The original publication is available at www.springerlink.com via the following link:

Males are sensitive — sex-dependent effect of rearing conditions on nestling growth

Balázs Rosivall · Eszter Szöllősi · Dennis Hasselquist · János Török

Abstract The sex-dependent effect of environmental conditions on nestlings has been extensively studied in size dimorphic birds. Whether males or females are more sensitive to poor conditions is not yet clear; however, the degree of sexual size-dimorphism, brood size and their interactions seem to influence the pattern. Much less is known about sex-dependent environmental sensitivity in size-monomorphic species, even though it may result in biased sex allocation. We altered the rearing conditions by brood size manipulation in the size-monomorphic collared flycatcher and then examined the sex-specific development of the nestlings. In all analyses, we controlled for the effect of paternity, because one may expect extra-pair young to be of better genetic quality and perform better at least under poor conditions. However, this was not the case, because we did not find any difference in growth rate or fledging size between extra- and within-pair young. We found that male nestlings had the potential for faster growth under favourable conditions, but suffered more under poor conditions. We found no sex × environment interaction for fledging size probably because the growth curves level off before fledging, and the disadvantaged nestlings can catch up with their siblings. The larger sensitivity of males does not explain the previously found seasonal shift in brood sex ratios and contradicts previous findings in another size-monomorphic species where females were more sensitive. This suggests that even in size-monomorphic species, no general rule exists, which determines the more sensitive sex.

Introduction

Sex differences in the effects of environmental conditions (e.g. food supply and brood size) on nestlings have been intensively studied in sexually size dimorphic birds. The common notion that the larger sex should be more sensitive (in terms of e.g. growth speed or final size) to poor conditions due to its larger nutritional need has not been unambiguously supported (reviewed e.g. in Råberg et al. 2005). Råberg et al. (2005) found that both brood size and the degree of sexual size dimorphism (SSD) are likely to influence the sensitivity of the sexes. In species with small broods and with large SSD, the larger sex was more sensitive as expected (e.g. Brommer et al. 2003; Velando 2002), while in species with relatively large broods and small SSD, the smaller sex suffered more under poor conditions (e.g. Råberg et al. 2005; Rowland et al. 2007). The latter relationship may be explained by the fact that the small difference in size may not result in considerable difference in energy requirement, but even a small size advantage can be beneficial in sibling competition when food is scarce. Though a recent meta-analysis (Jones et al.

Communicated by M. Leonard

B. Rosivall (✉) · E. Szöllősi · J. Török
Behavioural Ecology Group,
Department of Systematic Zoology and Ecology,
Eötvös Loránd University,
Pázmány Péter sétány 1/c,
1117 Budapest, Hungary
e-mail: rosi@ludens.elte.hu

D. Hasselquist
Department of Animal Ecology, Lund University,
Ecology Building,
22362 Lund, Sweden

2009) found different results, it also came to the conclusion that the interaction of brood size and the degree of SSD may influence which sex is more sensitive.

Interestingly, sex-dependent environmental sensitivity has been found even in the sexually size-monomorphic zebra finch (*Taeniopygia guttata*). Females were more sensitive: their growth rate, mortality after independence and metabolic rate in adulthood were more dependent on rearing conditions than that of males, though no such sex difference was found in size and immune response (de Kogel 1997; Martins 2004; Verhulst et al. 2006; Naguib et al. 2004). Due to lack of information, it is not yet clear whether female sensitivity is a general pattern in size-monomorphic species. Further studies on such species can provide important information also on what factors (other than SSD) may explain sex-dependent sensitivity.

Sex differences in the costs and benefits of rearing certain nestlings are expected to influence the allocation of parental care and may select for sex ratio adjustment. Sex-dependent environmental sensitivity is likely to affect the net benefit of rearing male and female chicks. Thus, we can predict that when rearing conditions of the nestlings are expected to be adverse (either due to poor condition of the parents or the environment), the less sensitive sex will be overproduced. Indeed, in some species, where both environmental sensitivity and sex ratios were examined, the observed patterns met the predictions. For example, the less sensitive males were overproduced in the zebra finch under poor food conditions (Bradbury and Blakey 1998; Kilner 1998; Martins 2004) and in the lesser black-backed gull (*Larus fuscus*) when the mothers were in poor body condition (Nager et al. 1999, 2000). Seasonal shift in brood sex ratios is also a common phenomenon in birds (Cordero et al. 2001; Dijkstra et al. 1990; Krebs et al. 2002; Rosivall et al. 2004), and one of the many explanations is related to sex-dependent environmental sensitivity (Hasselquist and Kempenaers 2002). That is because in temperate zones, food supply changes over the season, and if one sex is less sensitive to food conditions, this sex should be overproduced in the part of the season when food is limited.

In the present study, we examined environmental sensitivity in the size-monomorphic collared flycatcher (*Ficedula albicollis*). Our major goals were to investigate whether larger female sensitivity is the general pattern in size-monomorphic species and whether environmental sensitivity can explain the seasonal shift in brood sex ratio, which was observed earlier in our population. In our earlier paper (Rosivall et al. 2004), we found that males were overproduced late in the season when food conditions are usually deteriorating, so we predicted males to be less sensitive to situations when food is restricted. The same prediction follows from studies on zebra finches (see above). To alter the rearing conditions of the chicks, we manipulated brood size. However, in addition to nestling size measures, which have already been studied in another collared flycatcher population (Sheldon et al. 1998), we also measured nestling growth, which seems to be a more sensitive indicator of environmental conditions than size per se (see e.g. Martins 2004 versus Naguib et al. 2004).

Methods

Study species and field methods

Field data were collected from a nestbox-breeding population of collared flycatchers in the Pilis Mountains (47°43′N, 19°01′E), Hungary. The study plot is part of a continuous, unmanaged, oak-dominated woodland, a protected area of Duna-Ipoly National Park. The collared flycatcher is a small hole-nesting, long-distance migratory passerine bird that starts to breed in mid April. Adult males and females do not differ in tarsus length ($F_{1,1615}=0.03$, $p=0.858$; males, mean±SD= 17.41±0.49; females, mean±SD=17.43±0.49). Females usually lay five to seven eggs, and the eggs hatch approximately 12 days after the last egg was laid. Nestlings usually fledge 14–15 days after hatching.

We studied altogether 50 broods with six or seven eggs. Around the estimated hatching date, nests were inspected daily, and pairs of broods with the same hatching date were assigned. The original brood size of the brood pairs was the same in all but one case (in this case, the difference was one chick between the two broods). We partially cross-fostered broods 2 days after hatching so that four chicks were moved from nest A to nest B and two chicks were moved from nest B to nest A. As a result, we had enlarged (+2 chicks) and reduced (−2 chicks) broods consisting of approximately equal numbers of own and foster chicks that were selected randomly with respect to their size. An earlier paper (Török and Tóth 1990) found that parents do not fully compensate for the brood size manipulation in terms of feeding rate, so this manipulation is suitable to alter the food conditions, and as a result, fledgling size is smaller in enlarged broods (Török and Tóth 1990; Török et al. 2004). In the sister species, the pied flycatcher (*Ficedula hypoleuca*), a similar manipulation also resulted in reduced chick weight, increased heterophil/lymphocyte ratio and reduced PHA response (Ilmonen et al. 2003).

Each nestling was weighed on the day of swapping and marked individually by removing tufts of down on its head and back. Body mass of the nestlings was measured from day 2 (day 0=hatching date of the first chick) and the length of the third outer primary from day 8 (to the nearest 0.1 g and 0.5 mm, respectively) on every second day until day 14. On day 14, tarsus length was also measured (to the nearest 0.1 mm). Body size and growth measures are

analysed separately (see below), because they may have different importance. For example, preference for feather over body mass growth has been observed in a number of species (Nilsson and Svensson 1996; Rosivall et al. 2005), and feather length but not tarsus length or body mass influence the age when the nestlings fledge (Michaud and Leonard 2000).

Sex determination and paternity analysis

Blood samples were collected from 10- to 12-day-old nestlings. Parents were captured and sampled on the same day as their young. For molecular sexing, we used the primers 2550F and 2718R (Fridolfsson and Ellegren 1999) according to the protocol published in Rosivall et al. (2004). All of the adult samples were used as controls during molecular sexing and were always correctly sexed.

A previous study (Rosivall et al. 2009) did not find any difference in growth speed or size of extra-pair (EPY) versus within-pair young (WPY) in collared flycatchers under natural conditions. However, genetic quality differences may have more pronounced effects under poor environmental conditions (David et al. 2000), and consequently, the difference between EPY and WPY may also be larger (Garvin et al. 2006). So, we decided to control for the potential effects of paternity in our analyses. We assessed paternity by using four polymorphic microsatellite loci as described in Rosivall et al. (2009). The polymerase chain reaction products were run on 6% polyacrylamid gels and visualised using a FluorImager (Molecular Dynamics, Sunnyvale, CA, USA). The samples of all members of a family were run in the same gel so any mismatch in the genotypes between offspring and putative parents could be detected. Assuming Mendelian inheritance, we classified offspring as extra-pair young if they showed genotype mismatch with their putative father.

Data analyses

We had paternity data for 46 out of the 50 broods. Among these broods, 28 (60.87%) contained extra-pair young. Seventy of the 298 chicks (23.49%) were sired by extra-pair males. Chicks, which were reared by secondary or widowed females, and those that died due to predation or other reasons were omitted from the analyses, so the sample size was 278 chicks (reared in 45 broods; for some variables, the number of chicks may be smaller due to missing values). In those analyses when only mixed paternity broods were considered, the sample size was 146 chicks (reared in 35 broods). The sex ratio of the enlarged and reduced broods did not differ (generalized linear model; $p < 0.465$; average proportion of males in reduced broods=45.8%; in enlarged broods=50.3%).

Throughout the study, we used individual-based analyses (general linear mixed models) with the brood of origin and brood of rearing as random factors. Manipulation (i.e. whether the chick was reared in reduced or enlarged brood), sex and paternity of the chick were fixed factors. Because previous studies showed that hatching asynchrony and the resulting size hierarchy has a substantial influence on nestling growth in this species (Rosivall et al. 2005; Szöllősi et al. 2007), we controlled for this using the corrected 2-day body mass (CBM) of the chicks as a covariate. CBM was defined as the deviation of 2-day body mass from the mean body mass of the rearing brood divided by the mean body mass, and it is a good estimate of relative hatching time (Szöllősi et al. 2007). The two-way interactions, the sex × manipulation × CBM, paternity × manipulation × CBM and sex × paternity × manipulation interactions were involved in the initial models. Non-significant variables were deleted from the models one-by-one starting with the highest order interactions. Our dependent variables were 14-day body mass, 14-day tarsus length, 14-day feather length, feather growth rate and body mass growth rate. The growth of the primaries was linear between 8 and 12 days, so we calculated the slope of a linear regression for each nestling to describe feather growth rate. The body mass showed logistic growth in most chicks; however, it was rather linear in some late hatched chicks of the enlarged broods resulting in a poor fit of the logistic curve and poor estimation of the growth rate constant. So, instead of using the logistic growth constant, we rather estimated the maximum mass gain, which was the daily mass gain of the quasi-linear fast growing period. Depending on whether the chick was fast or slow growing, this linear period was either between 4 and 8 or 6 and 10 days (always the larger value was used). We found a significant CBM × manipulation interaction for all dependent variables, as previously reported on the same dataset (Szöllősi et al. 2007). These results will not be further discussed. All analyses were performed using the SAS 8.2 program. Nestling mortality was not analysed, because in broods where we had data on sex and paternity, only eight nestlings died.

Results

Both measures of nestling growth were influenced by the sex of the nestlings. However, the effect was different in enlarged and reduced broods, as indicated by the significant sex × manipulation interaction (Fig. 1a, b and Table 1). In reduced broods, male nestlings grew faster (feather growth, $F_{1,57}=7.47$, $p=0.008$; body mass growth, $F_{1,57}=2.15$, $p=0.149$), while in enlarged broods, they grew, though not significantly, slower (feather growth, $F_{1,127}=0.80$, $p=0.373$;
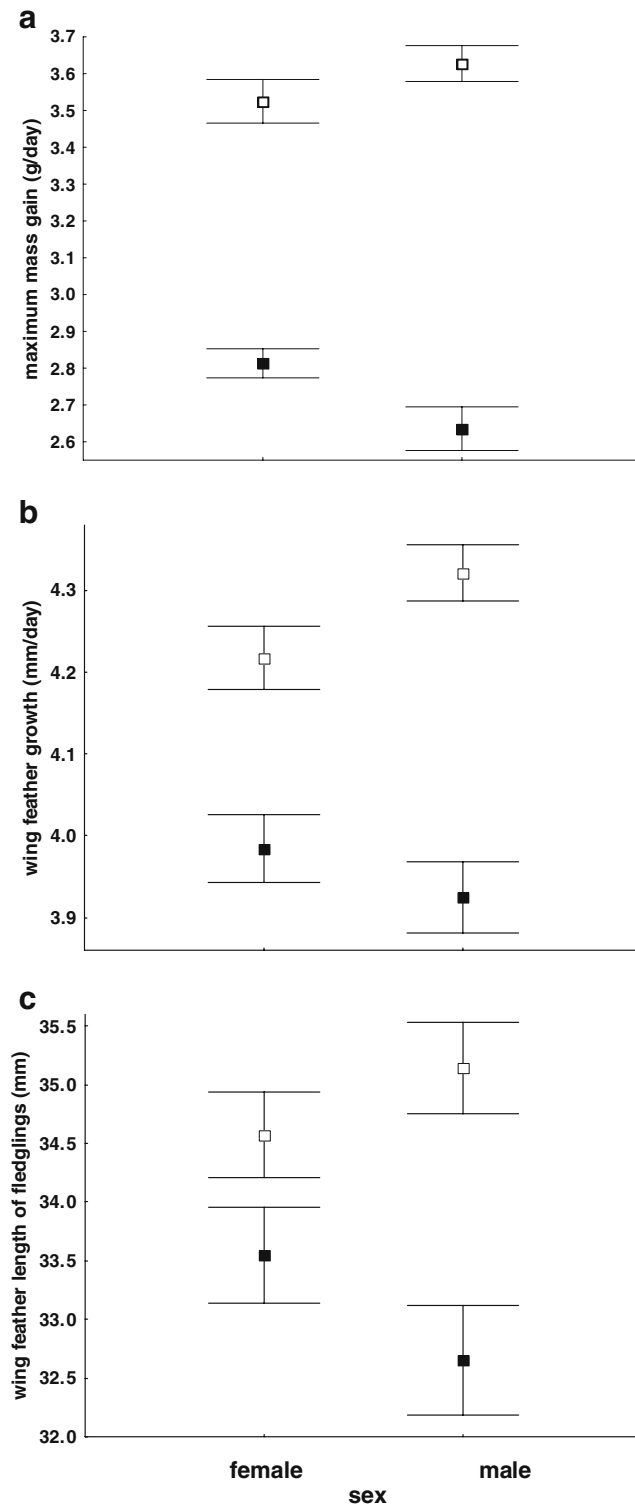
Fig. 1 The effect of sex on body mass growth (a), feather growth (b) and 14-day feather length (c) in reduced (*open squares*) and enlarged (*filled squares*) broods in the collared flycatcher (mean ± SE are indicated)

body mass growth, $F_{1,127}=2.45$, $p=0.120$), suggesting that males have the potential for faster growth, but are more sensitive to rearing conditions. As a result, we found no overall sex effect (Table 1).

We found no sex × manipulation interaction effect on 14-day body mass and feather length of the nestlings (Table 1), probably because growth already levelled off at this stage, and the slower growing nestlings could catch up. However, the pattern for 14-day feather length was very similar to that of the feather growth (Fig. 1c). Again, we found no overall sex effect for these two parameters (Table 1). On the contrary, 14-day tarsus length was smaller in males independent of brood size manipulation (Table 1).

Paternity had no effect on any measures of nestling growth and fledging size, and there was no manipulation × paternity interaction either (Table 1). This was true also when the analyses were restricted to mixed paternity broods (all $p>0.378$, details not shown). In all models, the interaction effect of sex and paternity and their interactions with manipulation or initial size of the nestlings were not significant (Table 1).

Discussion

In this study, our aim was to investigate the environmental sensitivity of male and female collared flycatcher nestlings. Based on the body mass and feather growth patterns, males were able to grow faster under favourable conditions. This is in line with our previous finding in unmanipulated broods (Rosivall et al. 2009). However, under poor conditions (i.e. in enlarged broods), males suffered more in terms of reduced growth rate and smaller size than female nestlings (Fig. 1). Thus, we conclude that males are more sensitive to environmental conditions during growth. However, at the time of fledging, feather length and body mass of the nestlings did not differ between the sexes. This can probably be explained by the fact that both growth parameters level off before fledging, and so, disadvantaged nestlings can catch up with their sibs. The significant difference found in 14-day tarsus length between males and females does not contradict the above results. In a previous study on unmanipulated broods (Rosivall et al. 2009), we found that despite their faster growth, male nestlings had shorter tarsus on day 14 than female nestlings. We showed that after reaching its maximum length, the tarsus of the males shortened more than that of the females (probably due to water loss from the tissues), and we argued that this may be because males were ahead of the females in development (Rosivall et al. 2009). Probably the same applies to the reduced broods of our current study. On the other hand, females in enlarged broods developed faster than males under the same condition, but slower than

Table 1 The effect of sex and paternity on nestling growth and fledgling size under different rearing conditions (in enlarged and reduced broods)

Variables	Mass growth			Feather growth			14-day mass			14-day feather length			14-day tarsus length		
	F	df	p	F	df	p	F	df	p	F	df	p	F	df	p
Sex	0.12	1,204	0.727	1.07	1,204	0.303	1.46	1,192	0.228	0.89	1,192	0.345	*20.33*	*1,189*	*<0.001*
Paternity	0.13	1,198	0.715	0.16	1,198	0.690	1.13	1,187	0.289	0.31	1,187	0.577	0.01	1,185	0.921
Manipulation × sex	*5.74*	*1,204*	*0.018*	*5.30*	*1,204*	*0.022*	0.39	1,185	0.533	2.26	1,186	0.134	2.03	1,184	0.156
Manipulation × paternity	0.04	1,194	0.849	0.24	1,194	0.621	0.08	1,183	0.782	0.80	1,184	0.372	1.00	1,182	0.319
CBM × sex	1.35	1,197	0.246	1.58	1,196	0.211	0.00	1,182	0.975	1.29	1,185	0.258	0.08	1,180	0.772
CBM × paternity	0.63	1,196	0.429	1.50	1,197	0.223	1.40	1,186	0.238	0.14	1,182	0.707	0.66	1,181	0.418
Sex × paternity	0.22	1,195	0.636	0.72	1,195	0.397	0.39	1,184	0.533	0.13	1,183	0.717	2.03	1,183	0.156
Manipulation × sex × CBM	1.41	1,193	0.237	1.18	1,193	0.278	1.44	1,181	0.232	0.15	1,180	0.699	0.52	1,178	0.472
Manipulation × paternity × CBM	0.08	1,191	0.773	0.14	1,192	0.708	0.18	1,179	0.676	0.00	1,179	0.956	0.00	1,177	0.985
Manipulation × sex × paternity	0.20	1,192	0.659	0.00	1,191	0.992	0.43	1,180	0.515	0.97	1,181	0.327	0.62	1,179	0.431
Background variables															
CBM	*32.93*	*1,204*	*<0.001*	*3.18*	*1,204*	*0.076*	*44.80*	*1,193*	*<0.001*	*300.35*	*1,193*	*<0.001*	*24.95*	*1,189*	*<0.001*
Manipulation	*119.00*	*1,204*	*<0.001*	*28.78*	*1,204*	*<0.001*	*16.41*	*1,193*	*<0.001*	*8.69*	*1,193*	*0.004*	*13.71*	*1,189*	*<0.001*
Manipulation × CBM	*32.04*	*1,204*	*<0.001*	*7.09*	*1,204*	*0.008*	*52.00*	*1,193*	*<0.001*	*39.28*	*1,193*	*<0.001*	*23.23*	*1,189*	*<0.001*

In addition to the variables in the focus of the study, in all analyses, we controlled for the following background variables: corrected 2-day body mass (CBM) of the nestlings, manipulation and the interaction of these variables because earlier, we found that they had significant effect (see Szöllősi et al. 2007). Variables retained in the final model are indicated in *italic*, significant effects are indicated in *bold*. Values indicated for removed terms are derived from the last model in which the given variable was included during the backward stepwise model selection. The brood of origin and the brood of rearing were included in all models as random effects, because the model fit was significantly better with than without these two effects (likelihood ratio test, all $p<0.001$)

Fig. 2 The relationship between timing of breeding, brood sex ratios and caterpillar abundance in 2002. *Dots* show brood sex ratios in relation to laying date, *dot size* indicates the number of cases (1, 2 and 3). In 2002, the collared flycatchers arrived in two migratory waves. The *hatched line* separates early and late broods. Caterpillar abundance is estimated by the amount of daily caterpillar frass fall. Frass was collected every 4–5 days; therefore, we indicate the average frass fall for each of these 4–5-day periods by *horizontal lines*. Caterpillar abundance is shown on the day of laying the first egg of each brood (**a**) and 18 days later (i.e. around hatching; **b**). During egg laying, caterpillar abundance increased with date parallel with brood sex ratios (**a**). However, when late broods were hatching, the caterpillar abundance was already small, thus male-biased broods faced unfavourable environment (**b**). The figure is modified from Rosivall et al. (2004); see more details on sex ratio data there
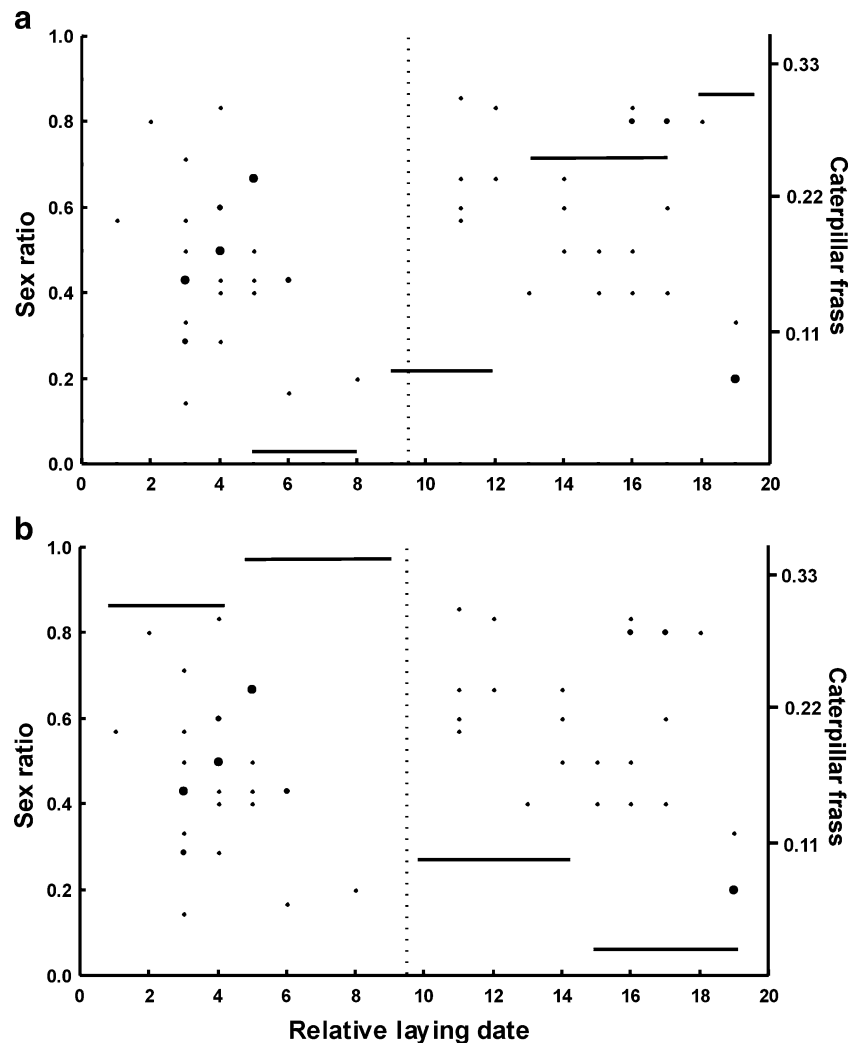
females in reduced broods. So, we argue that probably, none of the sexes could reach their maximum tarsus length on day 14 in enlarged broods, but females were closer to it. As a result, both in enlarged and reduced broods, females appeared to have longer tarsi.

A previous study of collared flycatchers on Gotland (Sweden) failed to find any sex difference in the environmental sensitivity of collared flycatcher nestlings (Sheldon et al. 1998). However, that study focused on body size measures at fledging. At fledging, we also failed to find sex difference or sex × manipulation effect for two out of the three variables. Instead, we found significant effects for the growth parameters, which were not measured in the previous study, and are likely to be more sensitive measures of environmental sensitivity (see e.g. Martins 2004 versus Naguib et al. 2004). It is because poor condition and reduced growth early in life may have long-term consequences on fitness, even if slow-growing individuals can catch up in size

later (Alonso-Alvarez et al. 2007; Birkhead et al. 1999; Blount et al. 2003; Metcalfe and Monaghan 2001).

Earlier studies suggested three hypotheses as an explanation for sex-dependent environmental sensitivity (reviewed e.g. in Sheldon et al. 1998). First, the larger sex has larger energy requirement; second, the heterogametic sex is more likely to be affected by sex-linked deleterious recessive alleles; third, higher testosterone level in males has antagonistic effects on some fitness-related traits. Later studies suggested that in birds, either males or females can be more sensitive depending on the direction of SSD (reviewed e.g. in Råberg et al. 2005), refuting the last two hypotheses. In addition, the role of size seems to be more complex than thought before, because depending on the degree of SSD, either the larger or the smaller sex can be more sensitive (see "Introduction" section). The results on sexually size-monomorphic species also suggest that there is no general rule for sensitivity, because studies on zebra

finches (de Kogel 1997; Martins 2004; Verhulst et al. 2006) found that females are more sensitive to poor conditions, while our study suggests that in collared flycatchers, males are more sensitive. Further studies are clearly needed to identify the factors, which determine sensitivity in different species. However, we cannot exclude the possibility that sex × environment interactions early in life reflect different allocation strategies of male and female nestlings rather than different sensitivity of the sexes. If so, different environmental factors may affect the sexes in different ways. Indeed, in some species, the conclusions on sensitivity were dependent on the environmental factor manipulated and the way the chick response was measured. For example, in the great tit (Parus major), a study by Oddie (2000) suggests that females perform worse when they are in competitive disadvantage, while Tschirren et al. (2003) found that male nestlings were more affected by parasite infections. In the blue tit (Parus caeruleus), brood size manipulation affected the body size of female nestlings more than that of male nestling (Råberg et al. 2005), while the immune response to a PHA challenge under poor conditions was reduced only in males (Dubiec et al. 2006). On the contrary, zebra finch studies with different manipulation methods, and a range of measured response variables came to similar conclusions showing that females were more sensitive (de Kogel 1997; Martins 2004; Verhulst et al. 2006).

In any case, if environmental conditions affect any fitness component in a sex-dependent manner, changing the relative costs or benefits of rearing male and female nestlings, selection may favour sex-biased allocation of parental resources and may lead to the evolution of sex ratio adjustment. Indeed, in some species, where both environmental sensitivity and brood sex ratios were examined, the less sensitive sex was overproduced under poor conditions (Bradbury and Blakey 1998; Kilner 1998; Martins 2004; Nager et al. 1999, 2000). One of our aims in this study was to investigate whether sex-dependent environmental sensitivity can explain the sex ratio patterns observed previously in the Hungarian population of collared flycatchers. In an earlier study, we found that males were overproduced late in the season (Rosivall et al. 2004), at a time when food availability is usually decreasing, making us predict that males were less sensitive to poor food supply. Surprisingly, our experiment revealed the opposite pattern. This suggests that the sex allocation pattern observed in 2002 (i.e. when the sex ratio pattern was examined) was not adaptive, because male-biased broods faced unfavourable conditions during growth (Fig. 2b). However, we have no information about sensitivity during the embryonic period. The amount of nutrients the mothers allocate into their eggs is known to vary with environmental conditions in this species (Hargitai et al. 2005), so one could argue that

increasing food availability during egg formation may favour the more sensitive sex in later laid broods (Fig. 2a) if sex differences exist also during embryonic growth. Hence, it is not yet clear whether environmental sensitivity can explain the observed sex ratio pattern.

Embryonic sensitivity and the relationship between food supply and sex ratio pattern should be further tested in the future, as well as the alternative explanations for seasonal sex ratio shift. These alternatives mainly focus on the sex difference in time of maturation. First, in some species, one sex often breeds as yearling, while the other sex does not. For example, Krebs et al. (2002) argued that the overproduction of females in early broods of crimson rosellas (Platycercus elegans) can be adaptive, because they are likely to breed as yearling, and thereby their lifetime reproductive success is more affected by the date of fledging than that of males. In other species, while both sexes can breed as yearling, its probability is dependent on fledging date only in one sex, and this sex is overproduced in early broods (Cordero et al. 2001; Daan et al. 1996; Dijkstra et al. 1990).

In summary, our results show that environmental sensitivity can be sex-dependent also in sexually size-monomorphic species. However, even in such species, no general rule exists, which determines the more sensitive sex. So, further studies are clearly needed to investigate the factors that may influence environmental sensitivity. Our data also draw attention to the fact that in birds, sensitivity during embryonic growth might also be important in shaping sex allocation patterns, and future studies should not focus exclusively on post-hatching sensitivity.

Ethical notes The authors declare that the experiment complies with the current laws of Hungary.

Conflict of interest The authors declare that they have no conflict of interest.

References

Alonso-Alvarez C, Bertrand S, Faivres B, Sorci G (2007) Increased susceptibility to oxidative damage as a cost of accelerated growth in the zebra finches. Funct Ecol 21:873–879

Birkhead TR, Fletcher F, Pellatt EJ (1999) Nestling diet, secondary sexual traits and fitness in the zebra finch. Proc R Soc Lond B 266:385–390

Blount JD, Metcalfe NB, Arnold KE, Surai PF, Devevey GL, Monaghan P (2003) Neonatal nutrition, adult antioxidant defences and sexual attractiveness in the zebra finch. Proc R Soc Lond B 270:1691–1696

Bradbury RB, Blakey JK (1998) Diet, maternal condition, and offspring sex ratio in the zebra finch, *Poephila guttata*. Proc R Soc Lond B 265:895–899

Brommer JE, Karell P, Pihlaja T, Painter JN, Primmer CR, Pietiäinen H (2003) Ural owl sex allocation and parental investment under poor food conditions. Oecologia 137:140–147

Cordero PJ, Viñuela J, Aparicio JM, Veiga JP (2001) Seasonal variation in sex ratio and sexual egg dimorphism favouring daughters in first clutches of the spotless starling. J Evol Biol 14:829–834

Daan S, Dijkstra C, Weissing FJ (1996) An evolutionary explanation for seasonal trends in avian sex ratios. Behav Ecol 7:426–450

David P, Bjorksten T, Fowler K, Pomiankowski A (2000) Condition dependent signalling of genetic variation in stalked-eyed flies. Nature 406:186–188

de Kogel CH (1997) Long term effects of brood size manipulation on morphological development and sex-specific mortality of offspring. J Anim Ecol 66:167–178

Dijkstra C, Daan S, Buker JB (1990) Adaptive seasonal variation in the sex ratio of kestrel broods. Funct Ecol 4:143–147

Dubiec A, Cichoń M, Deptuch K (2006) Sex-specific development of cell-mediated immunity under experimentally altered rearing conditions in blue tit nestlings. Proc R Soc Lond B 273:1759–1764

Fridolfsson A-K, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. J Avian Biol 30:116–121

Garvin JC, Abroe B, Pedersen MC, Dunn PO, Whittingham LA (2006) Immune response of nestling warblers varies with extrapair paternity and temperature. Mol Ecol 15:3833–3840

Hargitai R, Török J, Tóth L, Hegyi G, Rosivall B, Szigeti B, Szöllősi E (2005) Effects of environmental conditions and parental quality on the inter- and intraclutch egg-size variation in the collared flycatcher (*Ficedula albicollis*). Auk 122:509–522

Hasselquist D, Kempenaers B (2002) Parental care and adaptive brood sex ratio manipulation in birds. Phil Trans R Soc B 357:363–372

Ilmonen P, Hasselquist D, Langefors Å, Wiehn J (2003) Stress, immunocompetence and leucocyte profiles of pied flycatchers in relation to brood size manipulation. Oecologia 136:148–154

Jones KS, Nakagawa S, Sheldon BC (2009) Environmental sensitivity in relation to size and sex in birds: meta-regression analysis. Am Nat 174:122–133

Kilner R (1998) Primary and secondary sex ratio manipulation by zebra finches. Anim Behav 56:155–164

Krebs EA, Green DJ, Double MC, Griffiths R (2002) Laying date and laying sequence influence the sex ratio of crimson rosella broods. Behav Ecol Sociobiol 51:447–454

Martins TLF (2004) Sex specific growth rates in zebra finch nestlings: a possible mechanism for sex ratio adjustment. Behav Ecol 15:174–180

Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? Trends Ecol Evol 16:254–260

Michaud T, Leonard M (2000) The role of development, parental behavior, and nestmate competition in fledging of nestling tree swallows. Auk 117:996–1002

Nager RG, Monaghan P, Griffiths R, Houston DC, Dawson R (1999) Experimental demonstration that offspring sex ratio varies with maternal condition. Proc Natl Acad Sci USA 96:570–573

Nager RG, Monaghan P, Houston DC, Genovart M (2000) Parental condition, brood sex ratio and differential young survival: an experimental study in gulls (*Larus fuscus*). Behav Ecol Sociobiol 48:452–457

Naguib M, Riebel K, Marzal A, Gil D (2004) Nestling immunocompetence and testosterone covary with brood size in songbird. Proc R Soc Lond B 271:833–838

Nilsson J-Å, Svensson M (1996) Sibling competition affects nestling growth strategies in marsh tits. J Anim Ecol 65:825–836

Oddie K (2000) Size matters: competition between male and female great tit offspring. J Anim Ecol 69:903–912

Råberg L, Stjernman M, Nilsson J-Å (2005) Sex and environmental sensitivity in blue tit nestlings. Oecologia 145:496–503

Rosivall B, Török J, Hasselquist D, Bensch S (2004) Brood sex ratio adjustment in collared flycatchers (*Ficedula albicollis*): results differ between populations. Behav Ecol Sociobiol 56:346–351

Rosivall B, Szöllősi E, Török J (2005) Maternal compensation for hatching asynchrony in the collared flycatcher *Ficedula albicollis*. J Avian Biol 36:531–537

Rosivall B, Szöllősi E, Hasselquist D, Török J (2009) Effects of extrapair paternity and sex on nestling growth and condition in the collared flycatcher, *Ficedula albicollis*. Anim Behav 77:611–617

Rowland E, Love OP, Verspoor JJ, Sheldon L, Williams TD (2007) Manipulating rearing conditions reveals developmental sensitivity in the smaller sex of a passerine bird, the European starling *Sturnus vulgaris*. J Avian Biol 38:612–618

Sheldon BC, Merilä J, Lindgren G, Ellegren H (1998) Gender and environmental sensitivity in nestling collared flycatchers. Ecology 79:1939–1948

Szöllősi E, Rosivall B, Török J (2007) Is hatching asynchrony beneficial for the brood? Behav Ecol 18:420–426

Török J, Tóth L (1990) Costs and benefits of reproduction of the collared flycatcher, *Ficedula albicollis*. In: Blondel J, Gosler A, Lebreton J-D, McCleery R (eds) Population biology of passerine birds. Springer Verlag, Berlin, pp 305–319

Török J, Hegyi G, Tóth L, Könczey R (2004) Unpredictable food supply modifies costs of reproduction and hampers individual optimization. Oecologia 141:432–443

Tschirren B, Fitze PS, Richner H (2003) Sexual dimorphism in succeptability to parasites and cell-mediated immunity in great tit nestlings. J Anim Ecol 72:839–845

Velando A (2002) Experimental manipulation of maternal efforts produces differential effects in sons and daughters: implications for adaptive sex ratios in the blue-footed booby. Behav Ecol 13:443–449

Verhulst S, Holveck M-J, Riebel K (2006) Long-term effects of manipulated natal brood size on metabolic rate in zebra finches. Biol Lett 2:478–480