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Paternal expenditure is related to brood sex ratio in polygynous great reed warblers

Abstract In many polygynous animals, parents invest more heavily in individual sons than in daughters. However, it is unclear if these differences in investment are a consequence of sex differences in the demand of offspring related to sexual size dimorphism or a consequence of parental manipulation. Here, we report on parental food delivery frequency in relation to brood size and brood sex ratio in a wild population of polygynous great reed warblers *Acrocephalus arundinaceus*. We used the polymorphic microsatellite loci on the Z chromosome to sex chicks. We found that paternal feeding frequency (times/h per nest) increased not with brood size, but with the proportion of males in the brood, although the demand per nest was more closely related to brood size than to brood sex ratio. Additionally, the increase in rate of paternal feeding frequency in relation to the brood sex ratio was much higher than the increase in rate of nestling food demands. Maternal feeding frequency was independent of both brood size and brood sex ratio. These results strongly suggest that fathers preferentially invest in their sons. We propose that parents can afford sex-biased parental care in animals in which food provisioning is enough for all offspring to survive.

Key words Parental manipulation · Paternal feeding · Brood sex ratio · Microsatellite DNA · Great reed warbler

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Introduction

For polygynous animals in which variation in reproductive success among adults is influenced by parental investment (Trivers 1972; Clutton-Brock et al. 1984), it is predicted that parents should maximize their reproductive success by allocating a greater proportion of their resources to individual sons than to individual daughters (Willson and Pianka 1963; Trivers and Willard 1973; Maynard Smith 1980). Indeed, it has been reported that mothers invest more heavily in individual sons than in daughters in many polygynous and dimorphic mammals which have one offspring (Reiter et al. 1978, in northern elephant seal *Mirounga angustirostris*; Clutton-Brock et al. 1981, in red deer *Cervus elaphus*; Pickering 1983, in goats *Capra domestica*; Lee and Moss 1986; in African elephant *Loxodonta africana*; Trillmich 1986; Costa and Gentry 1986, in fur seal *Arctocephalus*; Anderson and Fedak 1987, in grey seal *Halichoerus grypus*; Hogg et al. 1992, in bighorn sheep *Ovis canadensis*; but see Byers and Moodie 1990; Pélabon et al. 1995). However, these differences in investment might appear to be a consequence of sex differences in the demand of offspring related to sexual size dimorphism rather than a consequence of parental manipulation (Lee and Moss 1986; Clutton-Brock 1991).

One way to distinguish between both explanations would be to compare to what extent brood size and brood sex ratio affect paternal investment. Bird species which have several offspring within broods are suitable for such a comparison. The only study of this kind, that of Yasukawa et al. (1990) on red-winged blackbirds *Agelaius phoeniceus*, found a stronger correlation of investment with brood size than with brood sex ratio. One reason for the scarcity of relevant studies is that it is impossible to accurately sex the chicks in the majority of bird species, though sexual size (Newton and Marquiss 1979; Holcomb and Tweist 1970; Fiala 1981b) or plumage colour dimorphism (Pinkowski

1974) can be used in some species. Recently, genetic techniques have become available for sexing chicks in several species (Quinn et al. 1990; Parker et al. 1991; Rabenold et al. 1991; Miyaki et al. 1992; Griffiths 1992; Graves et al. 1993; Longmire et al. 1993). Similarly, we have developed a new genetic method for sexing great reed warbler *Acrocephalus arundinaceus* chicks using two polymorphic microsatellite loci located on the Z chromosome.

The great reed warbler is a socially polygynous, slightly sexually dimorphic (males are 13% heavier than females), migrant passerine, exhibiting biparental care of young. Males direct most of their feeding effort to the primary (first hatching) nest (Ezaki 1990; Urano 1990a). In the Japanese population of the great reed warbler, nestling starvation is relatively rare (Ezaki 1990; Urano 1990a), even in situations in which the father does not provide parental care. However, it is predicted that males should invest in parental effort only when it will positively affect their reproductive success (Orians 1969; Maynard Smith 1977; Westneat et al. 1990). Here, we report on the relationship between parental feeding frequency and brood sex ratio and brood size in the great reed warbler. We also discuss the conditions necessary for paternal effort to be related to the brood sex ratio.

Methods

Field methods

We conducted research during the breeding seasons (late April to early August) of 1992–1994 in Deguchi Reed-bed Park, Osaka Prefecture, central Japan (34°48′N, 135°37′E). The park covers an area of about 4 ha and contains mainly common reed *Miscanthus sacchariflorus* and reed *Phragmites communis*. We located all great reed warbler nests and individually colour-marked all breeding adults (except one female in 1992) and nestlings. A blood sample was collected from a brachial vein of each individual in order to identify nestling sex. Data were collected on parental food provisioning behaviour by using video cameras placed near nests that had 2- to 10-day-old chicks. These data were collected on days with no rain ($n = 48$, mean 4.4 h, SD 2.1 h, per nest).

Sexing by the polymorphic microsatellite loci on the Z chromosome

The procedure of cloning microsatellite loci with GT repeats followed Ellegren et al. (1992) with some modifications. Polymerase chain reaction (PCR) was carried out according to Ellegren (1992), the annealing temperature being 58°C. The primer set sequences at the G61 and G62 loci are 5′-GAGCAGAAGCTACAGA AATC-3′ and 5′-GCAAAGTCTGATTGTAAGCAG-3′, and 5′-CTTGTGTGTGCTACAGATGG-3′ and 5′-AAGGGTAGA-GTTCTCACATG-3′, respectively. Adults were sexed according to sexual differences in incubation patches and songs (Kluyver 1955). All 58 adult females had only one kind of allele each for both loci. In contrast, the majority of the males showed two alleles for both loci (47/59 for G61, 37/59 for G62). Therefore, we concluded that both G61 and G62 loci are located on the Z chromosome (Fisher's exact probability test; $P = 8.7 \times 10^{-22}$, 2.2×10^{-15}, respectively). The sizes of alleles were determined by electrophoresis of an accompanying sequence ladder. Heterozygosity shown in Table 1 was derived from the data on 59 adult males.

In sexing chicks, we assumed two things. The first was that we correctly assigned maternity. Intra-specific brood parasitism has not been detected in this species (Hasselquist et al. 1995). The second assumption was of no mutation. An estimated mutation rate at dinucleotide microsatellite loci is 4.5×10^{-4} per meiosis (Kwiatkowski et al. 1992). Under these two assumptions, we decided that chicks that inherited their mother's band were males whereas those that did not inherit it were females.

An example of a PCR amplification of the G61 microsatellite locus in two families is shown in Fig. 1. Each major band is associated with one or a few fainter bands appearing in each of two base pairs below. These minor bands are inevitable artifacts in PCR amplification of dinucleotide microsatellites (Litt and Luty 1989; Weber and May 1989; Luty et al. 1990). In family A (Fig. 1), chicks c and d inherited the mother's band, namely the mother's Z chromosome, but chicks a, b and e did not inherit the mother's band. Therefore, we recognized the former chicks as males and the latter as females. In family B in which the mother's band is the same length as one of the father's bands (22 repeat), chick e has only the 22 repeat band, which should at least be from the father, but we could not estimate whether the chick inherited the mother's band because the presence of a band of the same length from the father interfered with the estimate. Therefore, we could not correctly sex this chick. Of 230 chicks 212 (92%) were sexed using two loci.

Analyses of feeding frequency

The data in the last quarter of the breeding season (after 21 July) were excluded because paternal feeding frequencies were significantly lower (Scheffé's $F = 8.3$, $P < 0.0001$, $n = 89$) and maternal frequencies significantly higher ($F = 4.7$, $P = 0.0044$, $n = 89$) than in the other quarters. Data from the same brood were combined because paternal feeding frequencies did not differ significantly among nestling stages (nestling day 2–4, 5–7, 8–10; mean 3.5, 4.1, 4.8 times/h per nest; n 23, 23, 17, respectively; Kruskal-Wallis ANOVA, $df = 2$, $H = 3.32$, $P = 0.19$). The same was true for maternal feeding frequencies (mean 7.8, 7.6, 8.6; n 24, 26, 21, respectively; $df = 2$, $H = 3.56$, $P = 0.17$). The data from nests with unsexed nestlings were excluded from the analysis of parental feeding and brood sex ratio. The data from broods with only one

Table 1 Attributes of microsatellite loci used to sex nestlings.

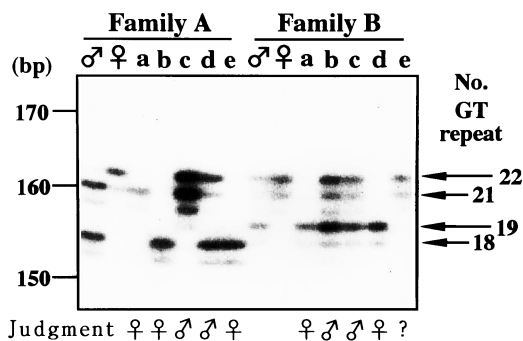| Locus	Fragment size (base-pair range)	Hetero-zygosity	Allelic frequencies (GT repeat number)														
			8	12	14	15	17	18	19	20	21	22	23	24	25	26	27	28
G61	133 to 173	0.797	0.006			0.006	0.017	0.364	0.034	0.131	0.108	0.199	0.068	0.011		0.011	0.034	0.011
G62	154 to 180	0.627		0.085	0.006		0.023	0.108	0.119	0.557	0.091	0.006			0.006			

Fig. 1 Sexing of chicks by using the polymorphic microsatellite loci. (♂ father, ♀ mother, *a–e* are nestlings, *GT repeat numbers* are on *right*, sizes of the fragments in base-pairs (*bp*) are on *left*, judgment of sex *below*)

nestling were excluded from the analysis of the relationship between maternal feeding frequency and brood sex ratio because maternal feeding frequency for such broods was significantly lower than for the other brood sizes (Scheffé's $F = 3.2$, $P = 0.023$).

The cost difference between sons and daughters has not been estimated in great reed warblers, although Weatherhead and Teather (1991) estimated that the cost difference is 20–50% less than the difference in their sizes in some other sexually size dimorphic birds. Great reed warbler males are 13% heavier than females. Therefore, we conservatively assumed that the excess cost of sons to daughters is less than 13%.

Results

Paternal feeding

Few males feed their polygynous second hatched broods before the offspring of first hatched broods become independent (about 15 days after fledging; Scheffé's $F = 7.4$, $P = 0.0001$, $n = 7$, Fig. 2). Males rarely feed the first hatched broods when they are guarding the second or third females (Scheffé's $F = 4.0$, $P = 0.049$, $n = 2$, Fig. 2). For these broods, the paternal feeding ratio (male visits/male+female visits) is not related to brood sex ratio ($n = 7$, two were excluded because of unsexed nestlings; Fig. 3). These broods were excluded from the following analyses ($n = 7$). The paternal feeding ratio increased with the proportion of males in the brood ($r_s = 0.47$, $P = 0.0052$, $n = 37$, Fig. 3). Similarly, there was a positive correlation between paternal feeding frequency (times/h per nest) and brood sex ratio ($r_s = 0.34$, $P = 0.040$, $n = 37$, Fig. 4a).

One possible explanation for these correlations is that fathers compensate for increasing demand in the brood related to the brood sex ratio as caused by sexual size dimorphism. If this was the case, paternal feeding frequency should correlate more strongly with brood size than with brood sex ratio, as found in the red-winged blackbird (Yasukawa et al. 1990). However, in the great reed warbler, the paternal feeding frequency was not significantly related to the brood size (Kruskal-Wallis ANOVA, $df = 4$, $H = 7.3$, $P = 0.12$, Fig. 5a).
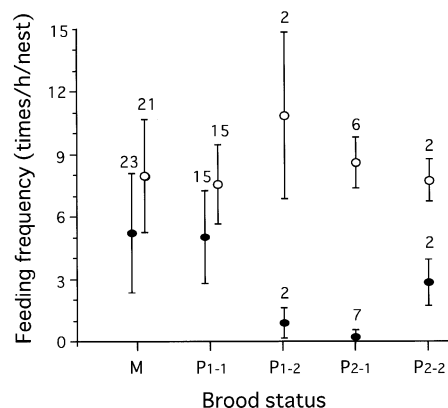

Fig. 2 Relationships between parental feeding and brood status. *Open* and *filled circles* indicate maternal and paternal feeding frequencies, respectively. Values are means (*circles*) ± SD (*vertical lines*) and *numbers* are sample sizes (number of broods). *M* indicates monogamous broods. *P1–1* and *P1–2* indicate the first hatched broods of polygyny when the second or third females were infertilizable and fertilizable, respectively. *P2–1* and *P2–2* indicate polygynous second hatched broods before and after the offspring of the first hatched broods became independent, respectively
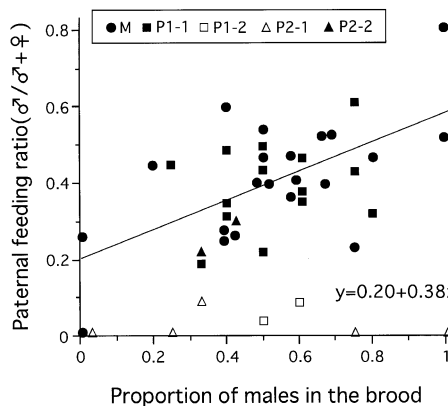

Fig. 3 Relationships between paternal feeding ratio and brood sex ratio. Abbreviations are the same as in Fig. 2. The simple *linear regression* is derived from the *filled symbols* only

This suggests that the cause of the increase in paternal feedings to male-biased broods can not be explained by an increase in brood food demands. Moreover, this is supported by the following. Great reed warbler males are only 13% heavier than females. Therefore, if fathers only compensate for increasing demand in the male-biased brood, we can expect that in the simple linear regression of Fig. 4a, the slope value should be less than 13% of the Y-intercept, namely less than 0.36. However, the value of the slope was 4.59, much higher than 0.36, and the lower value of the slope (95% confidence limit) was 1.09.

Maternal feeding

Maternal feeding frequencies were related neither to brood sex ratio ($r_s = 0.15$, $P = 0.36$, $n = 40$, Fig. 4b)
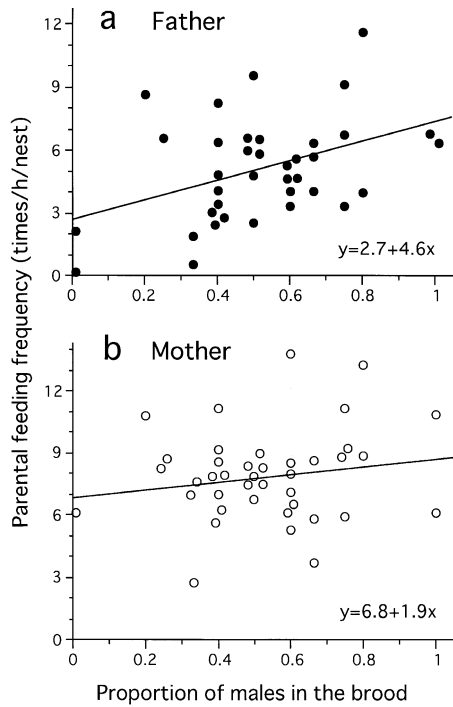
Fig. 4a, b Relationships between parental feeding frequency and brood sex ratio
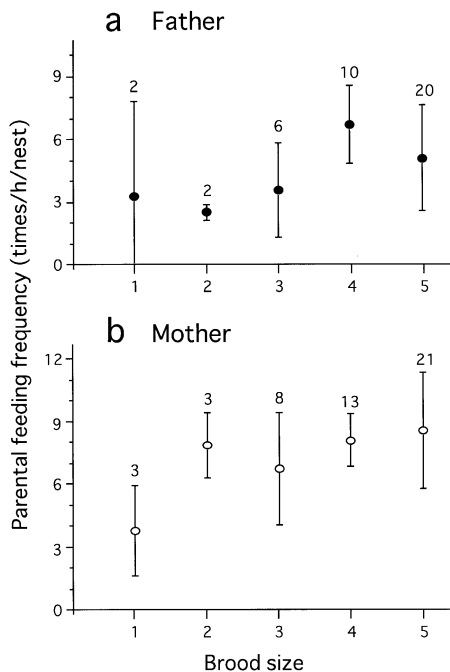

Fig. 5a, b Relationships between parental feeding frequency and brood size. symbols as in Fig. 2

nor to brood size except for one nestling broods (Kruskal-Wallis ANOVA, $df = 3$, $H = 2.1$, $P = 0.56$, Fig. 5b). Moreover, maternal feeding frequencies were independent of paternal feeding frequencies ($r_s = -0.063$, $P = 0.29$, $n = 45$; includes the data from the broods with unsexed nestling) and brood status (monogamy or polygyny; Scheffé's $F = 1.0$, $P = 0.42$, Fig. 2).

The importance of paternal care to offspring survival

The rate of starvation was relatively low (7.4% offspring, $n = 175$; 21% broods, $n = 52$; includes all nests in which at least one chick fledged, e.g. nests during the last quarter of breeding season or nests in which we could not record the feeding behaviour) and paternal feeding frequency did not affect starvation. Paternal feeding frequency between broods with (mean 4.1 times/h per nest, SD 3.0, $n = 5$) and without starvation (mean 4.3, SD 3.0, $n = 26$) did not differ significantly (Mann-Whitney U-test, $P = 0.90$; only includes nests in which at least one chick fledged during the first to third quarter of the breeding season).

Discussion

Behavioural mechanisms which yield correlations between paternal expenditure and brood sex ratio

We observed a correlation between paternal expenditure (feeding of chicks) and brood sex ratio, which could not be explained only by an increase in brood food demands related to sexual size dimorphism. Which parental sex and what behavioural mechanisms could yield this correlation? One possibility is that pairs are able to adjust the brood sex ratios (Gowaty 1991). For example, mothers might produce male-biased broods when they had signs of good male condition. However, this hypothesis is unlikely because there was no evidence for a sex-ratio bias in our population. There was no evidence of a skewed sex-ratio within broods in relation to female status [monogamy or polygyny (primary, secondary, and tertiary)], female age, clutch size, male status, male arrival order, hatching date and year in this population (I. Nishiumi, unpublished work). For example, the first-hatched broods within harems were composed of 70 females and 75 males (1:1.07), while second- and third-hatched broods combined had 30 females and 37 males (1:1.23). Although second- and third-hatched broods rarely received paternal feeding, they were never biased towards daughters.

The alternative hypothesis is that fathers can distinguish chicks' sex based on early sexual differences in behaviour. For example, young males might beg more often than females, as apparently occurs in the red-winged blackbird (Teather 1992). Unfortunately, we do not know whether great reed warbler fathers can distinguish chick sexes and if they use cues such as sex differences in chick activity. An interesting point is that

if the latter is true, the reactions of fathers to chick activity are different from that of mothers. Therefore, high paternal feeding contribution towards male-biased broods is likely to be a consequence of paternal strategy rather than female or chick manipulation.

Evolutionary significance of paternal extra feeding of male-biased brood

In the Japanese population of the great reed warbler, nestling starvation is relatively rare, even if the father does not provide parental care (Ezaki 1990; Urano 1990a). Paternal feeding of male-biased broods probably does not increase the survival of sons. Indeed, paternal feeding frequency did not differ between broods with and without starvation. This may be because starvation occurs only during long rainy periods and may mainly be influenced by weather-dependent feeding frequency (Urano 1990a). Anyway, paternal feeding can be looked upon as extra feeding which is dispensable for chick survival.

We have no direct evidence that the extra food differentially affects lifetime reproductive success of sons and daughters in great reed warblers because few warblers (5.6% males, $n = 54$, 4.4% females, $n = 45$) return to the natal area to breed. However, we have ample grounds for expecting this, as will be shown later. In birds, extra food would affect lifetime reproductive success of the young mainly in two ways. First, extra food results in faster growth and fledging at an earlier age (Stamps et al. 1987). The less time offspring spend in the nest the greater their survival may be (Sullivan 1989). Second, extra food results in greater structural growth, especially in body mass and tarsus length (Alatalo and Lundberg 1986; Boag 1987; Bryant 1989; Hochachka and Smith 1991). Greater survival would equally affect lifetime reproductive success of both sexes. On the other hand, greater structural growth would affect reproductive success more strongly for males than for females in the great reed warbler because large size in males contributes to success in competition for good territories and in attraction of more than one mate (Hasselquist 1994; Catchpole et al. 1985), and because variation in reproductive success on males is greater than on females (Urano 1990b). Therefore, we expect that allocating extra food to sons is adaptive.

The cause of difference between male and female feeding patterns

Assuming that extra food elevates the fitness of juvenile males, mothers will benefit just as much as fathers. Why should only fathers provide this extra food? One possibility is that by doing so, males increase the chances of their females laying subsequent clutches. For example, if females had to provide the additional food, they might have to delay the onset of the next clutch, as found in the budgerigar, *Melopsittacus undulatus* (Stamps et al. 1985). However, this hypothesis is unlikely in the great reed warbler because no female produces more than one successful clutch in the breeding season with the same male.

Alternatively, it may be that females cannot provide the extra food to male-biased broods because of a plateau in feeding frequencies, which was observed for experimentally enlarged broods in females of some bird species (the great tit *Parus major*, Smith et al. 1988; the red-winged blackbird, Whittingham 1989; the pied flycatcher *Ficedula hypoleuca*; Källander and Smith 1990; Moreno et al. 1995; but see Nur 1984). The plateau in feeding frequencies may be due to the need to avoid survival costs (Tuomi 1990) or future fecundity costs (Gustafsson and Sutherland 1988) for parents. A related explanation is that post-reproductive survival may drop precipitously and not linearly after a certain threshold in parental effort (Drent and Daan 1980). Great reed warbler males can shift their effort from mate attraction to feeding, as Urano (1990b) found a negative correlation between singing and feeding frequencies. Females may have no other effort they can shift to their feeding. To test this hypothesis, we need to measure the costs of feeding for each sex.

Trade-off between parental effort and mating effort

The reproductive success of males over the breeding season may be the result of a trade-off between parental effort and mating effort (Trivers 1972). Factors that affect this trade-off may include the probability of additional mating, brood size, brood sex ratio, nestling age, mate's parental effort, and paternity (Patterson et al. 1980; Westneat et al. 1990; Searcy and Yasukawa 1995). We found that in the great reed warbler the most important factor is brood sex ratio, unlikely in other polygynous birds (maternal care in the savannah sparrow *Passerculus sandwichensis*, Wheelwright et al. 1992; brood size and nestling size in the corn bunting *Miliaria calandra*, Hartley and Shepherd 1994; and in the yellow-headed blackbird *Xanthocephalus xanthocephalus*, Patterson et al. 1980; and in the red-winged blackbird, Whittingham 1989; Yasukawa et al. 1990; paternity in the red-winged blackbird, Weatherhead et al. 1994).

What is the difference between the great reed warbler and another polygynous species, the red-winged blackbird, in which there is little or no sex bias in provisioning (Fiala 1981a; Yasukawa et al. 1990; Teather 1992)? One possibility is the difference in variance in male reproductive success between these two species, because the greater the variance in male reproductive success, the greater benefit parents would gain by producing stronger sons. However, contrary to the prediction, the variance is greater in the blackbird than in

the warbler, because blackbird males acquire from zero to five females (Yasukawa et al. 1990), while warbler males only acquire from zero to three females. A second hypothesis is that there is a difference in the probability of additional mating. More females within the harem in the blackbird might indicate a higher probability of additional mating during the nestling period of the primary nest. If this was the case, the blackbird males might have to allocate much effort to mate attraction even if the brood sex ratio is male-biased. A third hypothesis is that parental investment influences lifetime reproductive success more in the warbler than in the blackbird, but this hypothesis is difficult to test.

Another hypothesis is that there is a difference in the importance of paternal care to offspring survival. In the blackbird the starvation rate is relatively high (19% offspring) compared to that in the warbler (7.4% offspring). Moreover, broods fed only by the female suffer higher losses than broods fed by both parents in the blackbirds (Yasukawa et al. 1990), which is unlikely in the warbler. In a monogamous bird, the rook *Corvus frugilegus*, in which starvation rate is high (67% broods), fathers do not offer sex-biased provisioning (Røskaft and Slagsvold 1985). In the domestic, monogamous budgerigar in which the starvation rate is low (9% broods in cage), paternal feeding frequency is negatively correlated with the proportion of males within brood (Stamps et al. 1987). Sex-biased provisioning may occur in animals in which paternal feeding does not affect chick survival of the sex that is discriminated against. In that case, low extra pair paternity would be more important for evolution of paternal care than in the case that paternal feeding increases the chick survival rate.

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