

Offspring sex ratio is related to male body size in the great tit (*Parus major*)

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Sex allocation theory predicts that the allocation of resources to male and female function should depend on potential fitness gain realized through investment in either sex. In the great tit (*Parus major*), a monogamous passerine bird, male resource-holding potential (RHP) and fertilization success both depend on male body size (e.g., tarsus length) and plumage traits (e.g., breast stripe size). It is predicted that the proportion of sons in a brood should increase both with male body size and plumage traits, assuming that these traits show a father–offspring correlation. This was confirmed in our study: the proportion of sons in the brood increased significantly with male tarsus length and also, though not significantly, with the size of the breast stripe. A sex ratio bias in relation to male tarsus length was already present in the eggs because (1) the bias was similar among broods with and without mortality before the nestlings' sex was determined, and (2) the bias remained significant when the proportion of sons in the clutch was conservatively estimated, assuming that differential mortality before sex determination caused the bias. The bias was still present among recruits. The assumption of a father–offspring correlation was confirmed for tarsus length. Given that both RHP and fertilization success of male great tits depend on body size, and size of father and offspring is correlated, the sex ratio bias may be adaptive. *Key words:* body size, great tits, *Parus major*; resource holding potential, sex allocation, sexual selection. [*Behav Ecol* 10:68–72 (1999)]

Natural selection favors offspring sex ratios that maximize fitness returns per unit parental investment. The allocation of resources to sons versus daughters should be sensitive to the potential fitness gains through either sex (Charnov, 1982). As an example, if male reproductive success increases more steeply with body size than does female reproductive success, a male-biased offspring sex ratio is predicted for large parents (Trivers and Willard, 1973), assuming that body size of parent and offspring is correlated.

In birds, evidence for sex allocation in relation to parental traits includes the zebra finch (*Taeniopygia guttata*) in captivity (Burley, 1981, 1986), and the blue tit (*Parus caeruleus*; Svensson and Nilsson, 1996) and the collared flycatcher (*Ficedula albicollis*; Ellegren et al., 1996) in wild populations. As predicted by sex allocation theory (Charnov, 1982), females mated to sexually attractive and/or high-quality males produced relatively more sons. Furthermore, female zebra finches bias the sex ratio toward daughters when they are relatively more attractive than their male mate (Burley, 1981, 1986). In the zebra finch the sex ratio bias may mainly arise through differential mortality after hatching (Burley, 1986; but see Oddie, 1998), whereas in blue tits and collared flycatchers, a sex ratio bias seems to occur before or at hatching (Ellegren et al., 1996; Svensson and Nilsson, 1996). Thus, both the timing and the mechanism of sex ratio modification can probably vary (Clutton-Brock, 1986; Oddie, 1998).

The great tit (*Parus major*) is a monogamous passerine with weak sexual size dimorphism (e.g., Perrins, 1979). Both parents feed their young at the nest. A manipulation of brood sex ratio did not result in a significant change of parental effort (Lessells et al., 1998), suggesting that raising male and female offspring may require a similar effort. Male great tits

compete both for territories and mates (Drent, 1983; Gosler, 1993; Perrins, 1979). Male body size, as estimated from tarsus length in field studies (e.g., Senar and Pascual, 1997), and plumage traits have been shown to correlate with measures of resource holding potential (RHP), such as priority for access to food (e.g., tarsus length: Garnett, 1981; Maynard Smith and Harper, 1988; breast stripe size: Lemel and Wallin, 1993; Maynard Smith and Harper, 1988; but see Wilson, 1992) and success in obtaining a breeding territory (tarsus length: Drent, 1983). Furthermore, male tarsus length in the great and blue tit correlates with both within-pair and extrapair fertilization success (Blakey, 1994; Kempenaers et al., 1992; Verboven and Mateman, 1997), and there is evidence that males with large breast stripes are preferred by females (Norris, 1990). For both tarsus length and breast stripe size, a parent–offspring correlation has been demonstrated. The two traits are heritable as well as sensitive to environmental conditions during growth (Gebhardt-Henrich and van Noordwijk, 1991; Norris, 1993).

We investigated the relationship between the proportion of sons in a brood and parental phenotypes in the great tit. Given the importance of body size and plumage traits for male fitness, we evaluated the assumption that offspring body size correlates with male body size, and predicted that the proportion of sons is positively related to the male parent's tarsus length and/or breast stripe size.

METHODS

The study was carried out in spring 1995 in a nest-box–breeding great tit population in the Bremgarten forest near Bern, Switzerland. The forest consists mainly of beech and pine trees with a few interspersed oaks and hornbeams. The habitat is of rather poor quality for breeding great tits, as indicated by a comparatively small average (mean \pm SD) clutch size (7.74 ± 1.38 , $N = 91$; cf. Oppliger et al., 1997; Smith et al., 1989). We visited nest-boxes regularly to record laying date, clutch size, start of incubation, hatching date, brood size, and

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fledging date. Nestlings were ringed 9 days after hatching with numbered aluminum rings. Fourteen days after hatching, we captured both parents, and for both nestlings and parents we recorded body mass (to the nearest 0.1 g using a Sartorius balance), tarsus length (to the nearest 0.1 mm using calipers), and wing length (to the nearest millimeter), and took a blood sample from the brachial vein. Parents were aged according to the color of the wing coverts as first-year or older birds (e.g., Gosler, 1993; Perrins, 1979). We photographed the ventral side of the males (holding the bird fully extended on its back and using a reflex camera with a 105-mm macro lens), and later determined breast stripe area from the slides projected onto a digitizing table. A reference scale (graph paper) was photographed together with every bird to calibrate the breast stripe measures of different birds. We measured the surface of the ventral breast stripe to the nearest square millimeter including the area of black feathers posterior to the edges of the white cheeks and anterior to the legs. The mean of three measures of breast stripe size from the same slide was used in the analysis. Photographing and measuring were each carried out by one person (P.H. and I.W., respectively). As expected for a heritable trait (Norris, 1993), breast stripe size was significantly repeatable for male birds that were measured in more than 1 year ($r' = .412$, $F_{39,49} = 2.557$, $p = .001$; Lessells and Boag, 1987). In the breeding seasons of 1996 and 1997, we recorded all the breeding birds to assess local recruitment into the local breeding population and the sex of the recruits.

For molecular sexing, blood was collected in capillary tubes (20 μ l) and transferred directly to an Eppendorf tube containing 100 μ l EDTA buffer. Samples were frozen the same day at -20°C . We extracted the DNA from a subsample of the blood using a commercial kit (Puregene, Gentra Systems, Minneapolis, Minnesota) following the manufacturer's protocol. Sexing was carried out using RAPD (random amplified polymorphic DNA) markers (Griffiths and Tiwari, 1993; Lessells and Mateman, 1998). Random primer sequences had previously been screened for their ability to amplify female-specific DNA fragments in great tits. Such a 10-mer primer was used for polymerase chain reaction (PCR) with the extracted great tit DNA, and the products were separated on an agarose gel. We identified females by the presence of a 941 base-pair DNA fragment that does not occur in males (for further details of laboratory procedures, see Lessells et al., 1996; Lessells and Mateman, 1998). In total, 48 out of 505 (=9.5%) eggs either failed to hatch or the chicks died before blood samples were taken. Nestlings of 64 broods were sexed. To test the accuracy of the molecular sexing method, the sexes of 69 individuals (31 females and 38 males) determined both at the nestling stage in 1995 (using RAPD markers) and as breeding adults in 1996 or 97 (using breast stripe size and the presence/absence of a brood patch; Gosler, 1993; Perrins, 1979) were compared. The molecular and morphological sex determinations agreed in all 69 cases.

Statistical analysis of the proportion of sons in a brood was carried out using logistic regression analysis with binomial errors and a logit link, taking the number of sons in a brood as the dependent variable, and brood size (number of sexed nestlings) as the binomial denominator. The statistical significance of a sex ratio bias in relation to an independent variable was assessed from the change in deviance (denoted as ΔD) when that variable was excluded first from (or included last into) the model (Crawley, 1993). The change in deviance is asymptotically distributed as χ^2 with corresponding degrees of freedom (Crawley, 1993). Statistical analysis of the proportion of sons in a brood was carried out using the statistical package GLMStat (Beath, 1997). We analyzed continuous de-

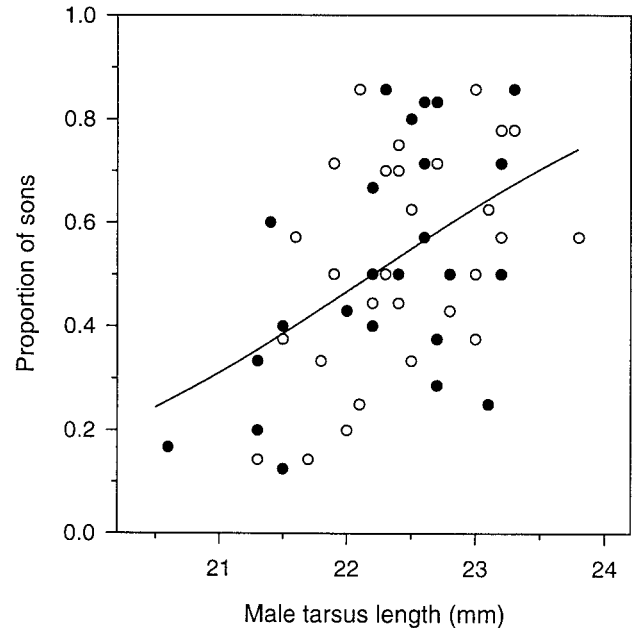


Figure 1

The proportion of sons in relation to the male parent's tarsus length (mm). Filled symbols represent broods with early mortality; open symbols represent broods without early mortality (all eggs hatched and all chicks could be sexed). The logistic regression line on the whole sample is shown.

pendent variables using the statistical package Systat (Wilkinson, 1989).

Of the original 64 broods, the breast stripe size of 7 males could not be measured either because the male had not been caught at the nest (3 cases) or the photographic slide was missing (4 cases). Thus, all analyses in the Results are based on a sample size of 57 broods. Experimental infestation of some broods with fleas as part of a different experiment had no significant influence on nestling sex ratio ($p > .53$), and the analysis was therefore performed on the pooled data. Parametric tests were only applied to continuous dependent variables with normal distributions. We used directed statistical tests when the direction of the association between two variables was specified by our hypothesis (Rice and Gaines, 1994). This is the case for the relationships between (1) the proportion of sons in a brood and both male tarsus length and size of breast stripe, (2) the proportion of sons among reproducing offspring and the nestling sex ratio, and (3) the correlation between parent and offspring tarsus length.

The proportion of male nestlings (age 14 days) in the local population was 51.9% (237 males and 220 females from 64 broods), and did not differ significantly from unity ($\chi^2_1 = 0.633$, $p > .30$). At the level of the brood, the observed distribution of the proportion of male nestlings tended to deviate from the binomial distribution [deviance in null model = 89.40 with 63 df; p (based on 1000 randomizations) = .07; see Westerdaal et al., 1997].

RESULTS

Proportion of sons among offspring

The proportion of sons in a brood was significantly and positively related to the male parent's tarsus length (Figure 1, Table 1), but not the female parent's tarsus length (Table 1). The proportion of sons also tended to be positively related to the size of male breast stripe (Table 1). In a model containing

Table 1

Individual logistic regressions for the relationships between the proportion of nestling sons in a brood and male tarsus length, breast stripe size, and female tarsus length

Parameter	(Δ) Deviance	(Δ) df	Slope (\pm SE)	Deviance ratio ^a	<i>p</i>
Null model	77.52	56			
Male tarsus length	16.36	1	0.68 (\pm 0.17)	0.211	<.001
Male breast stripe size	4.17	1	0.14 (\pm 0.07)	0.054	.051
Female tarsus length	0.73	1	-0.16 (\pm 0.18)	0.009	.392

The null model is the same for all three regressions. The *p* values in the table are sequentially Bonferroni-adjusted (Rice, 1989).

^a Indicates the proportion of deviance explained (corresponding to r^2).

breast stripe size, the inclusion of male tarsus length led to a further significant reduction in deviance ($\Delta D = 13.30$, $p < .001$). Conversely, in a model containing male tarsus length, the inclusion of breast stripe size led to no further significant reduction ($\Delta D = 1.11$, $p > .18$). This difference may be partly due to the observed correlation between breast stripe size and male tarsus length ($r = .27$, $n = 57$, $p = .042$). The proportion of sons was not significantly related to laying date ($\Delta D = 1.65$, $p > .19$), male age ($\Delta D = 0.17$, $p > .60$), female age ($\Delta D = 0.16$, $p > .60$), clutch size ($\Delta D = 0.39$, $p > .50$), and brood size ($\Delta D = 0.30$, $p > .50$). Brood size was not significantly correlated with male tarsus length (Pearson's $r = 0.21$, $n = 57$, $p > .10$). The absence of a significant correlation between male and female tarsus length ($r = -.03$, $n = 57$, $p = .83$) suggests that there was no size-assortative mating, indicating that the sex ratio bias in relation to male tarsus length did not arise indirectly via female tarsus length.

The observed nestling sex ratio bias could arise both by variation in the clutch sex ratio or differential mortality (e.g., Clutton-Brock, 1986). For 29 broods, all the eggs laid could subsequently be sexed; in 28 broods, either not all eggs hatched or nestling mortality occurred before blood sam-

pling. The relationship between the proportion of sons and male tarsus length was similar in the two types of broods (Figure 1; interaction term: $\Delta D = 0.001$, $p > .95$) and the proportion of sons did not differ between the two groups (Figure 1; $\Delta D = 0.003$, $p > .95$). These results suggest, but cannot firmly prove (see Fiala, 1980), a sex ratio bias in the eggs. A conservative test for a relationship between the proportion of sons in the eggs and male tarsus length can be made by assuming that differential mortality has caused the observed bias (Ellegren et al., 1996). If chick mortality before sex determination is taken as entirely son-biased in broods with fathers having a smaller tarsus than the one predicting a 1:1 nestling sex ratio (as calculated from the logistic equation; Figure 1), and entirely daughter-biased in broods with larger fathers, the relationship between the estimated proportion of sons in the eggs and male tarsus length remains positive and significant ($\Delta D = 5.76$, $p < .015$). Thus an association between sex ratio and male tarsus length was already present at egg laying.

Proportion of sons among local recruits

Thirty-six breeding pairs recruited at least one offspring into the local breeding population the following years. The proportion of sons among these recruits was, as expected, significantly related to the brood sex ratio at the nestling stage (null model: $D = 50.46$; $df = 35$; $\Delta D = 15.41$, $p < .001$). In a model containing nestling sex ratio, the inclusion of male tarsus length ($\Delta D = 0.43$, $p > .50$), male breast stripe size ($\Delta D = 0.07$, $p > .70$), or female tarsus length ($\Delta D < 0.001$, $p > .95$) led to no further significant reduction in deviance. As expected from the relationships between male tarsus and nestling sex ratio and nestling and recruit sex ratios, the proportion of sons among recruits tended to increase with male tarsus length ($\Delta D = 2.83$, $p = .058$). The total number of recruits of a pair was not related to male tarsus length (Spearman's $r_s = .05$, $p > .70$).

Parent-offspring correlation of tarsus length

In a stepwise linear regression including both brood size and laying date, mean offspring tarsus length was significantly related to the male but not to the female parent's tarsus length (Figure 2, Table 2). This pattern was similar for male and female offspring when analyzed separately (analyses not shown).

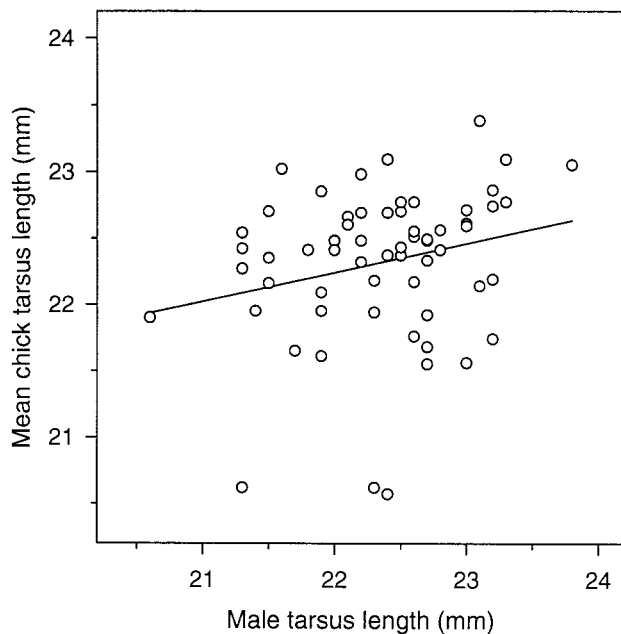


Figure 2

Mean chick tarsus length (weighted for the number of sons and daughters in a brood) in relation to the male parent's tarsus length. The least-square linear regression line is shown.

DISCUSSION

Our results indicate that random segregation of sex chromosomes during meiosis is not the only mechanism determining the sex ratio of offspring (Charnov, 1982; Krackow, 1995; Wil-

Table 2
Stepwise linear regression of mean chick tarsus length in relation to brood size, laying date, male tarsus length, and female tarsus length

Source of variation	df	F	Slope ^a (± SE)	p
Brood size	1	4.76		.033
Laying date	1	2.14		.150
Male tarsus length	1	6.26	0.26 (± 0.10)	.010
Error	54			
Rejected term: Female tarsus length	1	0.02	-0.03 (± 0.13)	.883

Mean chick tarsus length was calculated as the mean of the two within-sex means of nestling tarsus length to weight for variation in the number of sons and daughters per brood.

^a The slopes of the parent-offspring regression lines were calculated after correcting for brood size and laying date.

liams, 1979) in the great tit. As predicted for the great tit, in which male RHP and fertilization success correlate positively with tarsus length and size of breast stripe (see Introduction), the proportion of sons in the brood was significantly related to the male parent's tarsus length and tended to increase with the size of its breast stripe. The relationship with male tarsus length remained significant when breast stripe size was statistically controlled for, but the reverse was not the case. This result may partly be due to the positive correlation between breast stripe size and male tarsus length. The finding that the relationship between the proportion of sons and breast stripe size was weaker than tarsus length does not, however, necessarily indicate that breast stripe size is of no biological importance. Tarsus length is measurable with greater precision than breast stripe size and thus will show, due to lower measurement error, a higher correlation coefficient. It may also be noted that the proportion of deviance in brood sex ratio explained by breast stripe size (5.4%; Table 1) is in the range of the proportion explained by the white forehead patch in collared flycatchers (8.3%), another example of a sexually selected plumage trait (Ellegren et al., 1996).

Our findings suggest that the covariation between the proportion of sons and male tarsus length was already present at egg laying and cannot be explained purely by differential mortality (e.g., Dhondt, 1970), and that this sex ratio bias may be adaptive: offspring tarsus length was significantly correlated with the male parent's tarsus length, and the sex ratio at the nestling stage was a significant predictor of the proportion of sons among reproducing offspring in the local population. Thus, pairs with large males produce both relatively more and larger sons which, due to their large body size, may have a higher RHP and mating success than the relatively smaller sons of pairs with small males (see Introduction). Daughters may therefore yield higher fitness returns than sons to pairs with small males.

Three hypotheses could potentially explain the sex ratio bias in relation to male tarsus length in great tits. Under the first hypothesis, local resource or mate competition (see Gowaty, 1993) causes the observed sex ratio bias. In the Seychelles warbler (*Acrocephalus sechellensis*) daughters stay as helpers in the parental territory. In poor territories they compete with parents for resources and thus become costlier for parents than sons. Consequently, parents inhabiting poor habitats skew sex ratio in favor of sons (Komdeur et al., 1997). In great tits males disperse less after fledging than females (Gosler, 1993; Gowaty, 1993). To explain our result, the overall nestling sex ratio should be female biased (Gowaty, 1993), which was not the case. In addition, a positive relationship between offspring body size and postnatal dispersal distance would be required (i.e., small males disperse less than large males). This is unlikely in a species where RHP (e.g., territory

acquisition) depends on body size. As expected, there is no such trend in our data (sons: $r_s = .02$, $n = 28$, $p > .50$). Also, natal dispersal distance of sons was not significantly correlated with the male parent tarsus length ($r_s = -.283$, $n = 25$, $p > .15$).

Under a second hypothesis, females may adjust the sex ratio of offspring in the eggs to territory quality rather than to the quality of their male mate per se, and large males, due to their superiority in competition over territories (Drent, 1983), acquire and defend higher quality territories (Richner, 1993). In a good territory, parents may be more able to raise large offspring (Gebhardt-Henrich, 1990; Richner, 1989, 1992) and should therefore also produce a larger proportion of sons. The hypothesis implies that the parent-offspring correlation in tarsus length arises mainly through a correlation between territory quality and male tarsus length (Alatalo et al., 1986). The hypothesis predicts a stronger relationship between the proportion of sons produced and male tarsus length in poor-quality habitats holding a limited number of good territories. There competition is intense and male RHP may play an important role in the settlement of breeding pairs. Indeed, in a great tit population in the Netherlands where, contrary to our study population, food and thus probably good territories are plentiful, no significant relationship between hatchling sex ratio and measures of male body size was found (wing length and body mass: Lessells et al., 1996; tarsus length: Lessells CM, unpublished data). The surprising lack of an association between the proportion of sons and female tarsus length in the present study might indicate that male body size is more important than female body size in determining the quality of the breeding territory (Drent, 1983).

Under a third hypothesis, the correlation between the proportion of sons in a brood and male parent tarsus length could arise by a female mate preference for male genetic attractiveness (as predicted for the Fisher process) or quality (as predicted for the good genes process) (see Andersson, 1994). Both these processes imply that the parent-offspring correlation in tarsus length is mainly genetic and, in our case, would require a correlation between body size and genetic attractiveness or quality. Offspring of large males would inherit the large body size from their father, and these parents should therefore produce a higher proportion of sons. The result that the proportion of sons only increases with male but not female tarsus length would require that tarsus length (or the correlated sexually selected trait) is inherited from parents to offspring nonadditively (sensu Falconer and Mackay, 1996), e.g., through paternal genomic imprinting (Haig, 1997). Tarsus length is known to be heritable in the great tit (e.g., Gebhardt-Henrich and van Noordwijk, 1991), and it has also been shown that mate preference is related to male tarsus length for both great and blue tits (Blakey, 1994; Kempnaers

et al., 1992; Verboven and Mateman, 1997). Thus the potential for one or both these processes to operate may also exist. In this context it may also be noted that breast stripe size may be an indicator of male genetic quality (Norris, 1993).

We cannot disentangle, based on our data, whether the sex ratio bias arises as a response to body-size-related territory quality, genetic quality, or both. Offspring sex ratios should be measured in studies where the effects of territory quality and parental phenotype have been separated experimentally (e.g., Alatalo et al., 1986).

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