Body attributes of both parents jointly affect offspring sex allocation in a socially monogamous, size-monomorphic passerine

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Abstract Theory predicts that because males are more variable in reproductive success than females, a mother should produce more sons to maximize fitness return from the sex allocation if she is of high-quality (the female quality hypothesis) or mates with a high-quality male (the male quality hypothesis). While most previous studies have looked at each hypothesis, we tested both of them simultaneously in the white-rumped snowfinch Montifringilla taczanowskii, a socially monogamous, sexually monomorphic passerine where body size is a potential indicator of individual quality in intrasexual competition and territory defense. Brood sex ratios at the population level did not deviate from random expectation. Among individual broods, the proportion of sons did not depend on body size of either male or female parent, but on interaction of this trait of both parents. Further analyses revealed that brood sex ratios were independent of body size of male or female parents when their mates were smaller, but positively related with body size of male or female parents when their mates were larger. These results suggest that mechanisms underlying the two hypotheses may act jointly on offspring sex allocation. The mechanisms are expected to evolve through size-assortative mating which is often reached by sexual selection [Current Zoology 59 (2): 271–277, 2013].

Keywords Brood sex ratio, Parental quality, Size-assortative mating, White-rumped snowfinch

Ever since Trivers and Willard (1973), many evolutionary ecologists have attempted to investigate whether, how and why female birds are able to adaptively allocate the sex of their offspring (West, 2009). Relying on a basic premise that sons may be highly variable in reproductive success due to prevalence of polygynous or extra-pair mating among populations, whereas daughters usually experience lower risks of gaining no mates, several hypotheses have been proposed to address this issue. Of these, the female and the male quality hypotheses are two most influential. The former predicts that mothers in good condition would overproduce sons to obtain greater fitness returns providing that good condition is transferred to the offspring, while mothers in poor condition would give rise to more daughters to minimize the risk of reduced fitness (Trivers and Willard, 1973). The latter suggests that females mated to high-quality and thus sexually-attractive males will benefit from yielding more sons, since the sons may inherit their father’s traits and reach a greater success in social and extra-pair mating (Burley, 1981). However, while some empirical data support the female quality (Nager et al., 1999; Heg et al., 2000; Whittingham et al., 2002; Parker, 2002) or male quality hypotheses (Ellegren et al., 1996; Sheldon et al., 1999; Rutstein et al., 2005; Du and Lu, 2010; Zielińska et al., 2010), some others provided no evidence for either (the female quality: Genovart et al., 2005; the male quality: Saino et al., 1999; Dreiss et al., 2006).

In birds, males and females can mate assortatively with respect to various quality-related phenotypes such as body size (Olsen et al., 1998; Tryjanowski and Simnek, 2005), ornament size (Jawor et al., 2003), age or breeding experience (Cézilly et al., 1997; Ludwig and Becker, 2008; Taff et al., 2011). Sexual selection, which may act through either male-male competition (intrasexual selection), female or male choice (intersexual selection), or a combination of these mechanisms, has been appreciated the major contributor to formation of the mating pattern of many taxa (Crespi, 1989). The non-random mating is evolutionarily important because different combinations of males and females with specific traits may have different fitness consequences. It has well been known that the mated pairs consisting of both high-quality males and females enjoy an enhanced reproductive success by many ways (Andersson, 1994).
Given that manipulation of offspring sex ratio through the potential mechanisms associated with quality of either female or male parents is a fundamental part of successful reproductive strategies, we expect that the size-assortative mating can generate fitness benefits in terms of offspring sex allocation. In other words, the two hypotheses of adaptive sex allocation may operate simultaneously or they would be effective only when individual quality of both parents is combined. However, most previous empirical tests for theory only focused on one of the two mechanisms, and to our knowledge, only two studies of sex ratio manipulation have simultaneously taken traits of both parents into account (Dowling and Mulder, 2006; Addison et al., 2008).

Here we examine variation in offspring sex ratio for a socially monogamous, sexually size-monomorphic passerine, the white-rumped snowfinches Montifringilla taczanowskii. Although the birds are sexually size monomorphic, body size should still be important for individual quality because there is individual variation in this trait for each sex. Moreover, during the breeding season, both male and female snowfinches are frequently engaged in direct aggressive interactions including physical flights in which larger body sizes could be advantageous (Zeng, 2008). We correlate brood sex ratio not only with parental body condition — a quality indicator depending more on current ecological regimes (Moya-Laraño et al., 2008), but also with parental structural size — a quality indicator that signifies more genetic components (Kölliker et al., 1999; Blanchard et al., 2007). Specifically, we test the predictions that females with better condition or larger size would produce male-biased broods when they mate to a better-conditioned or larger male.

1 Materials and Methods

1.1 Field data collection

White-rumped snowfinches were studied during the breeding seasons of 2006 and 2007 at Gahai Natural Reserve (34°14′N, 102°20′E, 3450-3800 m elevation), in the northeastern Tibetan Plateau. Our previous work at this site (Zeng and Lu, 2009a, b) has shown that the birds nest in the burrows of the black-lipped pika Ochotona curzoniae, with a density of 0.13–0.17 nests per ha within the study area. Both male and female snowfinches reach sexual maturity at the second year after hatching. Mating system is socially monogamous. Males establish territories (size 0.1–0.5 ha) and guard their mates strongly from pair formation through egg-laying period; paired females participate in territory defense. Egg-laying occurs between late April and early June. Clutch size averages 4.7 (2–6). Some pairs (9%, n = 147) make two breeding attempts in a single year. There is no evidence that a pair produce a replacement clutch if nesting failure occurs during the middle of breeding period. Nest-building, incubation (lasting 13 days on average) and brooding are undertaken by females only, and both parents share young caring (21 days on average). Males do not feed their mates that are engaged in incubating or brooding.

We searched snowfinch nests within a 390-ha plot covered with alpine meadow throughout the breeding season every year. The snowfinch species is present in the study area year round. There was 71% of 24 breeding males and 50% of 30 breeding females marked in 2006 summer in the study plot were rediscovered in 2007 early spring. Of these resighted individuals, only 4% males and 10% females had nests located within the study plot and all of them remated. Young recruitment rates from 2006 to 2007 were 21% for males (n = 61) and 16% for females (n = 43), with 13% in males and 14% in females being found to nest within the plot.

We mist-netted adult females at the entrance of nesting burrows during the incubation period and adult males during the nestling period. It was difficult to check the nest contents that were inside the pika burrows. Therefore we captured nestlings by hand or mist-net when they received food from parents at the nesting burrow entrances shortly before fledging. As a result, this study only focused on brood sex ratio at fledging. Offspring sex ratios can be influenced by sex-specific mortality rates of nestlings. However, such effect was minor in this study because the snowfinch nestlings reared in burrows experienced little brood reduction (Lu et al., 2009; Zeng and Lu, 2009b).

For each individual, we measured body mass (with an electronic balance, to the nearest 0.1 g) and linear dimension (body length, beak length, tail length, wing length and tarsus length, with a calipers, to nearest 0.05 mm; Sutherland et al., 2004). A blood sample (10–20 μl) was taken from the femur vein of each individual, collected in a capillary tube and transferred to a tube containing 100 μl anticoagulant (5% EDTA in Sodium Chloride Physiological Solution) and 1 ml ethanol (95%) for preservation.

1.2 Molecular sexing

We sexed the birds using two primer-pairs of P2/P8 (Griffiths et al., 1996) and 2550F / 2718R (Fridolfsson...
and Ellegren, 1999). DNA was extracted from blood samples following the protocol of a DNA mini kit (SBS Genetech Co., Beijing). PCR reaction conditions (total volume = 10 μL) were conducted as follows: 1× PCR buffer (50 mM KCl; 10 mM Tris-HCl pH 9.0; 0.1% Triton X-100), 1.6 mM MgCl₂, 200 μM of each dNTP, 125 nM of each primer and 0.5 U of Taq DNA polymerase. Minimum 100 pg of genomic DNA was used as template. The initial denaturing was step at 95°C for 4 min, followed by 35–40 cycles of 51°C for 30 s, 72°C for 30 s and 95°C for 30 s; a final run of 51°C for 5 min and 72°C for 10 min. The products were run out on a 6% non-denaturing polyacrylamide gel stained with silver. Gels were scored as males having a single band and females having two bands. The method was demonstrated to be valid based on known-sex adult snowfinches.

1.3 Statistics

We sampled young from 62 broods (2006, 30; 2007, 32) produced by 51 different snowfinch pairs, including 11 pairs that had a second brood during a single season. To avoid non-independence of the samples, these second broods were excluded from analysis unless specified. Among the remaining 51 broods, there were 42 (including 33 single-brooded pairs and 9 double-brooded pairs) for which we had full data on both parents and all their nestlings. In the dataset, only one male and three females marked in 2006 breeding season were present as breeders in 2007 breeding season. Because all these rediscovered individuals paired with a novel mate so that our dataset included no brood that was produced by the same pairs across years. Therefore, to increase statistical power we did not use mixed models. We fitted a series of general linear models, with number of sons as in a brood as the dependent variable, and body mass of female parent, body mass of male parent, structural size of female parent, structural size of male parent, brood size, number of broods a pair produced during a breeding season, year and breeding start date as the potential explanatory variables. We did not use the residual of an ordinary least squares regression of body mass on tarsus length of an individual as a measure of its body condition because the two traits were uncorrelated. Structural size of a breeder was measured used factor scores extracted from the first principal component for the five linear measurements (accounting for 30.3% and 34.6% of total variance for females for males, respectively). The variables with greatest factor loadings on this component were body length (0.72) and tail length (0.85) for males. No correlation was evident between body mass and structural size for female ($r = -0.05$, $P = 0.74$) and male breeders ($r = -0.18$, $P = 0.26$), suggesting them to act independently. Breeding start date was estimated as the time of first egg relative to 17 April, the earliest recorded egg-laying date in the snowfinch population.

Akaike's information theory approach is a general method for choosing the best number of parameters to include in a model (Burnham and Anderson, 2002). Akaike's information criterion (AIC) was calculated with the formula: $AIC = n\ln(RSS/n) + 2K$, where $n$ is the number of data points, $ln$ is the natural logarithm, RSS is the residual sums of squares of the candidate model, $K$ is the number of parameters in the model. If $n/K < 40$, AIC requires a bias-adjustment: $AIC_c = AIC + (2(K+1))/(n-K-1)$. We ranked relative support for each competing model by comparing the value of a model ($AIC_c$) with that of he best approximating model ($AIC_{min}$): $\Delta AIC_c = AIC_c - AIC_{min}$. As a rule of thumb, $\Delta AIC_c < 2$ indicates that the models have similar support, and $\Delta AIC_c > 2$ indicates that the models have considerably less support. We further evaluated the relative likelihoods of each model given the data using weights ($W_{i,AIC}$): $W_{i,AIC} = \exp(-0.5\Delta AIC_i)/\sum_{i=1}^{l}\exp(-0.5\Delta AIC_i)$.

All analyses were performed using SPSS 16.0 (SPSS Inc., Chicago, IL, U.S.A.). Significance is two tailed and values are expressed as mean ± SE.

2 Results

Among 148 nestlings produced from 42 broods, 81 were males and 67 females, not significantly biased to any one sex (goodness-of-fit test, $\chi^2 = 1.32$, df = 1, $P = 0.25$). With nests as the unit of analysis rather than individuals, the average sex ratio of all 42 broods was 0.57 ± 0.02, again not deviating significantly from 0.50 (one-sample $t$ test: $t = 1.74$, df = 41, $P = 0.09$). It was the case for data from 2006 (0.63 ± 0.06, $n = 16$ broods, 34 males and 21 females; $t = 1.97$, df = 15, $P = 0.07$) and 2007 (0.54 ± 0.06, $n = 26$ broods, 47 males and 46 females; $t = 0.42$, df = 25, $P = 0.46$). No significant difference was detected between years (independent-samples $t$ test: $t = 0.97$, df = 40, $P = 0.34$). For the 9 double-brooded pairs, the sex ratios of offspring of both the first and second broods were not significantly biased to 0.50 (first brood: $0.63 ± 0.09$, $t = 1.44$, df = 8, $P = 0.19$; second broods: $0.48 ± 0.11$, $t = 0.18$, df = 8, $P = 0.86$), with no difference between two types of brood (paired-samples $t$ test: $t = 1.14$, df = 8, $P = 0.29$).
Out of the 9 priori candidate models tested for offspring sex ratio in relation to potential explanatory variables, the model 6 had lowest AICc, which had a difference of more than 2 from 8 other models (Table 1). In the model, only brood size and female × male structural size interaction were significant predictors of brood sex ratio (Table 2). To better understand this interaction, female and male parents were divided according to their structure size into smaller and larger, and then tests were made for correlations between brood sex ratio and the size of their mates in either case. The production of sons by a smaller female was independent of body size of her mate ($r = -0.40, n = 21, P = 0.08$); however, a positive effect of male body size on number of sons in a brood existed for males paired to large females ($r = 0.45, n = 21, P = 0.04$; Fig. 1A). In contrast, when male parents were smaller, brood sex ratios did not covary with body size of their mates ($r = -0.30, n = 21, P = 0.19$), but significantly favored to sons if fathers had larger body size ($r = 0.56, n = 21, P = 0.01$; Fig. 1B).

### Table 1

| Candidate models | AICc | ΔAICc | W_AIC |
|------------------|------|-------|-------|
| 1. Y = a + $\lambda_1 X_1 + \lambda_2 X_2 + \lambda_3 X_3 + \lambda_4 X_4 + \lambda_5 X_5$ | 6.01 | 3.20 | 0.136 |
| 2. Y = a + $\lambda_1 X_1 + \lambda_2 X_2 + \lambda_3 X_3 + \lambda_4 X_4 + \lambda_5 X_5 + \lambda_6 X_6$ | 6.59 | 3.78 | 0.061 |
| 3. Y = a + $\lambda_1 X_1 + \lambda_2 X_2 + \lambda_3 X_3 + \lambda_4 X_4 + \lambda_5 X_5 + \lambda_6 X_6 + \lambda_7 X_7$ | 9.66 | 6.85 | 0.009 |
| 4. Y = a + $\lambda_1 X_1 + \lambda_2 X_2 + \lambda_3 X_3 + \lambda_4 X_4 + \lambda_5 X_5 + \lambda_6 X_6 + \lambda_7 X_7 + \lambda_8 X_8$ | 13.08 | 10.27 | 0.001 |
| 5. Y = a + $\lambda_1 X_1 + \lambda_2 X_2 + \lambda_3 X_3 + \lambda_4 X_4 + \lambda_5 X_5 + \lambda_6 X_6 + \lambda_7 X_7 + \lambda_8 X_8 + \lambda_9 X_9 X_10$ | 5.96 | 3.15 | 0.038 |
| 6. Y = a + $\lambda_1 X_1 + \lambda_2 X_2 + \lambda_3 X_3 + \lambda_4 X_4 + \lambda_5 X_5 + \lambda_6 X_6 + \lambda_7 X_7 + \lambda_8 X_8 + \lambda_9 X_9 X_10$ | 2.81 | 0 | 0.154 |
| 7. Y = a + $\lambda_1 X_1 + \lambda_2 X_2 + \lambda_3 X_3 + \lambda_4 X_4 + \lambda_5 X_5 + \lambda_6 X_6 + \lambda_7 X_7 + \lambda_8 X_8 + \lambda_9 X_9 X_10$ | 12.50 | 9.69 | 0.001 |
| 8. Y = a + $\lambda_1 X_1 + \lambda_2 X_2 + \lambda_3 X_3 + \lambda_4 X_4 + \lambda_5 X_5 + \lambda_6 X_6 + \lambda_7 X_7 + \lambda_8 X_8 + \lambda_9 X_9 X_10$ | 8.16 | 5.35 | 0.008 |
| 9. Y = a + $\lambda_1 X_1 + \lambda_2 X_2 + \lambda_3 X_3 + \lambda_4 X_4 + \lambda_5 X_5 + \lambda_6 X_6 + \lambda_7 X_7 + \lambda_8 X_8 + \lambda_9 X_9 X_10 + \lambda_10 X_7 X_8$ | 12.07 | 9.27 | 0.001 |

The best model is the one with the lowest AICc. Relative support for a given model is measured by ΔAICc, and the probability that a given model provides the best fit of those tested by $W_{AIC}$.

### Table 2

| Explanatory term                        | F    | df | P    |
|-----------------------------------------|------|----|------|
| Intercept                               | 0.09 | 1,34 | 0.77 |
| Brood size                              | 9.60 | 1,34 | 0.004 |
| Number of brood produced per year       | 0.05 | 1,34 | 0.83 |
| Year                                    | 0.09 | 1,34 | 0.77 |
| Clutch start date                       | 0.69 | 1,34 | 0.41 |
| Female parent structural size           | 0.27 | 1,34 | 0.61 |
| Male parent structural size             | 0.26 | 1,34 | 0.61 |
| Female × male parent structural size    | 5.97 | 1,34 | 0.02 |

The terms female and male parent structural size remained in the model because they were part of a significant interaction.

**Fig. 1** Brood sex ratio as a function of the structural sizes of mated males (A) and females (B) when their mates were smaller (grey circles, $n = 21$) or larger (black circles, $n = 21$).
There was a significantly positive relationship in structural size between females and males of a mated pair ($r = 0.33$, $n = 42$, $P = 0.03$), whereas such a relationship was significantly negative in body mass ($r = -0.37$, $n = 42$, $P = 0.02$). In particular, although failing to reach significant levels, the correlation between structural size of both sexes was negative when females were smaller ($r = -0.30$, $n = 21$, $P = 0.22$), and the opposite was true when females were larger ($r = 0.35$, $n = 21$, $P = 0.12$; Fig. 2).

**Fig. 2** A relationship between structural sizes of mated males and females

The relationship tended to be negative when females were smaller (grey circles, $n = 21$) and positive when females were larger (black circles, $n = 21$).

### 3 Discussion

The white-rumped snowfinches are a socially-monogamous bird. During the breeding season, male snowfinches strongly guard their mates through territorial defense and mate proximity (Zeng and Lu, 2009a, b). This indicates a high probability of extra-pair paternity (Griffith et al., 2002), and thus potentially high variance in reproductive success among males, a selective pressure that promotes adaptive sex allocation. The current research fail to find the role of parental body mass in offspring sex allocation of the white-rumped snowfinches, and it also reveals that offspring sex ratios did not depend on structural size of either parent. However, the results show that body size of both parents combine to affect brood sex ratios: increased production of sons in association with a larger parent occurred only when his or her mate was larger as well; when either female or male parents were smaller, they would not adjust the sex of offspring according to body size of their mates.

These findings should be consistent with predictions jointly by the female quality (Trivers and Willard, 1973) and the male attractiveness hypotheses (Ellegren et al., 1996; Sheldon et al., 1999). In the two earlier studies that attempted to test the two hypotheses simultaneously, the authors did not include interaction of maternal and paternal traits into analysis (Dowling and Mulder, 2006; Addison et al., 2008). Consequently, they only demonstrated the role of phenotypic traits of each parent as a single variable in sex allocation. For the snowfinches, it was possible that females would adaptively produce more sons only when their own and mates both were in high quality, i.e. an additive mechanism.

Structural size in the white-rumped snowfinches should be a good phenotypic indicator of male attractiveness because during mating courtship, two males often perform face-to-face posturing behaviors or direct physical fighting in front of females. It could also signal dominance of females, which, like males, often engage in aggressive interactions during territorial defense through posturing behaviors (Zeng, 2008). Body structural attributes are more likely to have a genetic basis and to be heritable as reported in a variety of bird species (e.g. Marzluff and Balda, 1988; Merilä and Fry, 1998; Kölliker et al., 1999; Barbraud, 2000). Body mass as an indicator of the current energy reserves often relies strongly on breeding status and ecological environments (Moya-Laraño et al., 2008), and is unrelated with structural size in our study species. In its initial version, the female quality hypothesis suggested that body condition should be the predictor of offspring sex ratio for species with sexual size dimorphism because the mothers in good condition would be able to afford the increased investment in producing and rearing the large and thus energy-demanded sex (Trivers and Willard, 1973). This could explain why parental body mass did not arise as a significant predictor of offspring sex ratio in the study species with no sexual size dimorphism.

In the snowfinches, the joint effect of body size of both male and female parents on brood sex ratios should have an association with a size-assortative mating. The non-random mating pattern may result from sexual selection by either females or males for the opposite sex. While female choice according to male-male competition has been treated as a major form of sexual selection, there is a growing body of empirical studies demonstrating male mating preferences in species with conventional sex roles (Amundsen, 2000; Rosvall, 2011). The quality of mates may be more important for a male’s success in monogamous species, in contrast to
polygynous species where male success depends largely on the number of mates. Being choosy, either sex would improve its fitness through yielding more, or high-quality offspring. Möller (1991) showed that in the socially-monogamous swallow Hirundo rustica, preferred males obtain mates of high phenotypic quality and thus a fitness benefit in terms of breeding date and offspring number. In the study species, the benefit could lie in the overproduction of sons that have a potential advantage in future mating success.

In conclusion, this study shows that both maternal and paternal factors interact to affect sex allocation in the white-rumped snowfinch, suggesting that females may manipulate offspring sex according to their own and their mate quality. It seems that no previous study of birds has reported the additive effect of both parental attributes on offspring sex allocation. We propose that the fitness benefits of sex manipulation resulting from the mechanism may be one of the drivers of the evolution sexual selection, in which larger males and females tend to mate each other through intrasexual competition and intersexual choice. We acknowledge that conclusions based on our results should be viewed with caution because of our relatively small sample sizes. More evidence is needed for the white-rumped snowfinch and other species of birds.

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References

Addison B, Kitaysky AS, Hipfner JM, 2008. Sex allocation in a monomorphic seabird with a single-egg clutch: Test of the environment, mate quality and female condition hypothesis. Behav. Ecol. Sociobiol. 63: 135–141.

Amundsen T, 2000. Why are female birds ornamented? Trends Ecol. Evol. 15: 149–155.

Andersson M, 1994. Sexual selection. Princeton: Princeton University Press.

Barbraud C, 2000. Natural selection on body size traits in a long-lived bird, the snow petrel Pagodroma nivea. J. Evol. Biol. 13: 81–88.

Blanchard P, Hanuise N, Dano S, Weimerskirch H, 2007. Offspring sex ratio in relation to parental structural size and body condition in the long-lived wandering albatross Diomedea exulans. Behav. Ecol. Sociobiol. 61: 767–773.

Burley N, 1981. Sex-ratio manipulation and selection for attractiveness. Science 211: 721–722.

Burnham KP, Anderson DR, 2002. Model selection and multimodel inference: A practical information-theoretic approach. New York: Springer.

Cézilly F, Boy V, Tourenq CJ, Johnson AR, 1997. Age-asserotive pairing in the greater flamingo Phoenicopterus ruber roseus. Ibis 139: 331–336.

Crespi BJ, 1989. Causes of assorative mating in arthropods. Anim. Behav. 38: 980–1000.

Dawling DK, Mulder RA, 2006. Combined influence of paternal and maternal quality on sex allocation in red-capped robin. J. Evol. Biol. 19: 440–449.

Dreiss A, Richard M, Moyen F, White J, Moeller AP et al., 2006. Sex ratio and male sexual characters in a population of blue tits Parus caeruleus. Behav. Ecol. 17: 13–19.

Du B, Lu X, 2010. Sex allocation and paternity in a cooperatively breeding passerine: Evidence for the male attractiveness hypothesis? Behav. Ecol. Sociobiol. 64: 1631–1639.

Ellegren H, Gustafsson L, Sheldon BC, 1996. Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. Proc. Natl. Acad. Sci. USA. 93: 11723–11728.

Fräkolsson AK, Ellegren H, 1999. A simple and universal method for molecular sexing of non-ratite birds. J. Avian Biol. 30: 116–121.

Genovart M, Oro D, Forero MG, Igual JM, González-Solís J et al., 2005. Parental body condition does not correlate with offspring sex ratio in Cory’s shearwater. Condor 107: 161–167.

Griffith SC, Owens IPF, Thuman KA, 2002. Extra-pair paternity in birds: A review of interspecific variation and adaptive function. Mol. Ecol. 11: 2195–2212.

Griffiths R, Double M, Orr KCY, Dawson RJG, 1998. A DNA test to sex most birds. Mol. Ecol. 7: 1071–1075.

Heg D, DINGEMANSE NJ, LESSELLS CM, MATEMAN AC, 2000. Parental correlates of offspring sex ratio in the Eurasian oystercatcher. Auk 117: 984–990.

Jawor JM, Linville SU, BEALL SM, BREITWISCH R, 2003. Assortative mating by multiple ornaments in northern cardinals Cardinalis cardinalis. Behav. Ecol. 14: 515–520.

Kölliker M, Heeb P, Mateman AC, LESSELLS CM et al., 1999. Offspring sex ratio is related to male body size in the great tit Parus major. Behav. Ecol. 10: 68–72.

Lu X, Ke DH, Zeng XH, Yu TL, 2009. Reproductive ecology of two sympatric Tibetan snowfinch species at the edge of their altitudinal range: Response to more stressful environments. J. Arid Environ. 73: 1103–1108.

Ludwig SC, BECKER PH, 2008. Supply and demand: Causes and consequences of assortative mating in common tern Sterna hirundo. Behav. Ecol. Sociobiol. 62: 1601–1611.

Marzluff JM, Balda RP, 1988. Pairing patterns and fitness in a free-ranging population of Pinyon jays: What do they reveal about mate choice? Condor 90: 201–213.

Merill J, Fry JD, 1998. Genetic variation and causes of genotype-environment interaction in the body size of blue tit Parus caeruleus. Genetics 148: 1233–1244.

Moller AP, 1991. Preferred males acquire mates of higher phenotypic quality. Proc. R. Soc. Lond. B 245: 179–182.

Moya-Laraño J, Macías-Ordóñez R, Blanckenhorn WU, Fernández-Montraveta C, 2008. Analyzing body condition: Mass, volume or density? J. Anim. Ecol. 77: 1099–1108.

Nager RG, Monaghan P, Griffiths R, Houston DC, Dawson R, 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. Proc. Natl. Acad. Sci. USA. 96: 570–573.
Olsen P, Barry S, Baker GB, Mooney N, Cam G et al., 1998. Assortative mating in falcons: Do big females pair with big males? J. Avian Biol. 29: 197–200.

Parker TH, 2002. Maternal condition, reproductive investment, and offspring sex ratio in captive red junglefowl Gallus gallus. Auk 119: 840–845.

Rosvall KA, 2011. Intrasexual competition in females: Evidence for sexual selection? Behav. Ecol. 22: 1131–1140.

Rutstein AN, Gorman HE, Arnold KE, Gilbert L, Orr KJ et al., 2005. Sex allocation in response to paternal attractiveness in the zebra finch. Behav. Ecol. 16: 763–769.

Saino N, Ellegren H, Möller AP, 1999. No evidence for adjustment of sex allocation in relation to paternal ornamentation and paternity in barn swallows. Mol. Ecol. 8: 399–406.

Sheldon BC, Andersson S, Griffith SC, Örnborg J, Sendecka J, 1999. Ultraviolet colour variation influences blue tit sex ratios. Nature 402: 874–877.

Sutherland WJ, Newton I, Green RE, 2004. Bird Ecology and Conservation: A Handbook of Techniques. Oxford: Oxford University Press.

Taff CC, Freeman-Gallant CR, Dunn PO, Whittingham LA, 2011. Relationship between brood sex ratio and male ornaments depends on male age in a warbler. Anim. Behav. 81: 619–625.

Trivers RL, Willard DE, 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179: 90–92.

Tryjanowski P, Simek J, 2005. Sexual size dimorphism and positive assortative mating in red-backed shrike Lanius collurio: An adaptive value? J. Ethol. 23: 161–165.

West SA, 2009. Sex Allocation. Princeton: Princeton University Press.

Whittingham LA, Valkenaar SM, Poirier NE, Dunn PO, 2002. Maternal condition and nestling sex ratio in house wrens. Auk 119: 125–131.

Zeng XH, 2008. Study on breeding biology of the white-rumped snowfinch Montifringilla taczanowskii in northeastern Tibetan plateau. Ph.D. Dissertation, Wuhan University.

Zeng XH, Lu X, 2009a. Interspecific dominance and asymmetric competition with respect to nesting habitats between two snowfinch species in a high-altitude extreme environment. Ecol. Res. 24: 607–616.

Zeng XH, Lu X, 2009b. Breeding ecology of a burrow-nesting passerine, the white-rumped snowfinch Montifringilla taczanowskii. Ardeola 56: 173–187.

Zielinska M, Dubiec A, Zielinski P, 2010. Offspring sex ratio skew in the sexually monomorphic house martin. J. Avian Biol. 41: 591–596.