

Effect of extra-pair paternity and parental quality on brood sex ratio in the scarlet rosetfinch *Carpodacus erythrinus*

Authors: Poláková, Radka, Schnitzer, Jan, Vinkler, Michal, Bryja, Josef, Munclinger, Pavel, et al.

Source: Folia Zoologica, 61(3–4) : 225-232

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: <https://doi.org/10.25225/fozo.v61.i3.a6.2012>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Effect of extra-pair paternity and parental quality on brood sex ratio in the scarlet rosefinch *Carpodacus erythrinus*

Radka POLÁKOVÁ¹, Jan SCHNITZER², Michal VINKLER^{1,2}, Josef BRYJA¹, Pavel MUNCLINGER² and Tomáš ALBRECHT^{1,2}

¹ Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, v.v.i., Květná 8, 603 65 Brno, Czech Republic; e-mail: radkpol@centrum.cz, michal.vinkler@natur.cuni.cz, bryja@brno.cas.cz, albrecht@ivb.cz

² Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, 128 44 Praha 2, Czech Republic; e-mail: jan.schnitzer@centrum.cz, muncling@natur.cuni.cz

Received 22 April 2012; Accepted 16 July 2012

Abstract. The attractiveness hypothesis predicts that females should bias the sex ratio of their offspring towards sons when mated to attractive males. Females of many socially monogamous bird species commonly engage in extra-pair fertilizations (EPFs). Assuming that extra-pair males are more attractive to females than their social partners, and that sons inherit superior traits from their fathers, extra-pair young should be more likely males. According to the maternal condition hypothesis male-biased sex ratio in offspring should be also associated with better female body condition. We evaluated these ideas in the scarlet rosefinch (*Carpodacus erythrinus*), socially monogamous songbird with moderate level of extra-pair fertilizations. Contrary to the attractiveness hypothesis we have found no significant effect of paternity (within-pair or extra-pair) on the sex of individual offspring. Furthermore, data did not suggest that females mated to males with more elaborated plumage colour were more likely to produce sons. However, consistently with the maternal condition hypothesis, high-quality females produced more sons than daughters. Our results indicate that scarlet rosefinch females may not be able to manipulate the primary sex ratio of their offspring in relation to the attractiveness of their mate, but they may adjust it according to their own condition.

Key words: sex allocation, extra-pair mating, parental attractiveness

Introduction

Female birds are the heterogametic sex (ZW) and this circumstance might enable maternal control of the offspring sex ratio (Rutkowska & Badayev 2008). Sex allocation theory predicts that females should preferentially produce offspring of the sex with the greater fitness potential (Trivers & Willard 1973, Charnov 1982). One prediction derived from this theory is that females should bias the sex ratio of their broods towards sons when mated to attractive males, assuming that sons benefit more than daughters from inheriting their father's attractiveness traits (Burley 1981). Several recent studies have found a relationship between the attractiveness of males and the sex ratio

of their offspring in birds. Female blue tits (*Cyanistes caeruleus*) produce more sons when mated to a male with high survival prospect (Svensson & Nilsson 1996). In great tit (*Parus major*), the proportion of sons in a brood increases significantly with male body size (Kolliker et al. 1999) and females collared flycatchers (*Ficedula albicollis*) are able to manipulate the sex ratio of their offspring in relation to the phenotype of their mate (Ellegren et al. 1996, Sheldon et al. 1999). Extra-pair fertilizations (EPFs) have been found in most socially monogamous passerine species and may have evolved as female strategy to enhance own fitness (Griffith et al. 2002, Westneat & Stewart 2003, but see discussion in Albrecht et al. 2006). Genetic

benefit models of this adaptive behavior predict that females engage in EPFs with males of higher genetic quality compared to their social mates and thus obtain indirect benefits for their offspring (Griffith et al. 2002, Kokko et al. 2002). Indeed, females in several passerine species seem to increase their fitness through EPFs (Kempnaers et al. 1997, Foerster et al. 2003, Stapleton et al. 2007, Fossøy et al. 2008). The male attractiveness hypothesis may therefore apply to extra-pair paternity. If females are actually engaged in EPFs with more attractive males, they should benefit from biasing the sex ratio of their extra-pair offspring (EPO) towards sons (Leech et al. 2001).

Only few studies have examined the relationship between paternity (within-pair or extra-pair) and offspring sex ratio. Moreover, the vast majority of studies available to date found no evidence for adaptive manipulation of offspring sex ratio in response to extra-pair paternity [EPP] in birds (e.g. Westerdahl et al. 1997, Saino et al. 1999, Leech et al. 2001, Whittingham & Dunn 2001, Kraaijeveld et al. 2007). However, four studies found that offspring fathered by extra-pair sires were more likely to be males (blue tit *Cyanistes caeruleus*, Kempnaers et al. 1997; red-capped robins *Petroica goodenovii*, Dowling & Mulder 2006; red-backed shrike *Lanius collurio*, Schwarzova et al. 2008; house wren *Troglodytes aedon*, Johnson et al. 2009).

Apart from the effects of mate attractiveness, the maternal condition hypothesis (Trivers & Willard 1973) predicts that females in better body condition adjust their brood sex ratio toward male offspring and produce heavier sons. Mothers in poor condition have fewer resources to produce a son in a good condition, and thus should produce more daughters as these provide a less risky source of individual fitness (Trivers & Willard 1973). As reported in some species of mammals (bank vole *Clethrionomys glareolus*, Hansson 1987; red deer *Cervus elaphus*, Clutton-Brock et al. 1984) and also in birds (zebra finch *Taeniopygia guttata*, Bradbury & Blakey 1998; tree swallow *Tachycineta bicolor*, Whittingham & Dunn 2000, Whittingham et al. 2005; eastern kingbird *Tyrannus tyrannus*, Dolan et al. 2009), male-biased broods are indeed produced by heavy females.

Scarlet rosefinch (*Carpodacus erythrinus*) is sexually dimorphic cardueline finch with delayed plumage maturation in males. Adult males display a variable carotenoid feather ornament (Stjernberg 1979). Rosefinches are socially monogamous songbirds, but show moderate levels of extra-pair fertilizations (almost 40 % of nests contained extra-pair young, Albrecht

et al. 2007). EPFs considerably increase variance in reproductive success among rosefinch males (Albrecht et al. 2007) and the secondary carotenoid-based plumage of males is a good predictor of male extra-pair success in this species (Albrecht et al. 2009). In this study we investigated the relationship between offspring sex ratio, and paternity in the scarlet rosefinch using male ornamentation and male and female condition as covariates in the analyses. We were able to evaluate the following predictions: (1) extra-pair young are more likely to be males; (2) females mated to superiorly ornamented males and/or (3) high-quality (i.e. heavy) females bias the sex ratio of their offspring towards sons.

Material and Methods

Study population and field methods

Data were collected during the breeding seasons (from the end of May to early July) of 2000-2008 in the National Park Šumava, Czech Republic (48° 49' N, 13° 56' E). A detailed description of the study site and field procedures is given in Albrecht et al. (2007). Briefly, the study area was an isolated patch of a wet shrubby meadow (110 ha) surrounded by a rural landscape from one side and hills covered with forest from the other. There a colony of 10-20 breeding rosefinch pairs per year was studied (Albrecht 2004, Albrecht et al. 2007). Adult birds were captured into mist nets upon their arrival to the study plot. Blood samples (20-50 µl) were taken by venipuncture from adults and 7-day old nestlings and stored in 96 % ethanol. Since the nest survival at this study site was high (Albrecht 2004), only a few broods (less than 15 %) were lost before it was possible to sample the blood of the young. In all adult individuals we recorded tarsus length (done by digital calliper Kinex, type 6040.2, accuracy 0.01 mm) and body mass (spring balance, 60 g). Body mass, body condition (i.e. body mass divided by tarsus length) and colouration of ornamental feathers in males were considered as potential indicators of the individual quality. Male ornamentation has not been available for all males in the population. However, most males in their 3rd year or older (i.e., males with yellow to red carotenoid-based ornamentation of breast, Stjernberg 1979) were photographed for colour analysis of ornamental patches that range in colouration from yellow to red. All photographs were taken in standard conditions in the dark room of a nearby field station. A grey card and colour & grey chart (grey card GC 18 and colour & grey chart Q 14; Danes-Picta, Praha, Czech Republic) were used to standardize measurements. Photographs were analysed using ADOBE PHOTOSHOP

software (Adobe Systems Inc., San Jose, California). Hue (mean 1.32 ± 4.04 [SE], $n = 62$ males and 86 observations), saturation (mean 65.85 ± 9.71 [SE]) and brightness (mean 61.21 ± 11.75 [SE]; HSB colour space) of carotenoid ornaments were measured (for a detailed description of feather ornament analysis based on photography see Badyaev et al. 2001, Fitze & Richner 2002, Tschirren et al. 2003, Surmacki 2008, Albrecht et al. 2009). To assess the reliability of colour measurements based on photographs, we measured colouration using both reflectance curves obtained from AVANTES spectrophotometer with white standard WS-2 (following equations H_3 , S_8 and B_2 in Montgomerie 2006) and ADOBE PHOTOSHOP in 30 males. Estimates obtained by both methods were significantly correlated in hue ($r^2 = 0.73$, $p < 0.001$) and brightness (brightness_{320-700 nm}: $r^2 = 0.15$, $p = 0.023$; brightness_{400-700 nm}: $r^2 = 0.14$, $p = 0.025$) but marginally nonsignificant in chroma ($r^2 = 0.10$, $p = 0.054$). Hue itself was strongly inversely related with UV chroma_{320-400 nm} (equation S_1 in Montgomerie 2006; $r^2 = 0.62$, $p < 0.001$), suggesting that UV component is unlikely to bias conclusions based on colour estimates derived from photographs in our case. To avoid any confusion, we use the term lightness instead of brightness throughout the manuscript (see discussion in Andersson & Prager 2006).

Sexing techniques

Sex of birds was determined according to the presence of the PCR products of the CHD1-Z and CHD1-W genes using the primers P2 and P8 (Griffiths et al. 1998). DNA was extracted from the blood samples using the DNeasy®Tissue Kit (Qiagen, Hilden, Germany). PCR amplification was carried out in a total volume of 10 µL. The final reaction conditions were as follows: 0.25 mM of each dNTPs, 1× Taq DNA buffer (Fermentas), 1.5 mM MgCl₂, 0.2 µM of each primers P2 and P8 and 0.15 U of Taq DNA polymerase (Fermentas). An initial denaturing step at 94 °C for 4 min was followed by 35 cycles of 48 °C for 45 s, 72 °C for 45 s and 94 °C for 30 s. A final run of 48 °C for 1 min and 72 °C for 5 min completed the program. PCR products were separated in 2.5 % agarose gel containing GoldView™ and visualized under UV light. In the scarlet rosefinch the product amplified from the female-specific CHD1-W gene is approximately 50 base pairs larger (ca 400bp) than the product for the CHD1-Z (ca 350bp).

Parentage analysis

Parentage was assessed using a set of 15 microsatellite markers (Poláková et al. 2007) as described in Albrecht

et al. (2009). Offspring genotypes were first compared with the social mother (attendant female at the nest) and we did not find any genetic mismatches between offspring and their social mothers. We subsequently determined paternity using the Cervus 3.0 program (Kalinowski et al. 2007), the offspring's paternal alleles were compared with the alleles of its putative father (the female's social partner). The offspring was considered to be EPO if it mismatched the social male at 5-14 loci (mean = 9.44). Sires of EPO were determined using the exclusion approach (Jones & Ardren 2003). We compared the paternal alleles of EPO with the genotypes of all males in the population. Because we found no mismatches between within-pair offspring (WPO) and their parents, we also used strict criteria when attempting to identify the EPO sires. A male was assigned as an extra-pair sire if he was matched the offspring at all loci.

Statistical analyses

We used mixed effect model approach to evaluate the effect of paternity and parental attributes on offspring sex ratio in rosefinch nests. Depending on the analysis, either nest identity, female identity, or male identity (in some analyses, see below) were involved as random effects. Sex ratio was expressed as the proportion of male to female offspring in nests, with total number of offspring in nests treated as binomial denominator and assuming binomial distribution of this dependent variable. Minimal adequate models (MAM, sensu Crawley 2007), i.e. models with all terms significant, were selected based on backward elimination of full model containing main effects and two-way interactions of continuous variables with categorical variables, comparing changes of deviance of the model with the term of interest included and the model where the term was removed, starting with two-way interactions. The significance of a particular term in models was based on the change in deviance between the full and reduced/null models, distributed as χ^2 with degrees of freedom equal to the difference in the degrees of freedom between the models with and without the term in question (Faraway 2006). Analyses were performed with R 2.9.2.

Results

Paternity and brood sex ratio

Over the 2000-2008 study period the sex of 443 nestlings from 103 broods was determined; of these 242 (54.62 %) were males. The sex ratio in the total data set was close to balance ($\chi^2 = 2.159$, $p = 0.141$). However, we are aware of the fact that relatively low

sample size precluded rigorous test of deviation from balanced sex ratio in rosefinches. We identified one or more extra-pair offspring in 32 (33 %) of all broods examined. There was no indication of EPO being more likely males than females ($\chi^2 = 0.45$, Df = 1, $p = 0.50$). The sex ratio of offspring in broods with mixed paternity did not differ significantly from that in broods containing purely within-pair offspring ($\chi^2 = 0.158$, Δ Df = 1, $P = 0.691$). Also, the sex ratio of EPO and WPO examined only in mixed nests was not significantly different from the null model ($\chi^2 = 0.170$, Δ Df = 1, $P = 0.679$). Furthermore, in a mixed effect model with the male identity treated as a random effect and restricted to males that sired both within-pair and extra-pair offspring ($n = 23$ males) the sex ratio of extra-pair and within-pair offspring was equal ($\chi^2 = 0.59$, Δ Df = 1, $P = 0.4418$). In our data set paternity had no significant effect on the offspring sex.

Parental effect on brood sex ratio

We tested the effect of several variables of the parental quality on brood sex ratios in a subset of 90 nests with adequate data available (i.e., with male and female traits available simultaneously). In a model involving male ornamentation (hue, saturation, lightness), male and female body mass, male and female body condition, the occurrence of EPP (0 – no EPO detected, 1 – at least one EPO detected) and two way interactions of EPP and male/female traits, only female body mass and social male lightness were important predictors of brood sex ratio (Table 1). The minimal adequate model involving these two predictors was significantly different from the null model (female identity as random effect, $\chi^2 = 12.24$,

Table 1. Summary of minimal adequate model (i.e., model with all term significant) explaining sex ratio in broods of scarlet rosefinches. The initial model involved male ornamentation (hue, saturation, lightness), male and female body mass, male and female body condition, the occurrence of EPP (0 – no EPO detected, 1 – at least one EPO detected) and two way interactions of EPP and male/female traits. Sex ratio was expressed as the ratio of male and female offspring in 90 nests of 65 females. The results and model parameters are based on mixed effect modelling involving female identity as random effect and total number of offspring in nest as binomial denominator.

	Estimate	Std. error	χ^2	P
(Intercept)	-4.926154	1.868301		
Female body mass	0.174316	0.081879	4.61	0.032
Male lightness	0.020198	0.007834	6.47	0.009

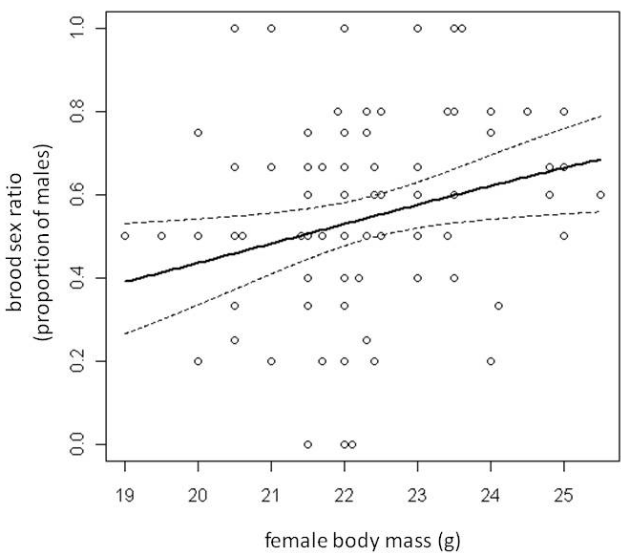


Fig. 1. Proportion of sons in brood in relation to the body mass of females over nine years (2000–2008). Line is from a linear regression but the relationship was tested with minimal adequate model.

Δ Df = 2, $P = 0.002$). In general, heavier females had more sons (Fig. 1), and, irrespectively of female body mass, more sons were identified in nests where male ornamental feathers had higher lightness (i.e., in less ornamented males, see Hill 2002, Fig. 2). The same relationship between male lightness and brood sex ratio was apparent when the analysis involved all offspring that a male sired both within- and extra-

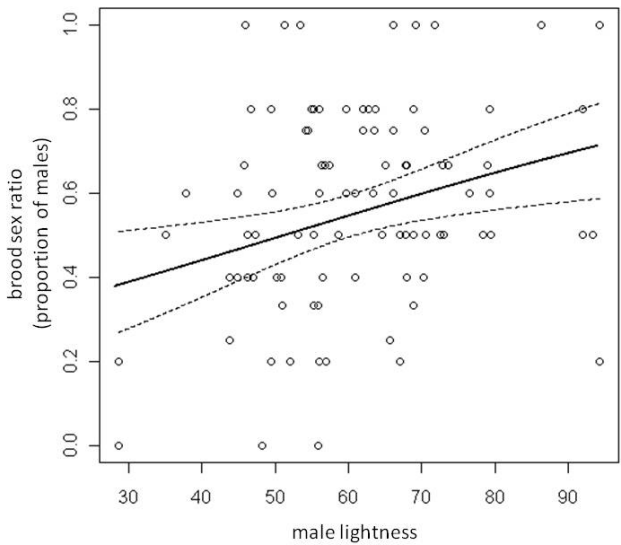


Fig. 2. Offspring sired by males with higher values of lightness are significantly more sons. Line is from a linear regression but the relationship was tested with minimal adequate model.

pair (60 males and 110 observations, male identity as random effect, MAM involving male lightness vs. null model, $\chi^2 = 4.52$, $\Delta Df = 1$, $P = 0.033$, slope: 0.019 ± 0.009 [SE]).

Discussion

Socially monogamous females commonly mate with higher quality males outside the pair bond. It is generally assumed that they prefer males of higher genetic quality compared to their social mate and thus obtain genetic benefits for their offspring (Griffith et al. 2002). Females mated to attractive EP males should produce more sons because these sons will inherit father's attractiveness traits and enjoy a great reproductive success (Burley 1981). Here we tested the prediction that females fertilized by extra-pair males produce more sons (Leech et al. 2001). However, we found no evidence that the offspring sired by extra-pair mates were significantly more likely males than were the offspring sired by within-pair mates. Our data thus do not confirm the idea that female rosefinches bias their offspring sex ratio towards sons when fertilized by EP males, passerine species where EPP success is biased towards elaborated males (Albrecht et al. 2009). In fact, there are only four studies in passerines suggesting that paternity source can influence sex allocation (Kempnaers et al. 1997, Dowling & Mulder 2006, Schwarzova et al. 2008, Johnson et al. 2009) and our result thus matches the findings of most previous studies in passerine birds, both observational (Westneat et al. 1995, Sheldon & Ellegren 1996, Westerdahl et al. 1997, Ramsay et al. 2003, Dietrich-Bischoff et al. 2006) and experimental (Saino et al. 1999). Moreover, there seems to be intraspecific variation in sex allocation in relation to extra-pair paternity. Although EPO were more likely to be males than WPO in a Belgian population of blue tits (Kempnaers et al. 1997), in another population of the same species Leech et al. (2001) found no such difference when using a molecular sexing technique (instead of a method based on morphology) and a larger data set. Our understanding of the evolutionary significance of EPP for female in birds is still weak (e.g., Eliassen & Kokko 2008, Forstmeier et al. 2011). However, our study clearly adds to the currently prevailing evidence that passerine females are not able to alter the sex of their offspring in response to the occurrence of extra-pair paternity.

Along with the prediction that paternity source affects the offspring sex we also tested the male attractiveness hypothesis. Although several studies of passerine birds have demonstrated significant correlations

between brood sex ratio and various indicators of male quality, including body size (Kolliker et al. 1999) and plumage characteristics (Ellegren et al. 1996, Sheldon et al. 1999), in the scarlet rosefinch we found no positive relationship between male-biased brood and condition-dependent traits such as body mass or the expression of ornamental feather colouration in males. Our data do not suggest that redder males (i.e. those with lower hue values) were more likely to produce sons and the results are consistent with other recent findings throwing doubts on the 'attractiveness hypothesis' of sex allocation (e.g. Saino et al. 1999, Radford & Blakey 2000, Ramsay et al. 2003). This result is surprising, because hue seems to be the most important colour component associated with male attractiveness both in rosefinches (Albrecht et al. 2009) and related house finches (Hill 2002). According to several models (Burley 1986, Sheldon 2000) sons of high-quality males should inherit some desirable traits from their fathers that may increase their subsequent survival or reproductive success. However, it still remains unclear what is the extent of heritability in carotenoid-based plumage ornaments in birds (e.g., Hill 1990, Fitze et al. 2003).

Somewhat surprisingly, our results indicate that females may bias the sex ratio of their offspring in favour of sons when mated to males with higher lightness of feather ornamentation (Andersson & Prager 2006). High plumage lightness may generally result from feather degradation by bacteria (e.g., Shawkey et al. 2007) and in scarlet rosefinch males it signalises impaired health state (Vinkler et al. 2012). One interpretation of our results is that colour lightness signalise the quality of parental care and males displaying less elaborated plumage have higher feeding efforts. However, in our study population neither the ornament lightness nor hue or saturation of the male ornamentation seems to indicate the amount of parental care (Schnitzer et al., submitted) and the relationship between ornament colouration and parental effort remains controversial in closely related species (e.g., Hill 2002, Duckworth et al. 2003). Any potential benefits arising to female rosefinches from the increased proportion of male offspring in their nests when mated to less elaborated males remain unclear and desire further investigation.

The maternal condition hypothesis (Trivers & Willard 1973) predicts that females should adjust their brood sex ratio according to their own body condition, assuming one sex has higher variance in reproductive success and thus is more risky to produce than the other. Initial studies of ungulate species revealed that

maternal condition can affect sex allocation, with mothers in good condition producing male offspring (e.g. Clutton-Brock et al. 1984, Kruuk et al. 1999). Similarly, there is an increasing body of evidence showing that maternal condition is correlated with male-biased sex ratio in birds (Wiebe & Bortolotti 1992, Bradbury & Blakey 1998, Nager et al. 1999, Parker 2002). Female mass presumably affects the quality of parental care and heavy females can be expected to raise high quality young that will later achieve high reproductive success. Biasing broods towards males is therefore predicted when variance in male success is high and females benefit by producing high-quality male offspring (Trivers & Willard 1973, Whittingham & Dunn 2000, Dolan et al. 2009). In the scarlet rosefinch, the variance in male reproductive success is much greater than that of females (Albrecht et al. 2007). We found significant relationship between female body mass and brood sex ratio and show that male-biased broods were produced by heavy females. Although the tarsus/body mass ratio (individual condition) did not enter the minimal adequate model, it is worth noting that both body mass and tarsus/body mass ratio were strongly correlated ($r^2 = 0.72$). Our findings imply that scarlet rosefinch females adjust

the primary sex ratio to the phenotypic quality of themselves and not to the genetic sire of their offspring. In summary, our results show that the sex ratio does not vary with the presence or absence of EP young in a nest. This finding contributes to the evidence suggesting that paternity source does not affect the offspring sex ratio in passerine birds. Present results do not support the hypothesis that brood sex ratios are adjusted by females scarlet rosefinch in relation to attractiveness of their mate. However, scarlet rosefinch females adjust the sex ratio of brood according to their own condition (body mass) at the time of reproduction potentially to increase their reproductive success.

Acknowledgements

We would like to thank Lubor Červa, Jaroslav Jelínek, František Zicha, Martin Lundák and Pavel Jaška for help with fieldwork. This study was funded by the Czech Science Foundation (project 206/06/0851), the Grant Agency of Charles University (project 191/2004/B-Bio) the Ministry of Education of the Czech Republic (project MS MT No. 0021620828), the Academy of Sciences of the Czech Republic (project AV0Z60930519), and by Research Centrum Nr. LC06073.

Literature

- Albrecht T. 2004: Edge effect in wetland-arable land boundary determines nesting success of scarlet rosefinches (*Carpodacus erythrinus*) in the Czech Republic. *Auk* 121: 361–371.
- Albrecht T., Kreisinger J. & Piálek J. 2006: The strength of direct selection against female promiscuity is associated with rates of extrapair fertilizations in socially monogamous songbirds. *Am. Nat.* 167: 739–744.
- Albrecht T., Schnitzer J., Kreisinger J., Exnerova A., Bryja J. & Munclinger P. 2007: Extra-pair paternity and the opportunity for sexual selection in long-distant migratory passerines. *Behav. Ecol.* 18: 477–486.
- Albrecht T., Vinkler M., Schnitzer J., Poláková R., Munclinger P. & Bryja J. 2009: Extra-pair fertilizations contribute to selection on secondary male ornamentation in a socially monogamous passerine. *J. Evol. Biol.* 22: 2020–2030.
- Andersson S. & Prager M. 2006: Quantifying colours. In: Hill G.E. & McGraw K.J. (eds.), *Bird colouration*, vol. 1. Mechanisms and measurements. *Harvard University Press, Cambridge, MA*: 41–89.
- Badyaev A.V., Hill G.E., Dunn P.O. & Glen J.C. 2001: Plumage colour as a composite trait: developmental and functional integration of sexual ornamentation. *Am. Nat.* 158: 221–235.
- Bradbury R.R. & Blakey J.K. 1998: Diet, maternal condition, and offspring sex ratio the zebra finch, *Poephila guttata*. *Proc. R. Soc. Lond. B* 265: 895–899.
- Burley N. 1981: Sex ratio manipulation and selection for attractiveness. *Science* 221: 721–722.
- Burley N. 1986: Sex-ratio manipulation in colour-banded populations of zebra finches. *Evolution* 40: 1191–1206.
- Charnov E.L. 1982: The theory of sex allocation. *Princeton University Press, Princeton*.
- Clutton-Brock T.H., Albon S.D. & Guinness F.E. 1984: Maternal dominance, breeding success and birth sex ratios in red deer. *Nature* 308: 358–360.
- Crawley M.J. 2007: The R Book. *John Wiley & Sons, Chichester*.
- Dietrich-Bischoff V., Schmoll T., Winkel W., Krackow S. & Lubjuhn T. 2006: Extra-pair paternity, offspring mortality and offspring sex ratio in the socially monogamous coal tit (*Parus ater*). *Behav. Ecol. Sociobiol.* 60: 563–571.
- Dolan A.C., Murphy M.T., Redmond L.J. & Duffield D. 2009: Maternal characteristics and the production and recruitment of sons in the eastern kingbird (*Tyrannus tyrannus*). *Behav. Ecol. Sociobiol.* 63: 1527–1537.

- Dowling D.K. & Mulder R.A. 2006: Combined influence of maternal and paternal quality on sex allocation in red-capped robins. *J. Evol. Biol.* 19: 440–449.
- Duckworth R.A., Badyaev A.V. & Parlow A.F. 2003: Elaborately ornamented males avoid costly parental care in the house finch (*Carpodacus mexicanus*): a proximate perspective. *Behav. Ecol. Sociobiol.* 55: 176–183.
- Eliassen S. & Kokko H. 2008: Current analyses do not resolve whether extra-pair paternity is male or female driven. *Behav. Ecol. Sociobiol.* 62: 1795–1804.
- Ellegren H., Gustafsson L. & Sheldon B.C. 1996: Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. *Proc. Natl. Acad. Sci. USA* 93: 11723–11728.
- Faraway J.J. 2006: Extending the Linear Model with R. *Chapman & Hall/CRC, London*.
- Fitze P.S., Köliker M. & Richner H. 2003: Effects of common origin and common environment on nestling plumage colouration in the great tit (*Parus major*). *Evolution* 57: 144–150.
- Fitze P.S. & Richner H. 2002: Differential effects of a parasite on ornamental structures based on melanins and carotenoids. *Behav. Ecol.* 13: 401–407.
- Foerster K., Delhey K., Johnsen A., Lifjeld J.T. & Kempenaers B. 2003: Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature* 425: 714–717.
- Forstmeier W., Martin K., Bolund E., Schielzeth H. & Kempenaers B. 2011: Female extrapair mating behavior can evolve via indirect selection on males. *Proc. Natl. Acad. Sci. USA* 108: 10608–10613.
- Fossøy F., Johnsen J. & Lifjeld J.T. 2008: Multiple genetic benefits of female promiscuity in a socially monogamous passerine. *Evolution* 62: 145–156.
- Griffith S.C., Owens I.P.F. & Thuman K.A. 2002: Extra-pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.* 11: 2195–2212.
- Griffiths R., Double M.C., Orr K. & Dawson R.J.G. 1998: A DNA test to sex most birds. *Mol. Ecol.* 7: 1071–1075.
- Hansson L. 1987: Vole sex ratios: the importance of mating systems and maternal condition. *Oikos* 49: 161–164.
- Hill G.E. 1990: Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Anim. Behav.* 40: 563–572.
- Hill G.E. 2002: A red bird in a brown bag: the function and evolution of colourful plumage in the house finch. *Oxford University Press, New York*.
- Johnson L.S., Thompson C.F., Sakaluk S.K., Neuhauser M., Johnson B.G.P., Soukup S.S., Forsythe S.J. & Masters B.S. 2009: Extra-pair young in house wren broods are more likely to be male than female. *Proc. R. Soc. Lond. B* 276: 2285–2289.
- Jones A.G. & Ardren W.R. 2003: Methods of parentage analysis in natural populations. *Mol. Ecol.* 12: 2511–2523.
- Kalinowski S.T., Taper M.L. & Marshall T.C. 2007: Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* 16: 1099–1106.
- Kempenaers B., Verheyen G.R. & Dhondt A.A. 1997: Extra-pair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behav. Ecol.* 8: 481–492.
- Kokko H., Brooks R., McNamara J.M. & Houston A.I. 2002: The sexual selection continuum. *Proc. R. Soc. Lond. B* 269: 1331–1340.
- Kolliker M., Heeb P., Werner I., Mateman A.C., Lessells C.M. & Richner H. 1999: Offspring sex ratio is related to male body size in the great tit (*Parus major*). *Behav. Ecol.* 10: 68–72.
- Kraaijeveld K., Ming M.A., Komdeur J. & Mulder R.A. 2007: Offspring sex ratios in relation to mutual ornamentation and extra-pair paternity in the black swan (*Cygnus atratus*). *Ibis* 149: 79–85.
- Kruuk L.E.B., Clutton-Brock T.H., Albon S.D., Pemberton J.M. & Guinness F.E. 1999: Population density affects sex ratio variation in red deer. *Nature* 399: 459–461.
- Leech D.I., Hartley I.R., Stewart I.R.K., Griffith S.C. & Burke T. 2001: No effect of parental quality or extra-pair paternity on brood sex ratio in the blue tit (*Parus caeruleus*). *Behav. Ecol.* 12: 674–680.
- Montgomerie R. 2006: Analyzing colours. In: Hill G.E. & McGraw K. (eds.), *Bird colouration*, vol. 1. Mechanisms and measurement. *Harvard University Press, Cambridge, MA*: 90–147.
- Nager R.G., Monaghan P., Griffiths R., Houston D.C. & Dawson R. 1999: Experimental demonstration that offspring sex ratio varies with maternal condition. *Proc. Natl. Acad. Sci. USA* 96: 570–573.
- Parker T.H. 2002: Maternal condition, reproductive investment, and offspring sex ratio in captive red junglefowl (*Gallus gallus*). *Auk* 119: 840–845.

- Poláková R., Vyskočilová M., Martin J.F., Mays H.L., Hill G.E., Bryja J. & Albrecht T. 2007: Multiplex set of microsatellite markers for the scarlet rosefinch (*Carpodacus erythrinus*). *Mol. Ecol. Notes* 7: 1375–1378.
- Radford A.N. & Blakey J.K. 2000: Is variation in brood sex ratios adaptive in the great tit (*Parus major*)? *Behav. Ecol.* 11: 294–298.
- Ramsay S.M., Mennill D.J., Otter K.A., Ratcliffe L.M. & Boag P.T. 2003: Sex allocation in black-capped chickadees (*Poecile atricapilla*). *J. Avian Biol.* 34: 134–139.
- Rutkowska J. & Badyaev A.V. 2008: Meiotic drive and sex determination: molecular and cytological mechanisms of sex ratio adjustment in birds. *Phil. Trans. R. Soc.* 363: 1675–1686.
- Saino N., Ellegren H. & Møller A.P. 1999: No evidence for adjustment of sex allocation in relation to paternal ornamentation and paternity in barn swallows. *Mol. Ecol.* 8: 399–406.
- Schwarzova L., Simek J., Coppack T. & Tryjanowski P. 2008: Malebiased sex of extra-pair young in the socially monogamous redbacked shrike (*Lanius collurio*). *Acta Ornithol.* 43: 235–240.
- Shawkey M.D., Pillai S.R., Hill G.E., Siefferman L.M. & Roberts S.R. 2007: Bacteria as agent for change in structural plumage colour: correlation and experimental evidence. *Am. Nat.* 169: 112–121.
- Sheldon B.C. 2000: Differential allocation: tests, mechanisms and implications. *Trends Ecol. Evol.* 15: 397–402.
- Sheldon B.C., Andersson S., Griffith S.C., Ornborg J. & Sendecka J. 1999: Ultraviolet colour variation influences blue tit sex ratios. *Nature* 402: 874–877.
- Sheldon B.C. & Ellegren H. 1996: Offspring sex and paternity in the collared flycatcher. *Proc. R. Soc. Lond. B* 263: 1017–1021.
- Stapleton M., Kleven O., Lifjeld J.T. & Robertson R.J. 2007: Female tree swallows (*Tachycineta bicolor*) increase offspring heterozygosity through extra-pair mating. *Behav. Ecol. Sociobiol.* 61: 1725–1733.
- Stjernberg T. 1979: Breeding biology and population dynamics of the scarlet rosefinch (*Carpodacus erythrinus*). *Acta Zool.* 157: 1–88.
- Surmacki A. 2008: Preen waxes do not protect carotenoid plumage from bleaching by sunlight. *Ibis* 150: 335–341.
- Svensson E. & Nilsson J.A. 1996: Mate quality affects offspring sex ratio in blue tits. *Proc. R. Soc. Lond. B* 263: 357–361.
- Trivers R.L. & Willard D.E. 1973: Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179: 90–92.
- Tschirren B., Fitze P.S. & Richner H. 2003: Proximate mechanisms of variation in the carotenoid-based plumage colouration of nestling great tits (*Parus major*). *J. Evol. Biol.* 16: 91–100.
- Vinkler M., Schnitzer J., Munclinger P. & Albrecht T. 2012: Phytohaemagglutinin skin-swelling test in scarlet rosefinch males: low-quality birds respond more strongly. *Anim. Behav.* 83: 17–23.
- Westerdahl H., Bensch S., Hansson B., Hasselquist D. & von Schantz T. 1997: Sex ratio variation among broods of great reed warblers (*Acrocephalus arundinaceus*). *Mol. Ecol.* 6: 543–548.
- Westneat D.F., Clark A.B. & Rambo K.C. 1995: Within-brood patterns of paternity and parental behavior in red-winged blackbirds. *Behav. Ecol. Sociobiol.* 37: 349–356.
- Westneat D.F. & Stewart I.R.K. 2003: Extra-pair paternity in birds: causes, correlates, and conflict. *Annu. Rev. Ecol. Evol. Syst.* 34: 365–396.
- Whittingham L.A. & Dunn P.O. 2000: Offspring sex ratios in tree swallows: females in better condition produce more sons. *Mol. Ecol.* 9: 1123–1129.
- Whittingham L.A. & Dunn P.O. 2001: Survival of extra-pair and withinpair offspring in tree swallows. *Behav. Ecol.* 12: 496–500.
- Whittingham L.A., Dunn P.O. & Nooker J.K. 2005: Maternal influences on brood sex ratios: an experimental study in tree swallows. *Proc. R. Soc. Lond. B* 272: 1775–1780.
- Wiebe K.L. & Bortolotti G.R. 1992: Facultative sex ratio manipulation in American kestrels. *Behav. Ecol. Sociobiol.* 30: 379–386.