Female starlings adjust primary sex ratio in response to aromatic plants in the nest

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Adjustment of offspring sex ratios should be favoured by natural selection when parents are capable of facultatively altering brood sex ratios and of recognizing the circumstances that predict the probable fitness benefit of producing sons and daughters. Although experimental studies have shown that female birds may adjust offspring sex ratios in response to changes in their own condition and in the external appearance of their mate, and male attributes other than his external morphology are also thought to act as signals of male quality, it is not known whether females will respond to changes in such signals, in the absence of any change in the appearance of the male himself. Here, we experimentally manipulated a male courtship display, the green plants carried to the nest by male spotless starlings (*Sturnus unicolor*), without changing any physical attributes of the male himself, and examined whether this influenced female decisions on offspring sex ratio. We found that in an environment in which female starlings were producing more daughters than sons, experimental enhancement of the green nesting material caused females to significantly increase the number of male eggs produced and thereby removed the female bias. This effect was consistent in 2 years and at two localities. This demonstrates that the green material, whose function has long puzzled biologists, conveys important information to the female and that she facultatively adjusts offspring production accordingly.

Keywords: primary sex ratio; adjustment of offspring sex ratio; courtship display; green nesting material; spotless starling

1. INTRODUCTION

When environmental or ecological circumstances differentially influence the relative fitness of sons and daughters, sex allocation theory predicts that parents should increase the production of the sex with the higher fitness benefit (Trivers & Willard 1973; Charnov 1982). Experimental support for this prediction is still scarce and controversial, particularly in vertebrate taxa, in which sex is chromosomally determined (Cockburn *et al.* 2002). In birds, females are the heterogametic sex and thus have the potential to control offspring sex before laying. Previous studies have shown that changes in male morphological ornaments may induce females to bias her offspring production in favour of sons (Ellegren *et al.* 1996; Sheldon *et al.* 1999), as sons sired by attractive males can attain higher mating success. The mechanisms whereby changes in offspring production occur are poorly understood. The females may be responding directly to the signal itself, but the results could also be induced by changes in male behaviour associated with his increased attractiveness. There are inherent difficulties in experimentally manipulating the signal itself without altering other aspects of male behaviour that might influence his performance. Furthermore, while male ornaments convey fixed information about their bearer, a behavioural trait, such as plant carrying, gives the possibility of the signal intensity being adjusted at the discretion of its performer

without affecting the male himself. Several male sexual behaviours other than his external morphology are also thought to act as signals of male mating status or male quality (Borgia & Gore 1986; Moreno *et al.* 1994; Fargallo *et al.* 2001; Duffy & Gregory 2002; Brouwer & Komdeur 2004). Therefore, it would be expected that experimental changes in such displays, which can be carried out without affecting the male himself, should induce changes in offspring sex ratios.

During courtship, male European starlings (*Sturnus vulgaris*) place green material into the nest (Gwinner 1997; Gwinner *et al.* 2000), which is then examined by the female and generally removed. The signal value and function of this display has puzzled biologists (Clark 1991; Hansell 2000). The amount of material brought by males is related to their circulating testosterone levels and territorial status (De Ridder *et al.* 2000; Pinxten *et al.* 2002; Veiga *et al.* 2002), and thus the display may convey important information on male quality or male status to the female (Gwinner 1997; Brouwer & Komdeur 2004). In this study, we present experimental evidence that the provision of green plants to the nest by male spotless starlings (*Sturnus unicolor*) influences offspring sex ratio. Offspring sex-ratio adjustment caused by the presence of aromatic plants in the nest might be a general pattern or the consequence of particular ecological conditions working with the green material carried by males during the reproductive time. We worked with two populations of spotless starlings, subjected to different ecological conditions, breeding in

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nest-boxes in central Spain. Like the European starling, male spotless starlings add aromatic fresh green plants to the dry nest material that they collect in their own territory during courtship and prior to egg laying (Gwinner 1997; Gwinner *et al.* 2000; Brouwer & Komdeur 2004). In this study, we altered the amount of green material in the nest during female inspections, and examined the effects on offspring sex ratio.

2. METHODS

(a) Study area and species

The spotless starling is a medium-sized passerine (mean body mass 92 g), double brooded and facultatively polygynous (Moreno *et al.* 1999; Veiga *et al.* 2001, 2002), closely related to the European starling. The study was conducted in two colonies of the spotless starling, spaced *ca.* 18 km apart, in Madrid province (central Spain), at 1000 m above sea level. The habitat is mainly pastureland with scattered trees (ash, *Fraxinus angustifolius*; oak, *Quercus pyrenaica*; and holm oak, *Quercus rotundifolia*). Fifty-four nest-boxes were placed in colony 1 (Manzanares) in 1997 and 40 nest-boxes in colony 2 (Villalba) in 1995. The nest-boxes were spaced *ca.* 35 m apart in Manzanares and 25 m apart in Villalba. The study was conducted between the end of March and mid-June in two successive years (2001 and 2002) in Manzanares and in 2002 in Villalba.

The spotless starling is a relatively long-lived species (we found that 75% of adults were still breeding after 6 years in monitoring the Villalba population). Females commonly lay two clutches per reproductive year, the first about mid-April and the second about the end of May. The studied populations differed in the average number of eggs laid in second clutches (3.9 versus 4.8 eggs laid, Villalba versus Manzanares, respectively) but not in first clutches (4.5 versus 4.7 eggs laid, Villalba versus Manzanares, respectively), probably related to differences in food availability later in the season. All breeding birds were marked with a numbered aluminium ring and a unique combination of coloured plastic rings for individual identification. At Manzanares, where birds were studied over 2 years, only females that were not subjected to experimental treatment in the first year (2001) were used in the second year (2002). These previously non-manipulated females were randomly assigned to control and experimental groups in 2002, and female identity was taken into account in the analyses.

(b) Experimental procedures

Male spotless starlings normally begin to incorporate green herbs into their nests 7–10 days before the onset of laying and cease this activity once the first egg appears, as the European starling does (Gwinner 1997). Therefore, for first clutches we began to add green plants 8–10 days before clutch initiation and for second clutches immediately after fledging of the first brood. Forty-seven boxes were randomly allocated to experimental manipulation of green nest herbs and 47 boxes remained as controls (27 in Manzanares and 20 in Villalba, both treatments). Breeding pairs were already formed when we assigned the nest-boxes to control or experimental groups. Assignment of nest-boxes to treatment groups was the same in first and second clutches of the same year. In the experimental nests we incorporated 35–40 g of fresh aromatic herbs daily of the species added naturally by starlings in these populations (mainly *Lavandula stoechas*, *Santolina rosmarinifolia*, *Geranium robertianum* and *Lamium purpureum*), shredded as naturally found in nests. The amount of fresh herbs in the nests was similar to the highest amount recorded in nests of polygynous males, and thus the stimulus created with our

experimental manipulation was within the range of natural levels experienced by the starlings in the wild. Aromatic plants were added to the nests until the first egg appeared. Control nests were inspected daily but no plants were added. To prevent differential stress that possibly could affect pre-laying females in the period in which fresh green plants were added, we spent the same daily time in the inspection and manipulation of experimental and control nests. Spotless starling females generally removed the green nesting material, both the experimental plants added by the researchers and those put into the nests by the males. Therefore, the experimental manipulation did not affect the behaviour of the males themselves.

Maternal condition was measured in 85.4% of clutches. Females were weighed (to the nearest 0.01 g) when their chicks were 5 days old. Mating status (monogamous versus polygynous) was determined in 60.4% of males, known by means of videotapes, captures into the boxes and visual observations.

(c) Sex determination

The sex of nestlings was determined from blood or muscle (the latter from dead nestlings or embryos from unhatched eggs) by using PCR amplification of two homologous genes (CHD1-W and CHD1-Z) following Griffiths *et al.* (1998), and with blind reference to sample origin. Excluding 48 infertile eggs (no apparent embryo) belonging to 43 clutches, and 70 nestlings (from 38 broods) that disappeared early from the nest, this study comprises a total of 735 individuals sexed from 805 fertile eggs laid, belonging to 188 broods (73 and 70 in Manzanares 2000 and 2002 respectively, and 45 in Villalba 2002). Therefore, we included in the study 150 completely sexed broods and another 38 broods with incomplete information on this variable.

(d) Data analyses

Sex ratio was calculated as the proportion of males per breeding attempt. Because this variable does not show a normal but a multinomial distribution, we used generalized linear mixed models (GLIMMIX; Krackow & Tkadlec 2001). We used logistic regression and binomial distribution fit to analyse brood sex-ratio variation in relation to the treatment (experimental versus control) and clutch order (first versus second clutches). We controlled for the possible effect of the year of the experiment and locality, including both variables as random factors. First and second broods of the same female in the same year were included in the analysis. To avoid pseudo-replication problems in relation to female identity, separate analysis when only each female was once used each year was considered. Statistical analyses were conducted using the generalized linear model GLIM package (Crawley, 1993). Data were weighted by the number of nestlings sexed within broods.

3. RESULTS

In both study populations, there was a female bias in the sex ratio of the control broods (figure 1). However, this was removed in the experimental nests, changing to equality (figure 1). Thus, clutches in nests with experimental additions of aromatic fresh herbs contained a significantly higher proportion of male offspring than clutches in control nests (experimental nests: 0.52 ± 0.27 s.d.; control nests: 0.41 ± 0.29 s.d.; table 1), and there were no differences in the proportion of males between first and second clutches (table 1). To examine whether any bias occurred as a result of incomplete information for 38 of the 188 broods (i.e. 16 control and 22 experimental broods), we also examined the
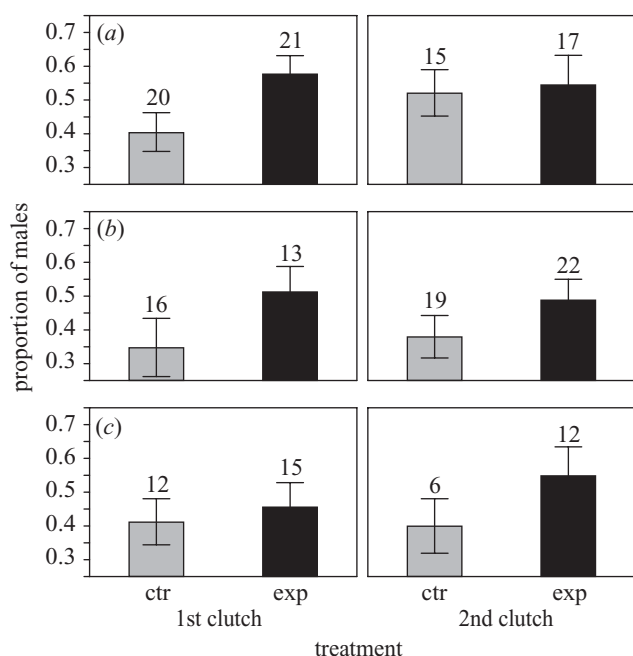
Figure 1. The proportion of males in broods of spotless starling in relation to experimental manipulation of the green nest material. Data (mean ± s.e.) and sample size are shown for broods in control (ctr) and experimental (exp) groups, in both first and second clutches and in 2 years and localities: (a) Manzanares, 2001 ($n = 73$); (b) Manzanares, 2002 ($n = 70$); and (c) Villalba, 2002 ($n = 45$).

Table 1. Results of a GLIMMIX with a binomial error structure and repeated measures analyses.
(The sex ratio at birth was examined as a function of treatment (control or experimental) and clutch order (first and second clutches). Locality, year of the study and female identity were included as random variables (see § 2). Results from logistic regression models are shown for the sample of 188 broods and for the 149 broods where a female was used only once each year.)

	sample of 188 broods		sample of 149 broods	
	$F_{1,181}$	p	$F_{1,143}$	p
treatment	11.08	0.0012	5.96	0.016
clutch order	0.84	0.36	0.035	0.85
treatment × clutch order	0.27	0.60	0.21	0.65

sex ratio only in the 150 completely sexed broods. The effect of the experimental addition of green nesting material on the sex ratio at birth was the same in both analyses (reduced sample: 0.51 ± 0.27 s.d. versus 0.40 ± 0.28 s.d., proportion of males in experimental versus control broods respectively; $F_{1,143} = 9.12$, $p = 0.003$). Furthermore, the majority of these 70 non-sexed nestling were late-hatched chicks in their broods and, although there is no evidence that sex is dependent on hatching order in this species (Cordero *et al.* 2001), simulating the worst case, i.e. that the missed nestlings had all been females, the difference in sex ratio between control and experimental nests was still significant (treatment effect: $F_{1,181} = 8.76$, $p = 0.0035$).

The effect of the experimental manipulation of green nesting material on the birth sex ratio was the same as for the total sample when only each female was used once each year in the analysis (149 females). Females with experimental enhancement of green nesting material produced more sons than control females (experimental nests: 0.52 ± 0.28 s.d.; control nests: 0.40 ± 0.27 s.d.; table 1), and there was a similar tendency in first and second broods (non-significant interaction term in table 1).

To test the robustness of our results further, we also performed a paired test comparing the sex ratio of broods of control and experimental females mated with the same polygynous males ($n = 21$ males). Again, experimental enhancement of nest material in one of the nests of the same male gave rise to a higher proportion of male offspring (experimental nests: 0.59 ± 0.28 s.d.; control nests: 0.41 ± 0.23 s.d.; $z = 2.5$, $p = 0.013$; Wilcoxon matched-pairs test).

The increased production of males in response to the experimental treatment was robust and consistent between populations (figure 1) and years (in Manzanares; see figure 1a,b), and there was a similar tendency in first and second clutches (interaction term treatment × clutch order: $F_{1,181} = 0.30$, $p = 0.59$). These results were not biased by any differences between experimental and control nests in two variables with a potential influence on sex ratio, female condition and male polygynous status. We have reliable information on male status and female condition in 80.85% and 76.06% of cases analysed respectively. There were no differences between treatments in male status (58.6% of control nests and 62.2% of experimental nests belonged to polygynous males; $\chi^2 = 0.21$, d.f. = 1, $p = 0.67$) or maternal condition (control: 85.2 ± 0.6 g; experimental: 85.6 ± 0.6 g; $F_{1,141} = 0.32$, $p = 0.57$).

4. DISCUSSION

The provision of green plants to the nests by male starlings during courtship (Gwinner 1997; Pinxten *et al.* 2002) has long puzzled biologists (Clark 1991; Hansell 2000). Its link to male hormonal and territorial status suggests that it provides important information on male quality (De Ridder *et al.* 2002; Pinxten *et al.* 2002; Brouwer & Komdeur 2004). The experiment presented here provides clear evidence that female spotless starlings respond to the amount of green material in the nest. They consistently altered the primary sex ratio of their offspring, and, by increasing male production, removed a female bias that occurred in both of our study populations. Why this female bias occurred in the first place is intriguing, and may itself be linked to differences in environmental or social circumstances. This tendency was also observed in several years before the manipulative control of the amount of green herbs was carried out, which prevented the experiment, *per se*, being the cause of this bias toward females. Significant deviations from 50 : 50 ratios have been found in some years or series of years in several bird species (Humple *et al.* 2001; Koenig *et al.* 2001; Krebs *et al.* 2002; Thuman *et al.* 2003). This has been linked to factors such as parental age (Heg *et al.* 2000), female social status (Westerdahl *et al.* 2000) or female body condition (Nager *et al.* 1999; Aparicio & Cordero 2001; Thuman *et al.* 2003), which may influence the relative fitness benefits of sons and daughters. Models

concerning the evolution of alternative mating tactics suggest that, when the costs of production of sons and daughters are different and population density is high, females might respond by skewing population sex ratios towards the less expensive and phylopatric sex (e.g. Pienar & Greeff 2003). Male spotless starlings are larger than females (2.3% in tarsus length and 5.8% in body mass) and the most phylopatric sex (Veiga 2002). However, the density of breeders and the pressure of floaters was comparatively high in both our study colonies (Cramp & Perrins 1994; Veiga 2002). Thus, females may benefit from producing more daughters in two ways, growing the less costly sex and preventing future female competence with their daughters. In addition, it has been shown that female birds increase the production of the smaller sex when maternal condition and male offspring survival are poor (Nager *et al.* 1999). However, we did not find any differences in body condition in our females, and there were no differences between sexes in the proportions of chicks and fledged (V. Polo, unpublished observations). Thus, the increased production of males in the experimental birds suggests that the advantages of being mated to a higher quality male offset the benefits of increased female production, presumably by somehow reducing the disadvantages that male offspring incur. Interestingly, in a previous experimental study conducted in the same study populations, spotless starling males that were implanted with testosterone spent more time in attracting additional mates and fed nestlings less than control males (Veiga *et al.* 2002). Thus, male offspring do not appear to benefit from better paternal care provided by high-quality fathers. Nonetheless, male offspring, by inheriting the high quality of their fathers, may render a higher fitness benefit.

A particularly interesting aspect of this study is that the female response was a result of the intensity of the signal alone, not of any changes in the male morphology. Also interesting is the fact that the effect does not disappear in second broods, even though the female would then appear to have more experience of the experimental male's true quality and the outcome of the breeding event. However, we cannot discard alternatively non-adaptive interpretations of our results. Although our results clearly demonstrate that the male behavioural trait is sufficient to induce sex-ratio adjustments, females may be concomitantly using other morphological or behavioural traits to attain a more accurate estimation of male characteristics that could be correlated with the intensity of the behavioural signal. Little is known about the use of different male courtship traits in mate choice and even less about their possible effects on how the female adjusts the proportion of sons in her offspring. Sexually selected male displays often involve multiple behavioural and morphological traits (Patricelli *et al.* 2003). For example, if more females are attracted to a nest by the males as a result of the experimentally added plants, there could be a concomitant increase in female aggressiveness that could cause hormonal changes in the female body (Whittingham & Schwabl 2002; Veiga *et al.* 2004), but little is known about this potential effect on sex-ratio variation. This aspect should be addressed in specifically designed studies in the future.

An obvious question arising from these results is why individual males do not increase the amount of material brought to the nest if this is indeed a signal of male pairing success (Brouwer & Komdeur 2004). Although collecting and carrying plants appears an inexpensive activity (Brouwer & Komdeur 2004), the costs of this behaviour have not been measured. Our ongoing study on spotless starlings indicates that males may carry plants to the nest at the same rate as when they feed nestlings. Furthermore, female spotless starlings frequently remove the green plants brought by their mate, possibly trying to induce him to work harder. This may render green plant carrying a behavioural trait as costly as other displays, such as stone carrying or complex nest construction, that induce differential mating responses by females (Soler *et al.* 1998; Moreno *et al.* 1999; Fargallo *et al.* 2001).

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