

# Is variation in brood sex ratios adaptive in the great tit (*Parus major*)?

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Life-history theory predicts skewed offspring sex ratios in a range of situations in which the costs and benefits of producing the two sexes differ. In recent years, many studies have demonstrated biased sex ratios in a variety of bird species. However, many of these investigations have been based on small sample sizes, on data from a single year, or both. Using a recently developed polymerase chain reaction-based molecular DNA technique, 912 great tit (*Parus major*) nestlings from 118 broods in 5 different years were sexed. As found in a number of previous studies on the same species, there were significant predictors of offspring sex ratio in individual years. However, there were no consistent trends across years, and none of the measured variables significantly predicted sex ratio over all years combined. Furthermore, brood sex ratio of the population did not depart from the expected binomial distribution. Although there are theoretical advantages to manipulating the sex ratio in this and other species, the physiological mechanism by which it is achieved in birds remains obscure. We argue that data from several years are needed to confirm whether facultative sex ratio manipulation is a consistent breeding strategy used by birds. *Key words*: great tits, molecular sexing, *Parus major*; sex ratios. [*Behav Ecol* 11:294–298 (2000)]

Fisher (1958) proposed that frequency-dependent selection should result in the equal allocation of reproductive resources to the production of male and female offspring. This has been confirmed mathematically (MacArthur, 1965; Shaw and Mohler, 1953) and further mathematical treatments have expanded the model (e.g., Charnov, 1975, 1982). Williams (1979) suggested that sex ratio variation among outcrossed vertebrates is mainly a result of automatic, Mendelian segregation of sex chromosomes at meiosis, with little or no scope for adaptive parental manipulation. To date, no physiological mechanism for facultative sex ratio adjustment in birds has been identified (Krackow, 1995). Despite this, there has been a recent accumulation of empirical evidence indicating that animals with chromosomal sex determination are capable of adjusting their offspring sex ratios in an adaptive way in response to a variety of factors (see, e.g., Bortolotti, 1986; Clutton-Brock et al., 1984; Lessells et al., 1996). Deviations from Fisherian sex ratios have been found at a populationwide level (e.g., Hamilton, 1967; Koenig and Dickinson, 1996), between individuals who have different resources available to them (e.g., Komdeur, 1996; Komdeur et al., 1997; Willson and Pianka, 1963), and between separate breeding attempts of the same individual (e.g., Bednarz and Hayden, 1991; Blank and Nolan, 1983; Olsen and Cockburn, 1991).

Great tits (*Parus major*) exhibit a number of life-history traits that may influence sex ratio variation. First, they are sexually dimorphic in body size (males are slightly bigger, with 4% larger wing and tarsus measurements than females; Perrins, 1963). The larger sex costs more to produce, requiring more resources, so the sex ratio will be biased toward individuals of the smaller sex to equalize overall expenditure (Fisher, 1958). Therefore, a female-biased population sex ratio is predicted in great tits.

Second, production of high-quality individuals of the more

expensive sex may be relatively more costly to mothers in poor condition than to those in good condition (Wiebe and Bortolotti, 1992). Further, if maternal condition has an effect on offspring condition that lasts into adulthood and the reproductive success (RS) of one sex is more strongly dependent on condition than it is in the other sex, mothers in better condition should bias offspring production toward the sex that yields relatively greater fitness benefits (Trivers and Willard, 1973). Extrapair fertilizations also occur in this study population of great tits, increasing variability in male RS relative to female RS still further (Blakey and Norris, 1994). Therefore, great tit females in good condition are expected to produce more sons and those in poor condition are expected to produce more daughters.

Third, when the attractiveness of a male depends in part on paternally inherited characteristics, and when those characteristics have a greater effect on male fitness than on female fitness, it is theoretically adaptive for females to adjust the sex ratio of their offspring in response to the attractiveness of their mates. Females mated to attractive males might be expected to favor the production of “sexy sons,” who are likely to father many grandchildren (Weatherhead and Robertson, 1979). Previous work on the great tit has suggested that female mate preference is related to the tarsus length of the male (Blakey, 1994) and size of the male breast stripe (Norris, 1990), rather than to the quality of his territory. Tarsus length and breast stripe size are heritable (Norris, 1993). Therefore, great tit females mated to large males (in terms of tarsus length) and/or those with wide stripes are predicted to “overproduce” sons.

Seasonality may also affect the survival and future RS of the sexes in different ways, and several trends in sex ratio with date have been observed (e.g., Dijkstra et al., 1990; Howe, 1977; Tella et al., 1996; Zijlstra et al., 1992) and modeled (Daan et al., 1996). A seasonally biased sex ratio could be selected for in great tits if fledging condition, which varies with hatch date, influences the likelihood of dispersal success. As females disperse more widely they may be overproduced early in the season when the feeding conditions are good, but males may be favored later in the season when there is a decline in food quality, especially in the proportion of caterpil-

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lars in the diet (Perrins, 1990). Alternatively, a greater abundance of food early in the season may favor overproduction of the more expensive sex (i.e., males), which would result in a seasonal decline in sex ratio.

In this study we tested the influence of all these parameters on offspring sex ratio using 5 years of data from a nest-box-breeding population of great tits.

## METHODS

### Data collection

Data were collected in 1991, 1992, 1993, 1996, and 1998 in Marley Wood, Oxfordshire, UK. We monitored all nest-boxes regularly throughout each breeding season to determine clutch size and lay date for each egg. Breeding birds were trapped at the nest using automatic spring-powered traps, on day 7 (day 1 = hatching) or later. We determined the age of each adult from plumage (Svensson, 1992), and in the analysis birds were classified as 1 year old or older. The following biometrics were determined for all captured birds: (1) wing length (maximum chord, in millimeters); (2) tarsus length (from the nuchal notch to the furthest extension of the leg with the foot held at a right angle, in millimeters); and (3) mass (to 0.1 g on a Pesola balance). In addition, a measurement (in millimeters) was taken of male breast stripe width across the sternum, which was assumed to be an indicator of quality used by females in mate choice (Norris, 1990). As expected for a heritable trait (Norris, 1993), breast stripe width was significantly repeatable for male birds that were measured in more than 1 year ( $r = .642$ ,  $F_{9,12} = 4.95$ ,  $p = .006$ ; Lessells and Boag, 1987). One person (J.K.B.) completed all measurements.

We visited nests every 3 days after the first egg hatched. All chicks were weighed, measured, and ringed on day 15, when a blood sample was also obtained by brachial venipuncture (under license from English Nature and the Home Office). Blood samples were kept cool in the field and stored at  $-20^{\circ}\text{C}$  in the laboratory until DNA extraction.

### Molecular sexing

Because the sex of great tit nestlings cannot be determined from morphological characteristics, we used a DNA test which uses the polymerase chain reaction (PCR) to amplify part of the W-linked avian chromo-helicase-DNA binding gene (*CHD-W*; unique to females) and part of its homologue, the *CHD-Z* gene, which is linked to the Z chromosome (occurs in both sexes; Griffiths et al., 1998).

DNA was extracted using a commercial kit (Puregene, Gen-  
tra Systems, Minneapolis, Minnesota) following the manufacturer's protocol. PCR reactions comprised 1  $\mu\text{l}$  DNA ( $\sim 0.2$   $\mu\text{g}/\text{ml}$ ), 0.2 mM of each dNTP (Pharmacia), 1.2 mM  $\text{MgCl}_2$ , 60 ng each of primers P2.3364 (5'-TCTGCATCGCTAAA-TCCTTT-3') and P8.3221 (5'-CTCCCAAGGATGAGRAAYTG-3'), 0.4 units of *Taq* polymerase (*Taq* supreme, Helena Biosciences Ltd.), and 1  $\mu\text{l}$  *Taq* buffer, in a total volume of 10  $\mu\text{l}$ . All PCR mixtures were overlaid with 15  $\mu\text{l}$  of mineral oil. Reactions were performed with the following temperature profile: initial denaturation at  $95^{\circ}\text{C}$  for 1 min; 30 cycles of denaturation at  $94^{\circ}\text{C}$  for 30 s, annealing at  $52^{\circ}\text{C}$  for 45 s, and template extension at  $68^{\circ}\text{C}$  for 45 s; and final annealing and extension at  $52^{\circ}\text{C}$  for 1 min and  $68^{\circ}\text{C}$  for 5 min, respectively.

We separated PCR products by electrophoresis at 7 V/cm for 1.5 h on 3% agarose gels. PCR products were visualized by UV transillumination after staining with 10 mg/ml ethidium bromide. We sexed birds according to the presence of the PCR products of *CHD-Z* (380 bases) and *CHD-W* (455 bases).

## Statistical analysis

We examined population sex ratios using *G* tests for goodness of fit and contingency. Most analyses were carried out using the brood as the unit of analysis. Analyses of brood sex ratios were performed using the GLIM package (version 4; NAG, 1993). The null model was specified with the number of males in a brood as the dependent variable and brood size as the binomial denominator, using binomial error distribution and a logit link. For linear models with several predictor variables, the backward-deletion model simplification procedure of Crawley (1993) was followed; the statistical significance of a sex ratio bias in relation to an independent variable was assessed from the change in deviance ( $\Delta D$ ) when that variable was excluded from the model. Other statistical tests were performed with MINITAB version 12 (Minitab, 1998).

We used tarsus length as an indicator of body size and the regression residual of weight on tarsus length as an indicator of body condition. To avoid pseudoreplication caused by the occurrence of the same individual in more than one year, one data point for each replicated adult (10 males, 12 females) was selected randomly for inclusion in the analysis across years. Brood size could not be entered into the model as a predictor because it was already present as the binomial denominator. Hence, we examined the effect of brood size on sex ratio using arcsine square-root transformed sex ratio data as the response variable in a general linear model.

The brood sex ratios were also tested for departure from binomial expectation using the deviance in the null model and a randomization procedure (supplied by C. M. Lessells as a GLIM macro routine). This randomly reallocated sexed chicks across broods, given the original brood sizes, thereby deriving binomial variation in sex ratio across broods. After each randomization, the deviance from the null model was compared to that observed in the original data; the proportion of randomizations (1000 were performed) in which the deviance is greater than the null model equates with the probability of obtaining the observed deviance by chance (e.g., Bradbury and Blakey, 1998).

## RESULTS

### Analysis at the level of the individual

In total, 95.5% of the chicks that hatched ( $n = 912$ ) in 118 broods from 5 different years were sexed; the remainder died before sampling. The chicks that died after hatching, but before being sampled, were evenly distributed between years ( $\chi^2 = 4.70$ ,  $\text{df} = 4$ ,  $p > .30$ ). Overall, 88.2% of the eggs laid in these broods were sexed; no unhatched eggs were collected for analysis. Unhatched eggs were also evenly distributed between sample years ( $\chi^2 = 4.70$ ,  $\text{df} = 4$ ,  $p > .10$ ). Subsequent analyses are based on sampled, hatched chicks.

Overall, 48.5% of 871 hatched chicks were male. This sex ratio did not differ significantly from unity ( $G_1 = .837$ ,  $p > .30$ ). The highest proportion of males was observed in 1991 (0.587) and the lowest in 1993 (0.437; Table 1). Sex ratios in individual years did not differ significantly from unity, except in 1993 (see  $G_1$  values in Table 1). The between-year variation in sex ratios was not significant ( $G_4 = 9.054$ ,  $p > .05$ ).

### Analysis at the level of the brood

Brood sex ratios varied between 0 and 1.0 ( $0.50 \pm 0.21$  SD,  $n = 84$ ), but the overall distribution (Figure 1) was not significantly different from the binomial expectation (randomization test:  $p = .286$ ).

Combining data across years, the overall proportion of sons did not vary with year ( $\Delta D_4 = 7.431$ ,  $p > .10$ ), male breast

**Table 1**  
**Proportion of male great tits in sexed broods in each year**

Year	1991	1992	1993	1996	1998	Overall
No. broods	15	19	33	24	27	118
No. chicks	104	151	284	147	185	871
No. males	61	78	124	65	94	422
No. females	43	73	160	82	91	449
Proportion males	0.587	0.517	0.437	0.442	0.508	0.485
$G_1$ value	3.13	0.166	4.57*	1.97	0.049	0.837

$G_1$  values are goodness of fit against the Mendelian expectation of equal numbers of both sexes (\* $p < .05$ ).

stripe size ( $\Delta D_1 = 1.587$ ,  $p > .20$ ), female condition ( $\Delta D_1 = 1.262$ ,  $p > .20$ ), male age ( $\Delta D_1 = 1.229$ ,  $p > .20$ ), female tarsus ( $\Delta D_1 = .531$ ,  $p > .40$ ), female age ( $\Delta D_1 = .460$ ,  $p > .40$ ), male tarsus ( $\Delta D_1 = .216$ ,  $p > .60$ ), or male condition ( $\Delta D_1 = .005$ ,  $p > .90$ ). There was also no trend in sex ratio with laying date ( $\Delta D_1 = .176$ ,  $p > .60$ ), and the proportion of male offspring was not related to brood size ( $F_{1,83} = .03$ ,  $p = .87$ ).

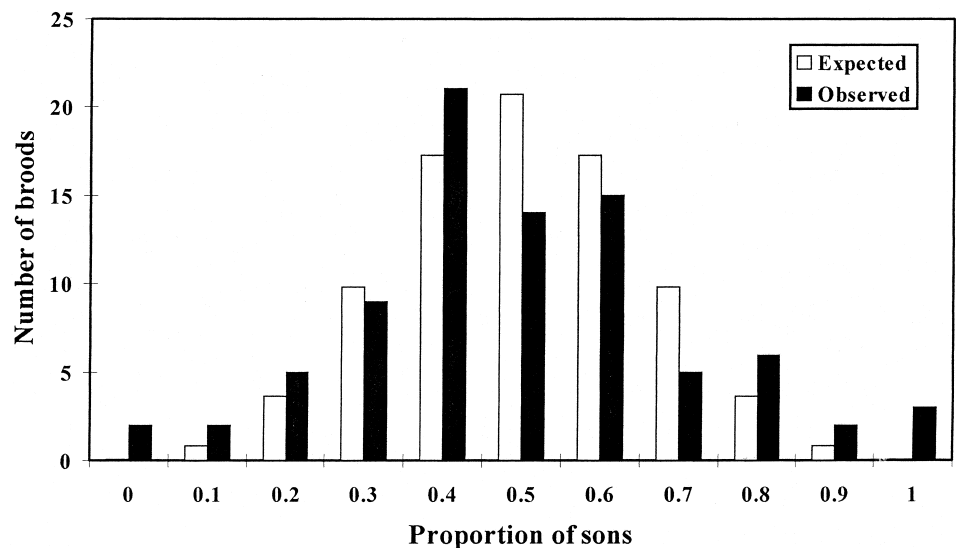
A similar analysis was carried out for individual years (Table 2). Although the odd predictor was significant in individual years, no single predictor was consistently significant across all years. The directional trends of individual correlates were never consistent across all years in the study (Table 2).

## DISCUSSION

Despite the theoretical prediction that even small relative fitness differences between the sexes may result in large shifts in sex ratio (Charnov, 1993), most studies of bird populations have found, at best, only weak evidence that this is the case. In practice, biased sex ratios are frequently found only in subsets of data, in studies where sample sizes are small (e.g., Burley, 1981) or in data from a single year (e.g., Ellegren et al., 1996; Kölliker et al., 1999; Lessells et al., 1996; Svensson and Nilsson, 1996). Comparing our study with others also conducted on the great tit shows the importance of investigating the effects of variables over a number of breeding seasons. For example, Lessells et al. (1996) found a significant correlation between hatching date and offspring sex ratio, but their findings were not corroborated by Kölliker et al. (1999). Our study found a significant relationship with lay date in only 1

of the 5 years (a seasonal increase in sex ratio in 1993) but not across years. The number of unhatched eggs and dead nestlings were equally distributed among the sample years, and comparisons between the years were not, therefore, confounded. A significant seasonal effect on sex ratio might only occur when laying dates of the population are relatively asynchronous, thereby increasing variability in lay and hatch dates. Nevertheless, in 1993 we found a significant seasonal increase in sex ratio but the most synchrony in lay dates of any of the years in our study.

The influence of lay date on sex ratio of offspring may vary between years, depending on fluctuations in food availability, the likelihood of procuring a breeding territory in the subsequent season (Smith and Arcese, 1989), or the level of local recruitment (Verboven and Visser, 1998). However, any facultative manipulation of brood sex ratio in response to parental size and quality should be detected across all years. Previous studies showing a significant influence of male quality (e.g., Ellegren et al., 1996; Kölliker et al., 1999; Svensson and Nilsson, 1996) have been based on data from a single year. We suggest that the findings from such studies should be treated with some caution. We found no significant effect on sex ratio of any parental biometrics across all years of our study. Also, no variable significantly predicted sex ratio in more than 2 of the 5 years when they were considered separately. Although this lack of significance might be explained by low sample sizes, it is much more difficult to account for a lack of consistency in directional trends of sex ratio correlates in the same way. For example, a significant effect of female tarsus length on sex ratio was found in 2 years; in 1991 an increase



**Figure 1**  
 Observed and expected brood sex ratios (proportion of sons) for 84 broods of great tits, ranging in size from 1 to 11 chicks.

**Table 2**  
**Correlates of the proportion of males among great tit broods in individual years**

Explanatory variable	1991 ( <i>n</i> = 12)	1992 ( <i>n</i> = 18)	1993 ( <i>n</i> = 30)	1996 ( <i>n</i> = 21)	1998 ( <i>n</i> = 20)
Lay date	0.000 (1)	0.897 (7)	4.154* (8)	1.578 (5)	2.002 (6)
Sign <sup>a</sup>	0	–	+	–	–
Male age	1.110 (4)	1.948 (8)	0.802 (5)	1.571 (7)	7.980*** (8)
Sign	+	–	–	+	–
Male tarsus	8.236*** (8)	0.401 (6)	0.103 (3)	3.216 (6)	0.115 (1)
Sign	–	+	–	–	+
Male stripe	2.736 (5)	0.611 (4)	0.446 (6)	1.131 (8)	1.567 (4)
Sign	+	–	–	–	–
Male condition	0.246 (3)	0.103 (3)	0.008 (1)	0.036 (1)	0.101 (2)
Sign	–	–	–	+	–
Female age	0.000 (2)	1.052 (5)	0.007 (2)	0.167 (2)	0.624 (3)
Sign	0	–	–	+	–
Female tarsus	7.858** (7)	0.011 (2)	1.044 (7)	1.036 (4)	5.514* (7)
Sign	+	–	–	+	–
Female condition	5.120* (6)	0.000 (1)	0.476 (4)	0.301 (3)	2.428 (5)
Sign	+	0	–	+	–

Values given are the increase in deviance in the model upon deletion of the variable; there was a change of one degree of freedom for every deletion ( $*p < .05$ ,  $**p < .01$ ,  $***p < .005$ ). Variables were deleted sequentially from a maximal model, dropping out in the order shown in parentheses (i.e., the least significant first).

<sup>a</sup> The sign represents the directional trend when the variable is plotted against the proportion of males in the brood. In the cases of male and female age, + implies that birds older than 1 year produce, on average, broods of a higher sex ratio than birds of 1 year of age; – implies the opposite.

in female tarsus resulted in an increased sex ratio, whereas the trend was negative in 1998. In addition, our results include trends in measures that differ from those of previous studies; although Kölliker et al. (1999) found a significant positive effect of male tarsus length on offspring sex ratio, we showed that male tarsus length was significantly negatively correlated with sex ratio in 1991. Also, despite the measured correlation between male stripe size and male tarsus length (Kölliker et al., 1999), the trends in 1991 and 1992 for these two measures were in opposite directions. Although this and previous studies have shown significant effects of measures on sex ratio in some years, the direction of the effects are not consistent across years, making it impossible to predict offspring sex ratio in any given year and making adaptive interpretation difficult.

Although we can identify possible advantages to manipulating offspring sex ratio in the great tit, no single parameter we have studied is sufficiently potent to overcome the frequency-dependent selection tending to keep the sex ratio at unity. At a population level, more of the smaller sex (i.e., females) were produced overall, but the bias was not significant. However, as the size dimorphism is only 4%, a large sample would be needed to find a significant difference in production of the sexes on the basis of this size differential alone. Also, potential competition between locally recruited sons and their parents, which might result in local resource competition (Clark, 1978), is rare in great tits (Greenwood et al., 1979). Brood sex ratio variation in any one individual is diluted out across the population and does not seem to be consistently important. Although adaptive strategies would result in manipulation of primary sex ratios, and so differential mortality of the sexes could have influenced the brood sex ratios determined here, it is the fledging sex ratio that is important in terms of future RS and survival. Also, there is no evidence of differential nestling mortality in this population (Blakey JK, unpublished data).

Given the variety of results found for different populations

of the same species (see Dhondt, 1970; Drent, 1984; Kölliker et al., 1999; Lessells et al., 1996; Slagsvold and Amundsen, 1992; Smith et al., 1989), further studies are needed to evaluate whether adaptive sex ratio manipulation is a consistently important breeding strategy in birds. Furthermore, despite speculation about putative mechanisms, the physiological basis of sex ratio adjustment in birds remains a mystery (Krackow, 1995). Apart from unusual circumstances, perhaps population sex ratios of 1:1 should not be surprising given the strong frequency dependence of the character (Fisher, 1958; Frank, 1990).

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