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## Brood sex ratio adjustment in collared flycatchers (*Ficedula albicollis*): results differ between populations

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**Abstract** Recently, a number of studies have found adaptive brood sex ratio (BSR) manipulation in birds. The reason for such manipulations is thought to be the different reproductive value of male and female nestlings. Several studies have found that parental quality and food supply can affect BSR, however results are sometimes inconsistent between species and populations. We investigated BSR patterns in a Hungarian population of Collared Flycatchers (*Ficedula albicollis*) and compared the results with those obtained in a previous study of the same species in Sweden. We found two significant differences. First, the male forehead patch size, a heritable, sexually selected trait, affected the brood sex ratio in the Swedish population, but not in our Hungarian study population. This difference might be a consequence of the different information content of the forehead patch size in the two populations. Second, a seasonal shift in BSR (more sons late in the season) was observed in the Hungarian, but not in the Swedish population.

**Keywords** *Ficedula albicollis* · Geographic variation · Male attractiveness · Seasonal patterns · Sex allocation

### Introduction

In the last decade an increasing number of studies have found that manipulation of brood sex ratio is an existing phenomenon in birds and that it may be adaptive for the parents (Bensch 1999; Hasselquist and Kempenaers 2002; Komdeur and Pen 2002). The adaptive value of this behaviour may be the potential for higher future reproductive success of nestlings of one sex given the current circumstances. For example, heritable parental quality/attractiveness may affect the future reproductive success of males more than that of females, if females show preference for high quality or attractive males. Hence, male-biased broods increase the fitness of females mated to preferred males more than female-biased or unbiased broods (Burley 1981; Ellegren et al. 1996; Sheldon et al. 1999).

Laying date has also been reported to affect the future reproductive success (FRS) differently for male and female nestlings. For example if only one sex starts to reproduce as yearlings, laying date has a higher impact on the FRS of this sex. In the crimson rosella (*Platycerus elegans*), females often breed as yearlings, while males do not, and it is therefore advantageous to produce female-biased broods early in the season (Krebs et al. 2002). Laying date effects, however, can also be the consequence of a seasonal change in food supply, because environmental sensitivity of the two genders may be different, especially in the case of sexually dimorphic species (Nishiumi 1998; Teather and Weatherhead 1989; Westerdahl et al. 2000). Thus, in several species brood sex ratio (BSR) adjustment has been observed in relation to laying date or food supply (see Table 1 in Hasselquist and Kempenaers 2002).

Brood sex ratio manipulation in birds is still a controversial issue, because results are often contradictory. In some cases, such contradictory results may be the consequence of different measurements of the same variable (e.g. male quality: Leech et al. 2001; Sheldon et al. 1999), while in other cases they may reveal actual differences between populations [in blue tits (*Parus caeruleus*):

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Leech et al. 2001; Svensson and Nilsson 1996; and in great tits (*Parus major*): Kölliker et al. 1999, Radford and Blakey 2000]. Comparable studies on different populations are therefore important, but so far scarce.

The mechanism of the sex ratio adjustment can also be responsible for differences between populations. Though this mechanism is not yet known (Krackow 1999; Oddie 1998), it may affect the probability of detecting brood sex ratio manipulations. This is because post-ovulatory mechanisms, such as the selective reabsorption of an ovulated egg, could result in a delayed completion of the clutch, resulting in an increased predation risk and possibly reduced egg viability (Emlen 1997). Hence, if sex is manipulated after ovulation, species with multiple-egg clutches should restrict sex ratio manipulation to the first egg of the clutch. If so, the probability of detecting sex ratio adjustment at the brood level would decrease and, as a consequence, the probability of yielding contradictory results should increase. This potentially confounding effect can be evaluated by investigating the sex of the first laid egg.

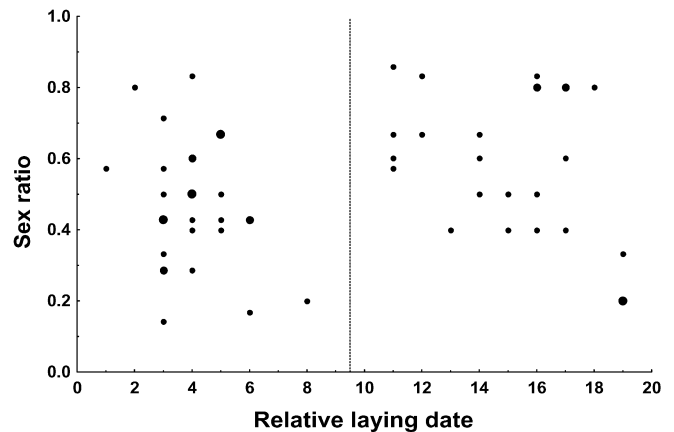
In the present study, we investigated brood sex ratios in a Hungarian population of Collared Flycatchers (*Ficedula albicollis*). In this species, we can expect adaptive modification of brood sex ratios, because two secondary sexual characters (i.e. the forehead patch and wing patch size of the males) have been shown to be heritable (Hegyi et al. 2002; Qvarnström 1999; Török et al. 2003) and play a role in social and/or extra-pair mate choice (Michl et al. 2002; Qvarnström et al. 2000; Sheldon et al. 1997; Sheldon and Ellegren 1999). Therefore, we predict that females mated to males with large patches will produce male-biased broods, an effect which has already been observed in relation to the forehead patch size in a Swedish population of this species (Ellegren et al. 1996). We therefore investigated the forehead and wing patch size, as well as a number of other traits (male size, female size, clutch size, and laying date), to compare BSR patterns between two populations of the same species. Because the mechanism of sex ratio adjustment is not yet known, we also investigated whether sex ratio adjustment is detectable only on the first egg, which is predicted in the case of post-ovulation mechanisms, or at the brood level (which is expected if sex ratio adjustment occurs before ovulation).

## Methods

### Study site and species

This study was conducted in an artificial nest box plot in the Pilis Mountains, Hungary, in 2002. The Collared Flycatcher is a small hole-nesting, long-distance migratory passerine bird. It has a predominantly monogamous social mating system and in our study area only ca. 8% of the males are socially polygynous (Török et al. 1999). However, the rate of extra-pair fertilizations is quite high as ca. 30% of the broods contain extra-pair young (Garamszegi et al. 2004).

The breeding season usually starts in mid-April, but its length is variable dependent on the arrival of the birds. In 2002, birds arrived in two separated migratory waves (Fig. 1.) and, as a consequence,



**Fig. 1** Secondary sex ratio of Collared Flycatcher (*Ficedula albicollis*) broods early and late in the season. Dot size indicates the number of cases (1, 2, 3)

the breeding season was long (the range of start of egg laying was 19 days for the broods included in the present study). Females usually lay 5–7 eggs.

Two of the conspicuous white plumage characters of the males have been reported to be important in sexual selection. The forehead patch is important for social and/or extra-pair mate choice (Michl et al. 2002; Qvarnström et al. 2000; Sheldon et al. 1997; Sheldon and Ellegren 1999), but may signal different qualities in different populations. It has been shown to be condition-dependent in a Swedish population (Gustafsson et al. 1995; Qvarnström 1999), but not so in our Hungarian study population (Hegyi et al. 2002). The wing patch is known to be important for extra-pair mate choice in the Swedish population (Sheldon and Ellegren 1999), and it is known to be condition-dependent in our study population (Török et al. 2003).

### Sex determination

Blood samples were collected from 9 to 13-day-old nestlings. Parents were captured on the same day as their young. Some of the adult samples were used as controls during molecular sexings. These adult samples were always correctly sexed ( $n=32$ ). PCR reactions were performed in 10- $\mu$ l volumes on a 9700 Thermal Cycler (Applied Biosystem) including 25 ng DNA, 0.5 units of Taq DNA polymerase, 0.4  $\mu$ M of each primer [2550F and 2718R (Fridolfsson and Ellegren 1999)], 1 $\times$ PCR buffer, 0.125 mM of each nucleotide and 3.0 mM MgCl<sub>2</sub>. Our thermal profile differed from the original protocol (Fridolfsson and Ellegren 1999) in that we used 10°C and 5°C lower annealing temperatures for the “touch down” and the following cycles respectively. PCR products were run in 2% agarose gels, pre-stained with ethidium-bromide, and detected in a FluorImager (Vistra).

In some of the samples, DNA was partially degraded, preventing us from sexing these offspring with the previous protocol. In these cases, we used a special asymmetric nested PCR protocol. The tests were performed separately for the male and the female band. For the male band, we used a PCR with the 3007 and 3112 primers (Ellegren and Fridolfsson 1997) and a thermal profile starting with ten “touch down” cycles from 50 to 40°C annealing temperature with 1°C decrease in each cycle followed by ten cycles at 45°C annealing temperature. One  $\mu$ l of this reaction was used in a second PCR with the 3007 primer together with a new primer, FalbZ on the CHD-Z intron (5'-TACAAAGATTTTGTATCTTA-3'). This time, the touch down thermal profile started at an annealing temperature of 55°C, followed by ten cycles at 50°C. Otherwise the conditions were the same as for the 2550F and 2718R primers. For the female band, we used the same thermal profiles, with the 2987 and 3112 primers in the first, and the 2987

and FalbW (5'-TTTACTTACATAACTCCTTA-3') primers in the second PCR.

#### Analysis of sex of the first egg

In 21 nests, eggs were numbered consecutively during egg laying. One day before hatching, we placed the eggs into an incubator (PL Machine SK75) and used dummy eggs to temporarily replace the clutch in the nest box. Nestlings were hatched at 37.2°C and 70–80% humidity. Hatching success was 100% for fertile eggs. After hatching, nestlings were marked individually with permanent ink on their stomach and delivered back to their nests immediately. Color marking was randomized in relation to hatching order. Nestlings were sampled for sexing 12 days after hatching. Because of infertile eggs, degraded samples and widowed females, we have data on the size of the paternal forehead patch and the sex of first egg in only 13 broods.

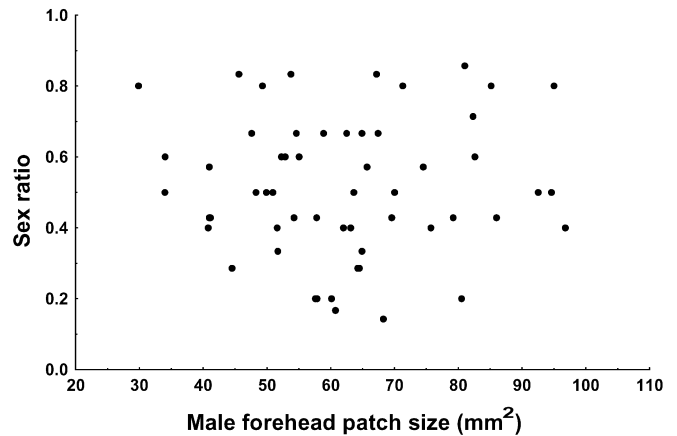
#### Statistical analysis

Throughout this study we used generalized linear models with binomial errors and logit link (Crawley 1993). To be able to compare the results with those obtained in a previous study on a Swedish population of Collared Flycatchers, the initial model of secondary BSR patterns included the same variables as in the study by Ellegren et al. (1996). After including the main effects, a step-wise backward deletion of factors was performed. Interactions were not included in the initial model, as including more than  $n/3$  ( $n$  = sample size) parameter is not recommended (Crawley 1993), but were instead tested after the first model simplification. Finally, we also tested two variables that were not included in the study by Ellegren et al. (1996), i.e. female body size and male wing patch size.

The variables included in the initial model were: the size of the male forehead patch, male body size (tarsus length), male age (subadult or adult: Svensson 1992), female minimum age (females not ringed as chicks were treated as 1 year old in the first year they were captured), clutch size and laying date. In 2002, birds arrived in two migratory waves resulting in a non-normal distribution of laying dates, we therefore assigned each brood to one of two laying date groups, i.e. either an early or a late brood (Fig. 1).

To the minimal model (model including the significant terms only) of the previous variables we added two new variables: female size (tarsus length) and the size of the male's wing patch. As the size of the male wing patch increases significantly from subadult to adult, the age and age  $\times$  wing patch interaction was also included in this model.

In cases where males were socially polygynous, we included only one nest from each male in the analyses (in four cases out of the five it was the primary brood of the male). In ten nests we failed to sex one nestling, because DNA was degraded. These nests were included in the analysis of secondary BSR, as we have no reason to believe that DNA degradation would occur non-randomly in respect to offspring sex. Moreover, exclusion of these nests did not change any of the results. For all nests ( $n=57$ ), we used the number of sexed nestlings when calculating the sex ratios. We used the SAS 8.02 GENMOD module (SAS 1990) for the statistical analyses. Because all generalized linear models of brood sex ratios had a scale parameter that was less than 1.0, and thus the samples were not over-dispersed, we tested the significance of the parameters using  $\chi^2$ -values. When we analyzed the sex of the first egg, the dispersion parameter was larger than 1.0 and we tested significance of parameters with  $F$ -tests (Crawley 1993; Krackow and Tkadlec 2001; the dscale option was used, SAS 1990). For calculating the 95% confidence limit of the deviance ratio we used a jackknife procedure (Sokal and Rohlf 1981).



**Fig. 2** Secondary sex ratio of Collared Flycatcher broods in relation to paternal forehead patch size

**Table 1** Effect of parental traits and laying date on secondary sex ratios in Collared Flycatchers (*Ficedula albicollis*) with parameter estimates and likelihood-ratio statistics from single-variate generalized linear models

Variable	Sample size	Estimate	$\chi^2$	$P$
Laying date	57	-0.4510	4.11	0.04
Male age	57	0.3237	1.97	0.16
Male tarsus	57	-0.0196	0.50	0.48
Forehead patch size	57	0.0006	0.01	0.93
Male wing patch size	54	-0.0003	0.18	0.67
Clutch size	57	-0.1310	0.70	0.40
Female age	56	-0.0883	1.00	0.32
Female tarsus	57	0.0317	2.62	0.11

## Results

In the initial model we included all the variables that were included in a previous study by Ellegren et al. (1996) on a Swedish population of Collared Flycatchers. After removing the non-significant factors, the single significant variable that remained was laying date ( $\chi^2=4.11$ ,  $df=1$ ,  $P=0.043$ ). The secondary sex ratio showed a shift to male-biased clutches late in the season (Fig. 1). Contrary to the results in the Swedish population, the brood sex ratio was not affected by male forehead patch size ( $\chi^2=0.01$ ,  $df=1$ ,  $P=0.933$ , deviance ratio = 0.0001, 95% CI =  $\pm 0.0012$ ; Fig. 2). Moreover, the brood sex ratio was not related to male body size, age, or wing patch size, nor to clutch size or female body size (for the results of single-variate analyses see Table 1).

Post-ovulation mechanisms of sex ratio adjustment predict that females laying multiple-egg clutches may restrict the sex ratio manipulation to the first egg of a clutch (Emlen 1997) and would reduce the probability of detecting sex ratio manipulation at the brood level. However, we found no effect of the forehead patch size of the father, i.e. the character found to be related to brood sex ratios in a previous study (Ellegren et al. 1996), on the sex of the first laid egg ( $F_{1,11}=0.70$ ,  $P=0.42$ ). Thus, even

when we assumed a sex manipulation mechanism that mainly affects the first laid egg, we found no evidence for an offspring sex-bias related to the forehead patch size of the father.

## Discussion

Our study revealed that the brood sex ratio in the Hungarian population of Collared Flycatchers was affected by different factors than in a Swedish population of the same species (Ellegren et al. 1996). There are so far very few species in which brood sex ratio patterns have been investigated in different populations. However, in some species inconsistencies between populations have been found (e.g. in great tit: Kölliker et al. 1999; Lessells et al. 1996; Oddie and Reim 2002; Radford and Blakey 2000). In blue tits, inconsistent BSR patterns in relation to male appearance quality may be explained by the fact that different measurements of male quality was used. In a Swedish population, the UV coloration of male blue tits was used as an indicator of male quality and it was found to affect the brood sex ratio (Sheldon et al. 1999), whereas when male size was used as an indicator of quality in an English population, it did not affect the brood sex ratio (Leech et al. 2001). However, when the same factor, i.e. male survival, was investigated in two different blue tit population there was no consistent effect on brood sex ratios (Leech et al. 2001; Svensson and Nilsson 1996). Because so few studies of BSR between populations or closely related species have been conducted, it is hard to draw any conclusions. So far, however, data suggest that BSR patterns may differ between populations of the same species. This has been used as an argument for the lack of BSR manipulation in birds, and that observed patterns are rather statistical artifacts than true biological effects (Krackow 1999). However, given the recent evidence for the occurrence of adaptive BSR manipulation in birds (Badyaev et al. 2002, 2003; Komdeur 1998; Sheldon et al. 1999), the other possibility is that BSR manipulation is a flexible mechanism that is affected by many different social and environmental factors and therefore prone to differ between populations and species.

One important difference between the studied populations of Collared Flycatchers is that, contrary to the result found in a Swedish population (Ellegren et al. 1996), in Hungary we did not find any relationship between brood sex ratio and the forehead patch size of the male, and this was true also when restricting the analysis to the sex of the first egg. In the analysis of the effect of forehead patch size on BSR, the deviance ratio (corresponding to  $r^2$ ) published by Ellegren et al. (1996) was 0.083, which is far outside the 95% confidence interval of our deviance ratio ( $0.0001 \pm 0.0012$ ). Hence the probability of obtaining these different patterns between the two population by chance is very low. Instead this between-population difference may be explained by other factors that differ between these two populations. In both popu-

lations, forehead patch size seems to be important for female social and/or extra-pair mate choice (Michl et al. 2002; Qvarnström et al. 2000; Sheldon et al. 1997; Sheldon and Ellegren 1999). However, in the Swedish population, male forehead patch size is condition-dependent (Gustafsson et al. 1995; Qvarnström 1999), while there is no such relationship in the Hungarian population (Hegyi et al. 2002). Thus, the payoff of benefits and costs of BSR adjustment may differ between these two populations such that only in the Swedish population can females accrue benefits from males with large forehead patches that are large enough to outweigh the costs of sex ratio manipulation.

In the Hungarian population, we found a significant relationship between laying date and BSR, so that an excess of sons was produced late in the season. If sex differences in nestling mortality rates are related to the food resources, either seasonal change in food supply (laying date effect) or seasonal changes in parental quality (i.e. low quality individuals arrive later: Hasselquist 1998; Møller et al. 2003) may result in a seasonal change of the secondary brood sex ratios in a way that nestlings of the less sensitive sex will be over-represented in late broods. This pattern can be the result of an adaptive primary sex ratio adjustment or sex-biased nestling mortality. However, a study of Swedish Collared Flycatchers does not support this idea, as males and females did not differ in environmental sensitivity (Sheldon et al. 1998). On the other hand, population differences may exist also in this factor, and given the quite large number of broods with some embryo or nestling mortality (42% in our dataset) further investigations are needed. Another explanation for the seasonal shift in BSR is based on the suggestion that steroid hormones may play a role in avian sex determination (Petrie et al. 2001). We have found that there is a seasonal shift in maternally transferred hormones, so that egg yolk of later laid clutches contain higher testosterone levels (Michl et al., unpublished data). According to the hypothesis proposed by Petrie et al. (2001), higher levels of testosterone in the egg yolk should result in male-biased broods, just as observed in the present study. Such a mechanism could be adaptive, if sons for some reason fare better when produced late in the season, but we have no direct evidence for this. However, the observed pattern of sex ratio bias related to a change in mean egg yolk testosterone levels could be non-adaptive, if testosterone adjustment is to induce rapid nestling growth in late hatched broods (Schwabl 1996), or if it is a consequence of changing levels of female aggression (Whittingham and Schwabl 2002), e.g. caused by a change in breeding density over the season. To draw firm conclusions of the laying date effect, however, long-term studies are clearly needed, as between year differences in seasonal BSR patterns may occur (Radford and Blakey 2000).

In the present study, we found a different pattern of BSR manipulation compared to a Swedish population of Collared Flycatchers. There was no relationship between BSR and male forehead patch size in our Hungarian study population whereas such a relationship was found in the



Swedish population. Instead, in Hungary we found that broods became more male-biased later in the season, a pattern that may have both adaptive and non-adaptive explanations. To be able to investigate the occurrence of and circumstances for adaptive brood sex ratio manipulation in birds, more studies of avian BSR patterns between years and populations, of the same species or closely related species, are clearly needed.

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## References

- Badyaev AV, Hill GE, Beck ML, Dervan AA, Duckworth RA, McGraw KJ, Nolan PM, Whittingham LA (2002) Sex-biased hatching order and adaptive population divergence in a passerine bird. *Science* 295:316–318
- Badyaev AV, Beck ML, Hill G, Whittingham LA (2003) The evolution of sexual size dimorphism in the house finch v. maternal effects. *Evolution* 57:384–396
- Bensch S (1999) Sex allocation in relation to parental quality. *Proc Int Ornithol Congr* 22:451–456
- Burley N (1981) Sex ratio manipulation and selection for attractiveness. *Science* 211:721–722
- Crawley MJ (1993) *GLIM for Ecologists*. Blackwell Science Ltd., Oxford
- Ellegren H, Fridolfsson A-K (1997) Male-driven evolution of DNA sequences in birds. *Nat Genet* 17:182–184
- Ellegren H, Gustafsson L, Sheldon BC (1996) Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. *Proc Natl Acad Sci USA* 93:11723–11728
- Emlen ST (1997) When mothers prefer daughters over sons. *Trends Ecol Evol* 12:291–292
- Fridolfsson A-K, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. *J Avian Biol* 30:116–121
- Garamszegi LZs, Møller AP, Török J, Michl G, Péczely P, Richard M (2004) Immune challenge mediates vocal communication in a passerine bird: an experiment. *Behav Ecol* 15:148–157
- Gustafsson L, Qvarnström A, Sheldon BC (1995) Trade-offs between life history traits and a secondary sexual character in male collared flycatchers. *Nature* 375:311–313
- Hasselquist D (1998) Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Evolution* 79:2376–2390
- Hasselquist D, Kempenaers B (2002) Parental care and adaptive brood sex ratio manipulation in birds. *Philos Trans R Soc Lond B* 357:363–372
- Hegyi G, Török J, Tóth L (2002) Qualitative population divergence in proximate determination of a sexually selected trait in the collared flycatcher. *J Evol Biol* 15:710–719
- Kölliker M, Heeb P, Werner I, Mateman AC, Lessells CM, Richner H (1999) Offspring sex ratio is related to male body size in the great tit (*Parus major*). *Behav Ecol* 10:68–72
- Komdeur J (1998) Long-term fitness benefits of egg sex modification by the Seychelles warbler. *Ecol Lett* 1:56–62
- Komdeur J, Pen I (2002) Adaptive sex allocation in birds: the complexities of linking theory and practice. *Philos Trans R Soc Lond B* 357:373–380
- Krackow S (1999) Avian sex ratio distortions: The myth of maternal control. *Proc Int Ornithol Congr* 22:425–433
- Krackow S, Tkadlec E (2001) Analysis of brood sex ratios: implications of offspring clustering. *Behav Ecol Sociobiol* 50:293–301
- Krebs EA, Green DJ, Double MC, Griffith R (2002) Laying date and laying sequence influence the sex ratio of crimson rosella broods. *Behav Ecol Sociobiol* 51:447–454
- Leech DI, Hartley IR, Stewart IRK, Griffith SC, Burke T (2001) No effect of parental quality or extrapair paternity on brood sex ratio in the blue tit (*Parus caeruleus*). *Behav Ecol* 12:674–680
- Lessells CM, Mateman AC, Visser J (1996) Great tit hatchling sex ratios. *J Avian Biol* 27:135–142
- Michl G, Török J, Griffith SC, Sheldon BC (2002) Experimental analysis of sperm competition mechanisms in a wild bird population. *Proc Natl Acad Sci USA* 99:5466–5470
- Møller AP, Brohede J, Cuervo JJ, de Lope F, Primmer CR (2003) Extrapair paternity in relation to sexual ornamentation, arrival date, and condition in a migratory bird. *Behav Ecol* 14:707–712
- Nishiumi I (1998) Brood sex ratio is dependent on female mating status in polygynous great reed warblers. *Behav Ecol Sociobiol* 44:9–14
- Oddie K (1998) Sex discrimination before birth. *Trends Ecol Evol* 13:130–131
- Oddie K, Reim C (2002) Egg sex ratio and paternal traits: using within-individual comparisons. *Behav Ecol* 13:503–510
- Petrie M, Schwabl H, Brande-Lavridsen N, Burke T (2001) Sex differences in avian yolk hormone levels. *Nature* 412:498–499
- Qvarnström A (1999) Genotype-by-environment interactions in the determination of the size of a secondary sexual character in the collared flycatcher (*Ficedula albicollis*). *Evolution* 53:1564–1572
- Qvarnström A, Pärt T, Sheldon BC (2000) Adaptive plasticity in mate preference linked to differences in reproductive effort. *Nature* 405:344–346
- Radford AN, Blakey JK (2000) Is variation in brood sex ratios adaptive in the great tit? *Behav Ecol* 11:294–298
- SAS Institute (1990) *SAS procedures guide*, version 6, 3rd edn. SAS Institute, Cary, N.C., USA
- Schwabl H (1996) Maternal testosterone in the avian egg enhances postnatal growth. *Comp Biochem Phys A* 114:271–276
- Sheldon BC, Ellegren H (1999) Sexual selection resulting from extrapair paternity in collared flycatchers. *Anim Behav* 57:285–298
- Sheldon BC, Merilä J, Qvarnström A, Gustafsson L, Ellegren H (1997) Paternal genetic contribution to offspring condition predicted by size of male sexual character. *Proc R Soc Lond B* 264:297–302
- Sheldon BC, Merilä J, Lindgren G, Ellegren H (1998) Gender and environmental sensitivity in Collared Flycatchers. *Ecology* 79:1939–1948
- Sheldon BC, Andersson S, Griffith SC, Örnberg J, Sendecka J (1999) Ultraviolet colour variation influences blue tit sex ratios. *Nature* 402:874–877
- Sokal RR, Rohlf FJ (1981) *Biometry*, 2nd edn. Freeman, New York
- Svensson E, Nilsson J-Å (1996) Mate quality affects offspring sex ratio in blue tits. *Proc R Soc Lond B* 263:357–361
- Svensson L (1992) *Identification guide to european passerines*. Mårstatträck, Stockholm
- Teather KL, Weatherhead PJ (1989) Sex specific mortality in nestling great-tailed grackles. *Ecology* 70:1485–1493
- Török J, Michl G, Garamszegi LZs, Tóth L (1999) Costs and benefits in a complex mating system from female perspective. *Adv Ethol* 34:185

- Török J, Hegyi G, Garamszegi LZs (2003) Depigmented wing patch size is a condition-dependent indicator of viability in male collared flycatchers. *Behav Ecol* 14:382–388
- Westerdahl H, Bensch S, Hansson B, Hasselquist D, von Schantz T (2000) Brood sex ratios, female harem status and resources for nestling provisioning in the great reed warbler (*Acrocephalus arundinaceus*). *Behav Ecol Sociobiol* 47:312–318
- Whittingham LA, Schwabl H (2002) Maternal testosterone in tree swallow eggs varies with female aggression. *Anim Behav* 63:63–67