Female biased hatching order in nestling bearded tits: a compensatory maternal tactic to reduce developmental differences

Dedicated to Professor Karel Hudec in honour of his 80th birthday

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A b s t r a c t . Deviation from an equal sex ratio has been observed in several avian species and there is now descriptive as well as experimental evidence that females are able to modify the sex of their offspring within a brood. Less attention has been paid to consequences of sex ratio manipulation and sex specific differences e.g. in competitive disparities of male and female siblings and parent tactics to compensate for such competitive differences. In this study we examine differences in chick development in relation to sex and hatching order in the socially monogamous bearded tit *Panurus biarmicus*. Our results revealed that significantly more female than male nestlings were the biggest in the brood. Allometric measurements seem to be a good predictor of age (hatching order). This consequently means that female nestlings frequently hatch earlier and have a higher initial body mass. In contrast male nestlings seem to develop much faster than female nestlings. By modifying the hatching order in favour of female nestlings, mothers seem to promote daughters to compensate for their slower growth.

Introduction

Deviation from parity in brood sex ratio has been detected in a number of bird species (D i j k s t r a et al. 1990, A p p l e b y et al. 1997) and in line with this, female ability to modify the sex ratio of their brood in a non-random and adaptive way has been suggested (B u r l e y 1981, E l l e g r e n & S h e l d o n 1997, K o m d e u r et al. 1997, K i l l n e r 1998, K o l l i k e r et al. 1999, N a g e r et al. 1999, S h e l d o n et al. 1999, V e l a n d o 2002, A r n o l d & G r i f f i t h s 2003, B l a n c o et al. 2003). One should be cautious, however, when talking about facultative capacity of female birds to vary offspring sex ratios. Meta-analyses, in fact, did not reveal that biased sex ratio or facultative offspring sex-ratio adjustment constitutes a characteristic biological phenomenon in birds (P a l m e r 2000, E w e n et al. 2004). Nonetheless, sex allocation theory predicts that females in good condition or living in a good environment should modify their brood sex ratio in response to differential benefits when increasing maternal investment into sons or daughters (T r i v e r s & W i l l a r d 1973, C h a r n o v 1982). There is now increasing knowledge about the mechanisms females may use to modify offspring sex (Y o u n g & B a d y a e v 2004, B a d y a e v et al. 2006).

Less attention has been paid to consequences of sex ratio manipulation and sex specific differences e.g. in competitive disparities of male and female nestlings which may affect development and offspring fitness (M a g r a t h et al. 2003).

The importance of sex specific competitive differences is e.g. suggested by the fact that, (i) hatching date differently affects age at first breeding for males and females, resulting in different fitness consequences (D i j k s t r a et al. 1990, D a a n et al. 1996, T e l l a et al. 1996, S m a l l w o o d & S m a l l w o o d 1998, P e n et al. 1999, C o r d e r o et al. 2001), (ii) for both sexes, nestling growth rates are strongly related to eventual adult body weight (B o a g 1987, S k a g e n 1988, K i l l n e r 1998, B a d y a e v et al. 2002) and, (iii) fecundity, attractiveness to mates and mortality correlates with nestling weight at fledging (d e K o g e l 1997, K i l l n e r 1998). However, these relationships may differ between the sexes (K i l l n e r 1998, B a d y a e v et al. 2002). During egg production, for example, females usually exploit their body reserves (H o u s t o n et al. 1995) and their fecundity is strongly related to their weight at fledging (H a y w o o d & P e r r i n s 1992). Thus, sex ratio adjustment to breeding dates might be adaptive and adults may therefore promote the weaker sex to increase its survival prospects. Females should be able to provision male and female eggs differentially depending on their fitness value (T r i v e r s & W i l l a r d 1973). However, natural selection may also favour maternal strategies that reduce resource expenditure without deteriorating offspring of the weaker sex (H i l l s t r ö m 1999, W i l l i a m s 2001, H e a t h et al. 2003). There might be sex-specific differences in resource requirements like sex hormones (e.g. S c h w a b l et al. 1997) which consequently may demand sex biased resolutions (see also S a s v a r i et al. 1999, A n d e r s s o n et al. 2003) without necessarily creating a trade-off for available resources. Thus females may be able to support the weaker sex and balance sex specific within-brood variation in sibling competition (M o c k & P a r k e r 1997, D r u m m o n d 2001), parental investment (A n d e r s o n et al. 1997) or nestling mortality differences between sexes (S l a g s v o l d et al. 1986, W e a t h e r h e a d & T e a t h e r 1991, H o w e 1997, T o r r e s & D r u m m o n d 1999).

In this study we examine within-brood sex ratio variation in bearded tits *Panurus biarmicus* in relation to hatching order and examine possible differences in chick development in relation to sex and hatching order. They are socially monogamous reed dwelling passerines and males are usually the sex with the higher variance in reproductive success, mainly because of extra-pair behaviour (H o i & H o i - L e i t n e r 1997) but also higher female mortality (S p i t z e r 1972, S a x & H o i 1998). Variation in reproductive success seems to be associated with a condition and age-dependent sexual male ornament, the black beard (H o f f m a n n 1994). For this reason male nestlings should be the sex which receives more parental support. However, in bearded tits there is mutual mate choice with males selecting females according to phenotypic traits as well. Furthermore, female condition does not only affect female fecundity but also settling strategies and quality of social and extra-pair males (H o i 1997, H o i & H o i - L e i t n e r 1997). Thus nestling females could be the favoured sex for parental investment as well. Finally in bearded tits there is evidence for maternal sex ratio manipulation (unpublished data).

Methods

The data have been collected in the years 2003 and 2005 in the extended reed stands at fish ponds near Veľké Blahovo (48°03'N 17°36'E) in Slovakia hosting a dense population of bearded tits. Submerged reeds *Phragmites australis* interspersed with cat tails *Thypha angustifolia* and *T. latifolia* and sedges *Carex* sp. are the primary vegetation of their habitat. Bearded tits usually start breeding at the end of March. We found no difference in clutch size,

Table 1. The role of being the first or last nestling in a brood in relation to sex. Given are the results of a GLMM analysis with nestling body mass as dependent factor and wing length (size measurement) as covariate. Hatching order (encoded as first or last), sex (male/female), and year are introduced as fixed and nest as a random factor.

	df	F	P
Hatching order (A)	1	7.65	<0.009
Sex (B)	1	0.15	>0.7
AB	1	4.75	=0.041
Year	1	0.12	>0.9
Nest	34	2.9	<0.01
Wing length (covariate)	1	4.51	=0.045

Total df = 67

nestling numbers (ANOVA, $p > 0.4$, for all) and no difference in body mass between the two study years (see Table 1). Therefore, and since no individual entered twice, the data of the two study years were pooled for the analyses. Nests were located either by observing pairs building the nest or later feeding chicks, or by systematically searching reed areas. Nests were regularly inspected to record reproductive events. Usually we followed the fate of a nest from laying to fledging. Since we had no unhatched eggs in the nests used for these analyses we can exclude that unhatched eggs may have influenced our results in particular hatching order (see below). We measured wing length (using callipers to the nearest of 0.1 mm) and body mass (using an electric balance to the nearest of 0.1 g) of nestlings between about seven to nine days.

Male and female nestling bearded tits differ in bill coloration. Male nestlings develop bright yellow bills whereas female nestlings keep their dull brownish bills (C r a m p & P e r r i n s 1993). The sex determination of nestlings was done by eye when nestlings were at least seven days old. Sex determination was repeated two days later when the first result was doubtful. This method of sex determination was approved by (i) genetically determining the sex of 53, randomly selected nestlings of 31 nests, and (ii) visual determination of their nestling sex (unpublished data not used in this study). The results revealed 100 % concordance between the two methods. The correctness of the method was further ascertained by determining the sex of individually colour marked nestlings (n = 142 nestlings of 32 nests) with seven to nine days of age which were later followed to adulthood in our breeding aviaries at the Konrad Lorenz Institute for Ethology. Again there was full agreement in the early sex determination and later sex.

The residual body mass on wing length was chosen as an indicator of condition as it has been found to be a good predictor of lipid reserves (B a c h m a n & W i d e m o 1999) or survival probability (T h u m a n et al. 2003). Nestling condition was the residuals from a regression with body mass (g) as the dependent and wing length (mm) as the independent variable (combined correlation model for both sexes: $r = 0.715$, n = 144, b = 0.195, $p < 0.0001$). In 2006 we additionally determined the daily body mass increase, for 53 nestlings (28 males and 25 females) of 14 nests measuring body mass, at four and nine day old nestlings.

Egg-laying and consequently hatching order has a significant affect on offspring fitness (B a d y a e v et al. 2002). Hatching order is clearly related to nestling size and body mass and furthermore, is a good predictor of laying order (see B a d y a e v et al. 2002, M a g r a t h et al. 2003).

We used an allometric measurement, wing length (mm), as a predictor of hatching order (see also results). To precisely measure the small wings at this early age is difficult (mean

length with one day of age: 3.3 mm $\pm$ 0.13, n = 49 nestlings of 12 nests). To avoid noise due to the imprecise measurements and consequently errors in the determination of the hatching order we compared only the nestlings with extreme wing lengths, namely the biggest and smallest nestling of a brood. To investigate the reliability of this method we used 12 nests of our aviary breeding population because in aviaries and using video equipment, we could follow the hatching process without disturbing the birds to much. In these 12 nests, where we followed the hatching order, hatching stretches over one to maximal two days. We found a significant difference in wing length of newly hatched nestlings in relation to hatching order (measured four to six hours after the last chick hatched). The first chick has always longer wings than the last hatched chick (paired t-test: $t = 8.08$, $p < 0.0001$, n = 12). After colour marking the biggest and the smallest nestling of each nest with a permanent marker and repeating the measurement on day 5 we found a 100 % concordance. The older was always the nestling with the longer wings. After that, nestlings have been individually ringed and another measurement of wing length on day 10 revealed again 100 % concordance. Thus we can conclude that wing length is a very good predictor for hatching order during at least the first ten days of the nestling phase.

We used parametric statistics except the data were inappropriate for such analyses, in which case we used nonparametric alternatives. All tests are two tailed and means $\pm$ SE are given throughout. To examine which sex hatched first or last within a brood we excluded single sex and single and two chick nests. We used a mixed generalized linear model (GLMM) to test the influence of hatching order and sex on nestling growth (condition). Therefore, nestling body mass was used as the dependent variable and wing length, as a size measurement, was used as a covariate. Nestling sex, hatching order (encoded as first and last hatched) and year were treated as fixed factors. Since chicks from a nest share both environment and genes they are not independent samples and to avoid pseudo-replication we included nest as a random factor. To examine sex specific differences in growth we used (i) the GLMM with body mass as the dependent variable and wing length as covariate (see above), (ii) a paired t-test to compare daily increase in body mass of 14 nests (measured in 2006), using the average for males and females of a nest and, (iii) nestling body mass at four
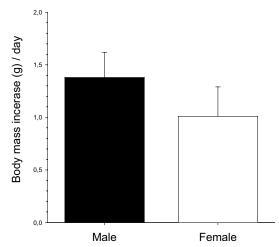

Fig. 1. Daily body mass increase (g) of male (filled bar) and female (open bar) nestlings. Given are means $\pm$ SE stratified / nest (for details see methods).
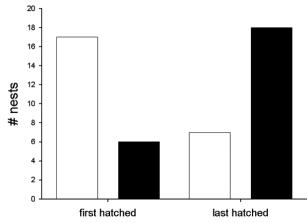
Fig. 2. Number of nests with males (filled bars) and females (open bars) being the first or last hatched in a nest.

days of age of these 14 nests. In Fig. 1 mean body mass of male and female nestlings was stratified per nest. Therefore, mean body mass of males and females of a nest has been used to calculate the overall mean for male and female nestlings.

Results

We found no obvious sex difference in nestling body mass (g) (see Table 1). However, the slope of the correlation between wing and body mass (for males: slope b = 0.269; SE = ± 0.028; r = 0.78, n = 59, p < 0.0001; for females b = 0.153, SE = ± 0.018; r = 0.675, n = 85, p < 0.0001), suggests that males seem to increase body mass significantly faster than females (t-test for different slopes: t = 2.1, p=0.012, n = 59, 85). The higher intercept for females (for females: i = 6.9, SE = ± 0.48, for males: i = 3.9, SE = ± 0.66) in contrast suggests that, females
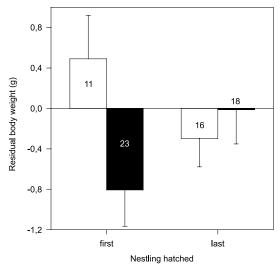

Fig. 3. Residual body mass (g) of male (filled bars) and female nestlings (open bars) in relation to hatching order (first / last). Given are means ± SE and numbers in bars indicate sample size.

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start with a higher initial body weight but develop slower. This sex specific developmental difference is also suggested by the significantly higher increase in daily body mass of male in comparison to female nestlings (paired t-test: $t = 2.53$, $p = 0.025$, n = 14 nests; Fig. 1) determined for 14 nests where we have repeated body mass measurements (see methods). The heavier initial body weight of female nestlings is also indicated when examining younger nestlings (average male body mass at four days of age: 7.3 ± 0.4, n = 20; female body mass at four days of age: 7.98 ± 0.41, n = 20, paired t-test: $t = -2.76$, p = 0.012, n = 20 nests).

Using wing lengths as an indicator of hatching order (see methods) we found differences in the sex which hatched first or last within a brood, excluding single sex nests or containing only one nestling. According to our results, significantly more females were the biggest nestling (hatched first) and significantly more males were the smallest (hatched latest) (binomial test: z = 3.18, $p = 0.0014$) (Fig. 2).

Finally, we found an affect of hatching order and sex on chick condition (Fig. 3). In fact we found a significant order effect and an interaction between hatching order (first or last) and sex which suggests that males do much better when hatching first (Fig. 3, Table 1) but females do not.

Discussion

Our earlier results on bearded tits reveal a profound within-brood deviation from a balanced sex ratio which suggests that females are able to modify the sex ratio towards either sex, probably depending on environmental or intrinsic quality of the mother (K i l l n e r 1998, V e l a n d o 2002, A r n o l d & G r i f f i t h s 2003, S u o r s a et al. 2003). This sex ratio bias results in more than 40 % of all nests containing single sex broods (D a r o l o v á , A., in press).

In this study we found evidence that also in mixed sex broods female bearded tits are able to modify the conditions for offspring. Besides manipulating offspring sex, females seem to differentially invest in male and female nestlings. Such sex specific differences in parental investment are known from other species in terms of nutrients, hormones and parental care (A n d e r s o n et al. 1997, L i p a r & K e t t e r s o n 2000, P e t r i e et al. 2001, S a i n o et al. 2003).

Our results revealed that there is evidence for a faster growth in male nestlings which is not obvious when just comparing average body mass of the two sexes (see results). However examining nestling development we found a sex specific difference in the slopes of the regression between body mass and size (wing length) suggesting that over the nestling period, females grew significantly slower than males. This result is also confirmed by the significant difference in daily body mass increase between male and female nestlings we found for a different sample of our data where we repeatedly measured nestling body mass (see Fig. 1). Such growth differences are also shown in other species (B l a n c o et al. 2003, M a g r a t h et al. 2003, Y o u n g & B a d y a e v 2004).

Sex specific differences in nestling growth may already start with oocyte growth (Y o u n g & B a d y a e v 2004) and continue during the embryonic (B l a n c o et al. 2003, M a g r a t h et al. 2003) and nestling period (B a d y a e v et al. 2001, R u t k o w s k a & C i c h o n 2002). How females recognize and support male and female offspring already prior to fertilization is not known. However, sex specific differences in growth rate may differentially expose male and female oocytes to maternal resources (Y o u n g & B a d y a e v 2004). Female nestlings grew slower and hence they may have more time for

resource uptake than male nestlings (Y o u n g & B a d y a e v 2004). This explanation is supported by our findings since (i) in contrast to the faster growth rate of males, female offspring seem to be provided with a higher initial body mass which may furthermore balance sex specific within brood competition, and (ii) bearded tits are one of the few bird species advertising their sex already during the nestlings period (C r a m p & P e r r i n s 1993). Therefore, this may be one possible maternal tactic how to compensate growth differences between sexes and bearded tit mothers seem to promote the weaker sex, in our case daughters, to compensate their growth rate disparities (M a g r a t h et al. 2003). Whether this is an active female tactic or a passive mechanism is not known but we further found that this difference in initial growth may have to do with hatching order. Mixed broods seem to have a skewed hatching order in relation to the sex of the nestlings (see also B a d y a e v et al. 2002). Significantly more females seem to be the first chick that hatch and significantly more males seem to be last. Skewing the hatching (laying) order of the sexes within a brood in favour of the weaker sex is one compensatory tactic known for some other bird species (see K i l l n e r 1998, N a g e r et al. 1999, L e g g e et al. 2001, B a d y a e v et al. 2002, B a d y a e v et al. 2006). In this way the earlier hatching nestling will have first access to food and grow larger by the time their younger siblings hatch (B o r t o l o t t i 1986, B e d n a r z & H a y d e n 1991, H o w e 1997). An alternative explanation could be that it is useful for the mother to partition the development of male and female offspring, e.g. for an optimal provisioning with sex specific resources necessary for a normal development (Y o u n g & B a d y a e v 2004). Both explanations are not exclusive and may apply to bearded tits. A compensatory female tactic is further supported by the fact that if male offspring hatch first they have a significant advantage over female offspring (Fig. 3), which may dramatically skew within brood competition. That females hatch first is probably not necessary for desynchronizing the development of sexes and for resource partitioning. A first step to understand the role of partitioning nestlings according to sex it would be important to investigate the hatching order of the whole clutch in relation to sex.

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