests were two-tailed.

Results

We determined the sex of 155 hatchlings from 37 nests. The overall hatchling sex ratio did not differ significantly from parity (0.503, binomial test, $P = 1.0$). There were no differences in laying date, brood size and body condition between socially monogamous, primary and secondary females ($F_{2,34} = 1.06$, 1.44 and 0.16, $P = 0.36$, 0.25 and 0.85, $n_1 = 19$, $n_2 = 8$ and $n_3 = 10$, respectively). The most parsimonious GLMM based on the AIC_c included social status (Table I). However, as five top candidate models had a substantial support ($\Delta_i \leq 2$; Table I), we employed model averaging in order to obtain reliable parameter estimates. It showed that only the social status appeared in all models as an important predictor of brood sex ratio, having high Akaike weight ($w_i = 1$) and 95% CI of its parameter estimate, which did not include zero.

Thus, hatchling sex ratios in nests of monogamous and primary great reed warblers were significantly male-biased ($z = 3.58$ and 2.51, $P = 0.0003$ and 0.012, respectively), whereas females of secondary mating status had a higher proportion of daughters in their clutches (Figure 1). All other potential predictors (see above) were not important, because 95% CIs of their parameter estimates included zero.

Table I. Selection of Generalized Linear Mixed Model (GLMM) explaining variation in great reed warbler brood sex ratio based on AIC_c. Explanatory variables included social status (monogamous, primary and secondary), brood size, laying date and female condition as fixed factor and the identity of the brood as a random factor. K – number of parameters in the model (incl. the random factor and intercept); $\Delta_i = AIC_{c(i)} - AIC_{c(min)}$, the most parsimonious model in bold.

Fixed effects in the model	K	AIC_c	Δ_i	w_i
social status	**3**	**208.55**	**0.00**	**0.32**
brood size + social status	4	209.3	0.75	0.22
brood size + laying date + social status	5	209.69	1.14	0.18
female condition + status	4	209.87	1.33	0.16
laying date + social status	4	210.4	1.85	0.13

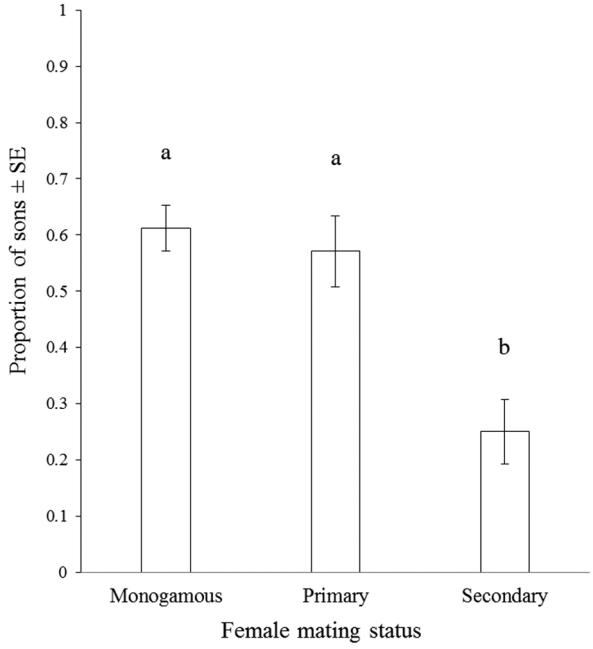

Figure 1. Hatchling sex ratio (m/(m+f)) in nests of monogamous and primary and secondary polygynous great reed warbler females.

Discussion

As predicted, monogamous and primary great reed warbler females produced a higher proportion of sons in their clutches than did secondary females in our study population. Thus, our data corroborate the results of previous studies on the yellow-headed blackbird *Xanthocephalus xanthocephalus* (Patterson et al. 1980), oriental reed warbler *Acrocephalus orientalis* (Nishiumi et al. 1996; Nishiumi 1998), house wren *Troglodytes aedon* (Albrecht & Johnson 2002) as well as earlier work on great reed warblers studied in Sweden (Westerdahl et al. 2000) that proposed adaptive explanation for observed patterns of sex ratios. This difference may lie in differences in resources for nestling provisioning that are higher at primary than secondary nests, due to greater feeding assistance of males at primary nests and in different costs imposed by sons and daughters (Trivers & Willard 1973; Bensch & Hasselquist 1994; Westerdahl et al. 2000). On the other hand, polygynous great reed warbler males are known to give assistance to their primary females similarly to that provided by monogamous males to their females (Sejberg et al. 2000). Moreover, four of eight tested primary females started lay their first egg at least six days before secondary female, and thus they did not have to be definitely aware of the presence of secondary female in the territory at the time when laying eggs. This also may partially explain similar hatchling sex ratio between monogamous and primary females found in our study.

However, because in previous studies mainly fledging sex ratios have been examined, it is not quite clear from existing findings if biased sex ratios resulted exclusively from female manipulation of offspring sex at laying or whether they might also result from sex-biased nestling mortality (Hasselquist & Kempenaers 2002; Gonzáles-Solís et al. 2005; Verhulst et al. 2006). In our study, however, we investigated brood sex ratio at hatching. Moreover, due to a very low proportion of unhatched (undetermined) eggs in examined nests, we can consider this sex ratio to be very close to the primary sex ratio. Therefore, our findings should not be confounded by sex-specific mortality in the brood after hatching. Thus, in spite of the small sample size, these results provide further evidence that great reed warbler females manipulate the sex ratio of their offspring in response to their rank in the harem.

Of course, we are aware of a smaller sample size considered in this study and that our data were collected during only one breeding season. Although sex ratio may vary from season to season (Ewen et al. 2004), no significant variation has been shown in Great reed warbler offspring sex ratio among years in previous extensive studies (Westerdahl et al. 1997; Dyrcz & Cichoń 2009). Moreover, our results are absolutely consistent with findings of these previous studies (Westerdahl et al. 2000) that are based on a much larger sample size. We believe, therefore, the obtained results reflect general pattern of biased hatchling sex ratio in relation to female mating status in our study population. However, further studies examining hatchling sex ratio from nests of second-mated great reed warbler females are welcome.

Furthermore, we found no differences in selected physical and breeding parameters between monogamous, primary and secondary females that would provide other mechanistic reasons for why secondary females had a lower proportion of sons in their

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broods than monogamous and primary females in our study population. One would argue that female biased sex ratio of secondary females could be influenced by breeding season because secondary females tend to initiate breeding later than primary females (Hansson et al. 1997; Trnka & Prokop 2010). Seasonal changes in brood sex ratios have been documented in many other species (for review see Dyrcz & Cichoń 2009). Nevertheless, no changes in sex ratio with a progress of breeding season were found in our and other great reed warbler populations (Westerdhal et al. 2000; Dyrcz & Cichoń 2009). On the other hand, negative relationship between brood size and time of season suggests that females generally reduce brood size as a response to less favourable feeding conditions later in season. These patterns were found also in other passerines (e.g., Goodenough et al. 2009; Jones et al. 2010). Therefore, reduced clutch sizes seem to be more effective strategies how to avoid starvation compared to relatively discrete manipulations with brood sex ratio.

Similarly, there could be expected the effect of female condition on offspring sex ratio where females in poor physical condition should produce more of the cheaper (smaller) sex (daughters) (Trivers & Willard 1973). We found no relationship between female physical condition and hatchling sex ratio in broods in our study population. However, because of generally low variability of physical condition between great reed warbler females, no definite conclusion can be made without experimental manipulation of female condition, and further research in this area is required.

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References

Albrecht DJ, Johnson LS. 2002. Manipulation of offspring sex ratio by second-mated female house wrens. Proceeding of the Royal Society of London, Ser. B 269:461–465.

Anderson DJ, Reeve J, Gormez JEM, Weathers WW, Hutson S, Cunningham HV, Bird DM. 1993. Sexual size dimorphism and food requirements of nestling birds. Canadian Journal of Zoology 71:2541–2545.

Bensch S, Hasselquist D. 1994. Higher rate of nest loss among primary than secondary females: infanticide in the great reed warbler? Behavioural Ecology and Sociobiology 35:309–317.

Burnham KP, Anderson DR 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Berlin: Springer-Verlag.

Charnov EL. 1982. The theory of sex allocation. Princeton: Princeton University Press.

Clotfelter ED 1996. Mechanism of facultaive sex-ratio variation in zebra finches (*Taeniopygia guttata*). Auk 113:441–449.

Cramp S. 1992. The Birds of the Western Palearctic, Vol. 6. Oxford: Oxford University Press.

Davies NB, Brooke ML. 1989. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. Journal of Animal Ecology 58:207–224.

Droge D, Gowaty PA, Weathers W. 1991. Sex-biased provisioning: a test for differences in field metabolic rates of nestling eastern bluebirds. Condor 93:793–798.

Du B, Lu X. 2010. Sex allocation and paternity in a cooperatively breeding passerine: evidence for the male attractiveness hypothesis? Behavioural Ecology and Sociobiology 64:1631–1639.

Dyrcz A, Cichoń M. 2009. Sex-specific fledgling success and brood sex ratio in the great reed warbler (*Acrocephalus arundinaceus*). Journal of Ornithology 150:839–844.

Ewen JG, Cassey P, Møller, AP. 2004. Facultative primary sex ratio variation: a lack of evidence in birds? Proceeding of the Royal Society of London Ser. B 271:1277–1282.

Forstmeier W, Kuijper DPJ, Leisler B. 2001. Polygyny in the dusky warbler, *Phylloscopus fuscatus*: the importance of female qualities. Animal Behaviour 62:1097–1108.

Freed LA, Cann RL, Diller K. 2009. Sexual dimorphism and the evolution of seasonal variation in sex allocation in the Hawaii akepa. Evolutionary Ecology Research 11:731–757.

Gonzáles-Solís J, Becker PH, Wendeln H, Wink M. 2005. Hatching sex ratio and sex specific chick mortality in common terns *Sterna hirundo*. Journal of Ornithology 146:235–243.

Goodenough AE, Elliot SL, Maitland DP, Hart AG. 2009. Variation in the relationship between lay date and clutch size in three cavity-nesting woodland passerines. Acta Ornithologica 44:27–36.

Griffiths R, Double MC, Orr K, Dawson RJG. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

Griggio M, Hamerstrom F, Rosenfeld RN, Tavecchia G. 2002. Seasonal variation in sex ratio of fledgling American kestrels: a long term study. Wilson Bulletin 114:474–478.

Griggio M, Tavecchia G, Biddau L, Mingozzi T. 2003. Mating strategies in the rock sparrow *Petronia petronia*: the role of female quality. Ethology, Ecology and Evolution 15:389–398.

Gwinner H, Schwabl H. 2005. Evidence for sexy sons in European starlings (*Sturnus vulgaris*). Behavioural Ecology and Sociobiology 58:375–382.

Hansson B, Bensch S, Hasselquist D. 1997. Infanticide in great reed warblers: secondary females destroy eggs of primary females. Animal Behaviour 54:297–304.

Hartley IR, Griffith S, Wilson K, Shepherd M, Burke T. 1999. Nestling sex ratios in the polygynously breeding corn bunting *Miliaria calandra*. Journal of Avian Biology 30:7–14.

Hasselquist D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. Ecology 79:2376–2390.

Hasselquist D, Kempenaers B. 2002. Parental care and adaptive brood sex ratio manipulation in birds. Philosophical Transactions of the Royal Society of London Ser. B 357:363–372.

Husby A, Saether BE, Jensen H, Ringsby TH. 2006. Causes and consequences of adaptive seasonal sex ratio variation in house sparrows. Journal of Animal Ecology 75:1128–1139.

Johnson LS, Kermott LH, Lein ML. 1993. The cost of polygyny in the house wren *Troglofytes aedon*. Journal of Animal Ecology 62:669–682.

Johnson LS, Wimmers LE, Johnson BG, Milkie RC, Molinaro RL, Gallagher BS, Masters BS. 2005. Sex manipulation within broods of house wrens? A second look. Animal Behaviour 70:1323–1329.

Jones SL, Dieni JS, Gouse PJ. 2010. Reproductive biology of a grassland songbird community in Northcentral Montana. Wilson Journal of Ornithology 122:455–464.

Kelly CD 2006. Replicating empirical research on behavioural ecology: How and why it should be done but rarely ever is. Quarterly Review of Biology 81:221–236.

Komdeur J, Pen I. 2002. Adaptive sex allocation in birds: the complexities of linking theory and practice. Philosophical Transactions of the Royal Society of London Ser. B 357:373–380.

Leisler B, Wink M. 2000. Frequencies of multiple paternity in three *Acrocephalus* species (Aves, Sylviidae) with different mating systems (*A. palustris, A. arundinaceus, A. paludicola*). Ethology, Ecology and Evolution 12:237–249.

Lessells CM, Mateman AC, Visser J. 1996. Great tit hatchling sex ratios. Journal of Avian Biology 27:135–142.

Lifjeld JT, Slagsvold T. 1989. Allocation of parental investment by polygynous pied flycatcher males. Ornis Fennica 66:3–14.

Maddox DJ, Weatherhead PJ. 2009. Seasonal sex allocation by common grackles? Revisiting a foundational study. Ecology 90:3190–3196.

Nishiumi I. 1998. Brood sex ratio is dependent on female mating status in polygynous great reed warblers. Behavioural Ecology and Sociobiology 44:9–14.

Nishiumi I, Yamagishi S, Maekawa H, Shimoda C. 1996. Paternal expenditure is related to brood sex ratio in polygynous great reed warblers. Behavioural Ecology Sociobiology 39:211–217.

Palmer AR. 2000. Quasi-replication and the contrast of error: lessons from sex ratios, heritabilities and fluctuating asymmetry. Annual Review of Ecology and Systematics 31:441–480.

Patterson CB, Erckman WJ, Orians GH. 1980. An experimental study of parental investment and polygyny in male blackbirds. American Naturalist 116:757–769.

Philip SA, Oommen MM, Baiju KV. 2010. Linear sex ratio change in the clutch sequence of *Melopsittacus undulatus*. Current Science 98:1520–1523.

R Development Core Team. 2010. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Radford AN, Blakey JK. 2000. Is variation in brood sex ratios adaptive in the great tit (*Parus major*)? Behavioural Ecology 11:294–298.

Sejberg D, Bensch S, Hasselquist D. 2000. Nestling provisioning in polygynous great reed warblers (*Acrocephalus arundinaceus*): do males bring larger prey to compensate for fewer nest visits? Behavioural Ecology and Sociobiology 47:213–219.

South JM, Wright TF. 2002. Nestling sex ratios in the yellow-naped amazon: no evidence for adaptive modification. Condor 104:437–440.

Teather KL. 1992. An experimental study of competition for food between male and female nestlings of the red-winged blackbird. Behavioural Ecology and Sociobiology 31:81–87.

Teather KL, Wetherhead PJ. 1988. Sex-specific energy requirements of great-tailed grackle (*Quiscalus mexicanus*) nestlings. Journal of Animal Ecology 57:659–668.

Trivers RL, Willard DE. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92.

Trnka A, Prokop P. 2010. Does social mating system influence nest defence behaviour in great reed warbler (*Acrocephalus arundinaceus*) males? Ethology 116:1075–1083.

Trnka A, Prokop P. 2011. Polygynous great reed warblers suffer more cuckoo parasitism than monogamous pairs. Journal of Avian Biology 42:192–195.

Trnka A, Prokop P, Batáry P. 2010. Infanticide or interference: Does the great reed warbler selectively destroy eggs? Annales Zoologici Fennici 47:272–277.

Velando A. 2002. Experimental manipulation of maternal effort produces differential effects in sons and daughters: implications for adaptive sex ratios in the blue-footed booby. Behavioural Ecology 13:443–449.

Verhulst S, Holveck MJ, Riebel K. 2006. Long-term effects of manipulated natal brood size on metabolic rate in zebra finches. Biology Letters 2:478–480.

Westerdahl H, Bensch S, Hansson D, Hasselquist D, von Schantz T. 1997. Sex ratio variation among broods of great reed warblers *Acrocephalus arundinaceus*. Molecular Ecology 6:543–548.

Westerdahl H, Bensch S, Hansson B, Hasselquist D, von Schantz T. 2000. Brood sex ratios, female mating status and resources for nestling provisioning in the great reed warbler *Acrocephalus arundinaceus*. Behavioural Ecology and Sociobiology 47:312–318.

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