



Sibling competition and not maternal allocation drives differential offspring feeding in a sexually size-dimorphic bird

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Sex allocation models still fail to predict the complex sex ratio patterns in broods of vertebrates. A major problem when studying mother–brood interactions is the difficulty in disentangling hypotheses involving maternal preferences from processes that do not imply maternal manipulation. We studied maternal resource allocation in mixed-sex, same-sex and single-chick broods in the great bustard, *Otis tarda*. Females normally rear a single chick, and previous work has shown that maternal investment influences male more than female breeding success. Therefore, mothers of two-chick broods were assumed to be in good condition and candidates to show a preference for sons. Results showed that male chicks of mixed-sex broods remained close to the mother for twice as long as their sisters, and received double the number of maternal feedings. However, sex differences in maternal feeding rate disappeared when considering only simultaneous begging approaches from both siblings. Proximity to the mother and its interaction with begging approach intensity were the factors determining the higher begging success of male chicks. In single-chick broods, females did not receive fewer maternal feedings than males. Overall, our results suggest that female chicks of mixed-sex broods become outcompeted by their larger brothers, which remain close to the mother much longer, preventing their sisters from taking a larger share of maternal feedings. We conclude that mothers do not show a preference for feeding male over female chicks, and that the sex differences in feeding rate are determined by the higher food requirements of male chicks due to their sexually selected, much faster growth rates. The higher mortality of females in mixed-sex broods contrasts with the pattern of male-biased mortality typical in this species, and supports our interpretation of an asymmetric competitive ability of male offspring as the mechanism responsible for the sex bias in maternal expenditure.

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Four decades after Fisher (1930) presented his famous theory on equal parental investment among offspring of both sexes, Trivers and Willard (1973) proposed that when resources allocated to offspring of one sex provide greater fitness returns, parents in good condition, or in years with more resources, are expected to invest more in that sex. This hypothesis was later generalized (Charnov, 1982; Frank, 1987; Leimar, 1996; Lessells, 1998), and various extensions and new hypotheses were proposed (advantaged daughter, attractiveness, local mate competition, local resource competition, repayment, cost of reproduction, male exploitation, brood reduction hypotheses; reviewed in Clutton-Brock, 1991; Cockburn, Legge, & Double, 2002; Frank, 1990; Hardy, 1997; Sheldon, 1998; Sheldon & West, 2004; Uller, 2006). These hypotheses raised enormous

interest and numerous empirical studies have provided evidence for differential investment in sons and daughters (reviewed in Cameron, 2004; Clutton-Brock, 1991; Clutton-Brock, Albon, & Guinness, 1982; Cockburn et al., 2002; Froy, Walling, Pemberton, Clutton-Brock, & Kruuk, 2016; Gomendio, Clutton-Brock, Albon, Guinness, & Simpson, 1990; Hewison & Gaillard, 1999; Robert, Schwanz, & Mills, 2010; Sheldon & West, 2004; Uller, 2006; West, 2009). However, despite this vast literature, sex allocation theory has been very successful in predicting sex ratio adjustment in haplodiploid insects, but not in birds and mammals, where sex ratio control by parents is still poorly understood.

In birds and mammals, adjustments predicted by theoretical models often fail, probably because (1) these models do not incorporate the complexities of their life histories (Krackow, 2002; Pen & Weissing, 2002; Uller, 2006; West, Reece, & Sheldon, 2002; West & Sheldon, 2002), (2) it is difficult to predict sex ratio

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adjustment when several offspring of the same litter compete for limited resources (Carranza, 2004; Frank, 1990) or (3) current models still lack an appropriate integration of theory and empirical data (Carranza, 2002; Clutton-Brock, 1991; Godfray & Werren, 1996). For example, Carranza (2004) and Uller (2006) suggested that sex asymmetries in competitive ability, cooperative behaviour and even noncompetitive interactions among offspring have not been sufficiently incorporated in previous models, and concluded that investigating these interactions should increase our knowledge of sex ratio strategies in vertebrates. In addition, most authors agree that another major problem with sex allocation hypotheses is that their predictions are difficult to distinguish from those of evolutionary processes that do not imply maternal manipulation (Clutton-Brock, 1991; Cockburn et al., 2002; Krackow, 2002). For example, a bias in offspring sex ratio is predicted by the Trivers–Willard and cost of reproduction hypotheses, but also by the differential mortality hypothesis, since the faster growth rates and greater nutritional requirements of young males of many species (e.g. most mammals, polygynous birds) make them more vulnerable to starvation than young females (Cockburn et al., 2002). A clear indication of whether any mechanism of maternal expenditure division among sons and daughters is a consequence of active parental manipulation or of ecological constraints ultimately determined by other evolutionary forces such as, in this case, sexual selection is only likely to be achieved by well-designed experiments (see e.g. Merckling et al., 2015; Nager, Monaghan, Griffiths, Houston, & Dawson, 1999) or detailed studies of the way in which parents treat individual offspring and of the fitness consequences of sex-specific sibling interactions (Clutton-Brock, 1991; Cockburn et al., 2002; Uller, 2006).

Here we present the results of one such detailed study, on maternal expenditure in great bustards, *Otis tarda*. Since we were interested in investigating whether mothers in good condition decide to expend more effort in their sons, we primarily studied the behaviour of families with two chicks of different sex, henceforth 'mixed-sex broods'. By selecting families of two chicks we ensured that mothers in our study were in better than average condition, since great bustard females usually rear one chick, and only in years with good environmental conditions do experienced mothers rear two or, exceptionally, even three chicks (Magaña, 2007; Morales, Alonso, & Alonso, 2002). We also studied families with two chicks of the same sex, henceforth 'same-sex broods', and families of one chick, hereafter 'single-chick broods', and used them as controls for the sex-related differences in mother–offspring or sibling interactions observed in mixed-sex broods. In two-chick broods, based on observations of the behaviour of mother and both offspring during maternal feedings, we tried to discern whether active maternal discrimination between son and daughter was a plausible mechanism involved in mother–offspring interactions. Specifically, we looked for (1) aggression, (2) refusal to feed a soliciting chick, (3) differential maternal feeding rates when both siblings solicited food under identical circumstances, i.e. when they either started a begging approach to the mother from identical distances to her or approached her simultaneously (see specific parameters in Tables 1 and 2). In addition, to evaluate whether the consequences of these mother–chick interactions could be relevant for population sex ratio as predicted by sex allocation theory, we examined whether mortality differed between siblings in mixed-sex broods. According to the differential mortality hypothesis, we should expect a higher mortality of male siblings, which are much larger and thus more vulnerable to starvation than their sisters (Clutton-Brock, 1991; Clutton-Brock, Albon, & Guinness, 1985; Kalmbach & Benito, 2007; Stamps, 1990).

In principle, the great bustard should be a good candidate to expect differences in expenditure on sons and daughters by

mothers in good condition. First, this lekking species shows the highest sexual size dimorphism among birds (Alonso et al., 2009). Strong sexual dimorphism develops very early during juvenile development, suggesting that rapid growth of young males is evolutionarily selected (Alonso et al., 2009). Second, young birds are precocial and feed themselves shortly after hatching, but have prolonged maternal dependence periods (6–18 months), during which they receive additional feedings from the mother (Alonso & Alonso, 1992; Alonso, Martín, Alonso, & Morales, 1998). As in some polygynous ungulates, in great bustards we found evidence of maternal care having a critical influence on the breeding success of sons but not of daughters. Young males that fed at higher rates or received more feedings from their mothers became independent at a younger age, integrating earlier into adult male flocks and settling earlier at their definitive leks, which suggests clear fitness advantages from early maternal care (Alonso et al., 1998). These relationships were not found in young females. However, these benefits of rapid growth are counterbalanced by a higher male mortality from starvation when food is scarce (Martín et al., 2007), which results in a female-biased sex ratio that appears at an age of 2–3 months and continues into adulthood in all populations (Alonso, Martín, Palacín, Magaña, & Martín, 2003; Alonso, Martín, Palacín, Martín, & Magaña, 2005; Alonso, Palacín, et al., 2005). Finally, the great bustard is also highly polygynous, with probably the strongest documented skew in male mating success among birds, with weight being one of the main factors favouring a high rank of males within the lek and facilitating their access to females (Alonso, Magaña, Palacín, & Martín, 2010).

METHODS

Study Area and Species

The study was conducted in the Wildlife Reserve Lagunas de Villafáfila (33 000 ha), northwest Spain. The climate is characterized by hot, dry summers, rainy autumns and springs and cold winters. The landscape is treeless and flat to gently undulating, and consists of extensive, 2-year rotation dry cereal farmland (ca. 80% of the surface), with alfalfa fields (8%), pasture land (7%) used for sheep grazing, and scattered vineyards and other minor crops (5%; details in Alonso & Alonso, 1990).

Male and female great bustards live in separate flocks all year round, and meet in early spring at traditional lek arenas, where males display to attract females. After mating in April, most males abandon the lek site, while females take on all breeding duties. The chicks depend on their mother for 6–18 months (Alonso et al., 1998). They follow her closely and remain isolated from other nonbreeding or unsuccessfully breeding females until late September, when they start flocking with other females (Martín, 1997). The first months of life are crucial for the development and survival of male chicks and for their future success as adults (Alonso et al., 1998, 2010). Young males grow much faster than young females soon after hatching, being significantly heavier at an age of only 10 days (Litzbarski, Jaschke, & Jaschke, 1983). The early appearance of sexual size dimorphism allows experienced observers to distinguish the sex of chicks just a few weeks old, and unmistakably during August–September, when chicks are 2–4 months old (Alonso, Martín, et al., 2005; Alonso, Palacín, et al., 2005, 2009, Martín, 1997).

Mother–Chick Feeding Interactions and Mother's Intake Rate

Between mid-August and early October 1993–1994 we searched for families with two chicks. These are uncommon, since (1) on average, only one in 8–10 females is successful in rearing chicks up

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