Sex ratio of *Parus major* and *P. caeruleus* broods depends on parental condition and habitat quality

Michael Stauss, Gernot Segelbacher, Jürgen Tomiuk and Lutz Bachmann

Brood sex ratio was studied in 88 families of *Parus caeruleus* (blue tit) and 95 families of *P. major* (great tit) in deciduous and mixed forest habitats differing in food availability. As a food specialist, the blue tit is expected to be more sensitive to the nutritional differences between the habitats than a food generalist such as the great tit. A shift of brood sex ratio towards males was detected for great tits in the high quality habitat, but there was no significant impact of parental condition or the number of nestlings. In contrast, brood sex ratio of blue tits was not affected by habitat quality. In blue tits, male condition correlated positively with a male-biased sex ratio. Habitat quality, however, affected the body mass differences of male and female blue tit siblings, and nestlings developed differently. The low quality habitat had a negative effect on the sexual dimorphism of siblings in male-biased broods, and the condition of offspring was bad. Nevertheless, sexual dimorphism cannot explain the differences between great and blue tits with respect to the correlation of sex ratio and individual condition.

Sex ratio theory intends to explain the frequently observed variation in the proportion of male and female offspring in natural populations. According to theoretical considerations, sex allocation in offspring is efficient if males compete for good resources, and selection operates on mate choice. In these cases, females may invest in the sex that has the highest probability for survival and future reproductive success. If females are able to predict the relative reproductive value of their offspring, those mating with high quality males are expected to skew the brood sex ratio towards sons. Accordingly, females in good condition would increase their fitness by producing sons of high quality, while females in poor condition would enhance their fitness by producing daughters rather than sons of poor quality (Trivers and Willard 1973, Charnov 1982, Trivers 1985).

Chromosomal sex determination (CSD) is expected to hamper the facultative adjustment of sex ratios (Maynard Smith 1978, Williams 1979, Charnov 1982). However, recent studies on various taxa with CSD have reported striking shifts in offspring sex ratios that are in line with the assumption of selection (Wiebe and Bortolotti 1992, Korpimäki et al. 2000, Whittingham and Dunn 2000, Whittingham et al. 2002). These studies indicate that the sex ratio is not completely constrained by CSD. However, the data are not consistent. Thus, whether the observed shifts might just represent sample-
size dependent noise around the expected binomial distribution is in discussion (Williams 1979, Palmer 2000, Krackow 2002).

West and Sheldon (2002) described two situations with a definite theoretical prediction as to the direction of sex ratio adjustment. In addition, they showed that birds can also adjust the offspring sex ratio in the predicted direction.

i) Females produce more sons when mated to an attractive male because sons have an increased fitness inherited from their high-quality father.

ii) In cooperatively breeding species, where one sex helps more than the other, adjusted to the respective environmental conditions offspring sex ratio is biased toward the sex that provides more reproductive help. This, however, is not the case for Parus species and will not be considered further.

Selection of facultative sex ratio variation is only expected when the increase in fitness due to this behaviour exceeds the costs. Accordingly, the most extreme and precise sex ratio variation will be seen in species where the fitness benefits of facultative sex ratio adjustment are high and the costs low (West and Sheldon 2002).

Unfortunately, very little is known about the way in which selection acts on sex ratio variation in natural populations. Complex life histories can influence sex allocation in many ways, and selection for a particular form of sex allocation behaviour might be obscured. Furthermore, if selection varies over time and/or between genetically connected populations, it is unlikely that populations can reach local optima with respect to sex allocation. Thus, estimating sex ratios of total populations can provide highly unreliable information about sex allocation. Patterns of sex ratios can even be inconsistent across species (West and Sheldon 2002). Our approach to these problems is to analyse sex ratio in broods of blue tits (Parus caeruleus) and great tits (P. major) from two habitat types that differ in resource quality. The high quality habitat is located in deciduous forests and the low quality habitat is dominated by coniferous trees. Availability of food is the major criterion for classifying the habitats since the abundance of caterpillars, which is the bulk of nestling food, is on average 50 times higher in deciduous trees than in coniferous trees (van Balen 1973).

As a food specialist, the blue tit is expected to be strongly affected by the nutritional differences between the habitats. As a food generalist, the great tit (Gibb and Betts 1963, Cowie and Hinsley 1987, 1988) should be affected much less by the differing habitats.

The following hypotheses will be tested:

i) Habitat quality and/or the body condition of parents affect the sex ratio in broods of blue and great tits. Thus, male-biased sex ratios are expected in high habitat quality and when parental conditions are good. For example, females in good condition are more likely to produce male offspring than females in poor condition.

ii) The low quality habitat differently affects the body conditions of sons and daughters. Thus, male development is more negatively affected by bad environmental conditions than that of females. Also, such differences are more pronounced in broods of specialised blue tits than in broods of the generalist P. major.

Material and methods

The breeding performance of great and blue tits (Parus major and P. caeruleus) was studied in three study plots near Tübingen, southwest Germany (48°33′N, 9°00′E). Two plots (high quality habitat) are ~1 km apart and consist of woodland (9 ha and 16 ha, respectively; with 90% deciduous trees (mainly beeches and oaks: Fagus sylvatica (67%), oaks Quercus robur (21%) and some other deciduous trees (3%) and a small number of coniferous trees as pines Pinus sylvestris and larches Larix decidua (9%)). The third study area (low quality habitat) is a 35 ha forest dominated by 60% coniferous trees (scots pines and spruces, for more detailed information see Stauss 2000, Stauss et al. 2005).

In total, 95 great tit and 88 blue tit families were studied comprising of 665 and 670 sexed offspring, respectively, during the breeding seasons in 1999 and 2000. Nests were checked regularly during the breeding seasons of 1999 and 2000. First laying date, clutch size, number of hatched young and fledglings were recorded. Nestlings and parents were weighed (to the nearest 0.1 g using a Sartorius balance) and tarsus lengths (to the nearest 0.1 mm using calipers) were measured 14–16 days after hatching. Parents were aged and sexed according to Svensson (1992). All birds were banded with a numbered aluminium ring.

Blood samples (~50 μl) were obtained through tapping the Vena ulnaris and subsequently stored in 250 μl EDTA-buffer in plastic vials to be frozen until further processing. DNA was isolated using the DNA Blood Mini Kit (Qiagen). The gender of the offspring was determined by PCR (Griffiths et al. 1996, 1998). The primers P8 (5′-CTCCCAAGGATGAGRAAYTG-3′) and P2 (5′-TCTGCATCGCTAAATCCTTT-3′) were used to amplify a sex-specific region of the CHD-1 gene on sex chromosomes (Griffiths et al. 1998).
Statistical methods

Two measurements of individual condition were calculated:

i) The overall condition was estimated as the ratio of body mass and tarsus length.
ii) Residuals were determined from the regression between tarsus length (independent variable) and body mass (dependent variable) per year across habitats.

However, no differences were observed when using overall condition instead of residuals in the subsequent analysis. Therefore, only data based on overall condition will be shown.

Mean values of nestling mass, tarsus length and condition for each sex in each brood were used in order to avoid pseudoreplication. Data were standardised for each year across habitats using z-transformation with mean = 0 and variance = 1 in order to eliminate year effects (for all parameters except residuals).

When brood sex ratio is considered as a dependent variable, generalised linear models with the number of sons were used as response variable, and the number of sexed nestlings were used as binomial denominator (procedure gennmod, SAS 1997). These models are binomial, and the option link = logit and type 3 for the likelihood ratio statistics w was used. The effects that habitat type and sex ratio has on the development of broods (differences in body traits between male and female offspring) were tested using a generalised linear model (procedure glm with type III, SAS 1997).

Results

In total, 95 great tit and 88 blue tit families were studied comprising of 665 and 670 sexed offspring, respectively. There was no significant deviation from the expected 50:50 sex ratio of offspring across broods in both habitats (testing for binomial distribution, p > 0.05; great tit (male/male + female): 0.54 ± 0.02 (se) in deciduous forest, 0.50 ± 0.03 in coniferous forest; blue tit: 0.49 ± 0.04 in deciduous forest, 0.48 ± 0.02 in coniferous forest).

First correlations between pairs of all estimated parameters, i.e. habitat quality, number of nestlings, clutch size, laying date, body mass and tarsus lengths, and condition of adult females and males, were analysed. Habitat quality, number of nestlings, condition of adult females and males were found to be statistically uncorrelated parameters. These could be used as effectors on sex ratio in broods in the generalised linear model. Laying date, clutch size, body mass and tarsus lengths statistically correlated with one or more of the above mentioned parameters and were thus excluded from further analyses.

Great tit

i) The analyses revealed a significant impact of habitat quality on brood sex ratio (p = 0.03, Table 1) with a male-bias in the high quality habitat. In contrast, no statistically significant impact of the number of nestlings (p = 0.64, Table 1) and the parental condition (p > 0.08, Table 1) on brood sex ratio could be detected.

ii) Brood sex ratio and habitat quality together have a significant impact on the development of siblings. This is depicted by the significance of the statistical model (p = 0.03, Table 2). In contrast, habitat quality, sex ratio and sex ratio nested within habitat individually have no significant effect on the development of siblings (0.053 < p < 0.107, Table 2).

iii) Depending on the brood sex ratio, sexual dimorphism in siblings develops differently in both habitats (Fig. 1a). Differences in body mass between male and female siblings increases more in male-biased broods in the high quality habitat (p = 0.01) than in the low quality habitat. In the low quality habitat, brood sex ratio does not affect sexual dimorphism in broods (p = 0.95).

Blue tit

i) There was no statistically significant impact of habitat quality and number of nestlings on brood sex ratio (p > 0.57, Table 1). However, male condition correlated positively with a high proportion of male offspring (p = 0.01, Table 1). Although there is no habitat effect per se, the tendency of habitat quality influencing brood sex ratio via parental condition (p = 0.04, p = 0.06, Table 1) may be assumed.

ii) The differences in body mass between male and female siblings significantly depended on habitat quality (p < 0.01, Table 2). Furthermore, nestlings developed differently in response to habitat quality (p = 0.001, Table 2) and sex ratio (p = 0.001, Table 2).

iii) Differences in body mass between male and female siblings increased in male-biased broods in the high quality habitat (p = 0.01). However, the low quality habitat has a negative effect on the sexual dimorphism of siblings in male-biased broods (p = 0.02).
Habitat quality determines the physical conditions of resident individuals. Accordingly, life history traits of specialist species such as the blue tit (*Parus caeruleus*) should be differently affected by environmental variation than those of sympatrically occurring generalist species such as the great tit (*P. major*).

In the present study, we observed a significant habitat effect on brood sex ratio for populations of great tits. In accordance with the hypothesis of Trivers and Willard (1973), great tit broods from deciduous forests (high quality habitat) contain more male offspring than those from the mixed woodland (low quality habitat). Individual condition, however, had no statistically significant effect on offspring sex ratio.

At first glance, our data seem to contrast the results obtained by Leech et al. (2001) who did not detect any correlation between parental quality and offspring sex ratio in blue tit populations from the UK. However, this may be due to different analysis procedures. We noticed that it is crucial to exclude correlated parameters from the analysis. Otherwise effects can be obliterated, and the significant correlations described here would have remained undetected.

As food generalists, great tits respond to variation of resource availability on a population level through plasticity of life history traits. In contrast, individual-based response strategies towards habitat quality were detected for the food specialist blue tit. The condition of adult males positively correlated to a male-biased sex ratio. Such correlation of parental body condition and sex ratio of offspring is also in accordance with the hypothesis of Trivers and Willard (1973). This hypothesis states that females mating with males in good condition would increase their fitness by producing sons rather than daughters. Conversely, females mating with males in poor condition would invest in daughters. This was observed in blue tits, tree swallows (*Tachycineta bicolor*) and house wrens (*Troglodytes aedon*). In these species, females in good condition produced male-biased broods and sons in good condition at the time of fledging (Svensson and Nilsson 1996, Whittingham and Dunn 2000, Whittingham et al. 2002). The observation in American (*Falco sparverius*) and European (*F. tinnunculus*) kestrels that females in good condition raised female-biased broods seems to contrast our data. Yet in these falcons, females are the larger sex demanding more resources (Wiebe and Bortolotti 1992, Korpinmäki et al. 2000).

Males of blue tits are found to be the philopatric sex (Dhondt and Hublé 1968, Greenwood et al. 1979), suggesting that competition for good territories and resources is likely to be stronger among males than females. The assumption that the condition of blue tit males also mirrors their fitness could explain the female bias in offspring sex ratio.

**Table 1.** Dependency of sex ratio on habitat quality, number of nestlings, condition of females and males, respectively, in *P. major* and *P. caeruleus* broods. The analysis of variance is based on a generalised linear model (procedure genmod: SAS 1997). The results of likelihood ratio analyses (type 3) are listed. Significant effects are indicated by + (excess of sons) if high quality habitat and/or good parental conditions correlate with a male bias. Bold: significant at the 5% level.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th><em>P. major</em></th>
<th></th>
<th><em>P. caeruleus</em></th>
<th></th>
<th>sex ratio bias</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df approx. $\chi^2$</td>
<td>p</td>
<td>df approx. $\chi^2$</td>
<td>p</td>
<td></td>
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<tr>
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<td></td>
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</tr>
<tr>
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<td></td>
</tr>
<tr>
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<td></td>
<td></td>
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<tr>
<td>Interaction with habitat quality:</td>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>number of nestlings</td>
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<td>0.128</td>
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<td>0.773</td>
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<tr>
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<td></td>
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</tr>
<tr>
<td>female condition</td>
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<td>0.00</td>
<td>0.964</td>
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<tr>
<td>deviance</td>
<td>84</td>
<td>92.20</td>
<td></td>
<td>72</td>
<td>74.13</td>
</tr>
</tbody>
</table>

*only statistically uncorrelated parameters are considered.

**Table 2.** Effect of habitat (coniferous vs deciduous forest) and sex ratio on the development of broods of *P. major* and *P. caeruleus* expressed as the differences in the body mass of male and female offspring. Only broods with more than five nestlings were analysed (procedure glm, type III; SAS, 1997).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>P. major</th>
<th></th>
<th>P. caeruleus</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>mean square sum</td>
<td>F-value</td>
<td>p</td>
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<tr>
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<td>3.24</td>
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</tr>
<tr>
<td>Error</td>
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<td>0.671</td>
<td>66</td>
<td>0.139</td>
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<tr>
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<td>0.107</td>
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<tr>
<td>Sex-ratio</td>
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<td>2.384</td>
<td>3.56</td>
<td>0.063</td>
</tr>
<tr>
<td>Sex-ratio (habitat)</td>
<td>1</td>
<td>2.607</td>
<td>3.89</td>
<td>0.053</td>
</tr>
</tbody>
</table>

**Discussion**

Habitat quality determines the physical conditions of resident individuals. Accordingly, life history traits of specialist species such as the blue tit (*Parus caeruleus*) should be differently affected by environmental variation than those of sympatrically occurring generalist species such as the great tit (*P. major*).

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breeding partner’s alteration of the sex allocation. Sheldon et al. (1999) detected a skewed offspring sex ratio in blue tits as a female response to male quality (survival) indicated by ultraviolet plumage ornamentation. Faivre et al. (2003) found that in blackbirds (Turdus merula) the secondary sexual traits (bill colour) can reflect physiological quality such as the status of the immune system. Our data also indicate that in natural populations of blue tits individual females can assess the condition of the mate and react on it by skewing the offspring sex ratio.

The data presented here revealed no significant association between female and male condition in breeding pairs of blue tits. Thus, the generally accepted view of mate choice being female dominated is maintained. Additionally, female constitution is relevant for the sex ratio of the offspring (Table 1). They can skew the sex ratio and maternally contribute to the fitness of their offspring. Therefore, the nutritional restrictions of low quality habitats can act against the advantage of male-biased sex ratio. Interestingly, we found significantly smaller size differences in blue tit male and female offspring in male-biased broods (Fig. 1b). This might be due to the higher energy demand of males for a normal development that cannot be fulfilled in a low quality habitat (Stauss et al. unpubl.). Other studies (Pickering, 1980, Godfray 1986, West et al. 1999, Nager et al. 2000) have also shown that interactions between different sexes of offspring can change the sex ratio or the relative reproductive value of the two sexes. The consequences of such intra-brood competition were studied at the population level (Godfray 1986, West et al. 1999, Werren and Hatcher 2000). However, context-dependent effects of competition between the sexes may impede the detection of sex ratio adaptation at the individual level in response to environmental conditions (West et al. 2002). Finally, paternal effects on sex ratio might be obliterated when sex dimorphism is not very pronounced as in the two Parus species (adults exhibit only ~3% sexual dimorphism in mass and size (males >females, own data). Therefore, larger sample sizes are necessary in order to demonstrate differences. Nevertheless, in a recent meta-analysis Sheldon and West (2004) found greater sex ratio shift in ungulate species with greater sexual dimorphism. Thus, the relationships were stronger when sexual size dimorphism was more male-biased. In the generalist great tit the results were as expect. A male-bias in offspring is found in the high quality habitat, regardless of parental conditions. Conversely, in the specialist blue tit the overall effect, i.e. good male condition, correlates with male-biased broods, causing reduced fitness of male-biased broods in the low quality habitat. Consequently, non-male-biased broods seem to have an advantage considering the future reproductive value of offspring.

It has previously been reported that offspring sex ratio can change in the course of a breeding season (Howe 1977, Blank and Nolan 1983, Clutton-Brock and Jason 1986, Dijkstra et al. 1990, Olsen and Cockburn 1991, Zijlstra et al. 1992, Daan et al. 1996). For example, fitness of male fledglings can be reduced when hatching late in the breeding season due to a lower survival rate (Nilsson 1989, Dijkstra et al. 1990, Visser and Verbomen 1999) and/or a reduced success in settling into a good territory in the next breeding season (Nur 1984, Tinbergen and Boerlijst 1990, Verbomen and Visser 1998, Oddie...
Thus, in good quality habitats parental fitness should be highest when producing male offspring in good condition early in the breeding season. However, in accordance with other studies (Svensson and Nilsson 1996, Leech et al. 2001) we found no seasonal decline of the male ratio in both habitats and species.

Our study demonstrates that even closely related species respond to their environment differently in adjusting the sex ratio of their offspring in different habitats. This adaptation is in good congruence with the theory of sex ratio adjustment.

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References


Clutton-Brock, T. and Jason, G. 1986. Sex ratio variation in


mammals. – Am. Nat. 146: 90–92.

Dhondt, A. A. and Hublé, J. 1968. Fledging-date and sex in

variation in the sex ratio of kestrel broods. – Funct. Ecol. 4: 143–147.

variation in the sex ratio of kestrel broods. – Funct. Ecol. 4: 143–147.

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