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Authors: Liu, Chang-Jing, Du, Bo, Liu, Nai-Fa, Bao, Shi-Jie, and Zhang, Shengxiang

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Sex-Specific Parental Care Strategies via Nestling Age: Females Pay More Attention to Nestling Demands than Males Do in the Horned Lark, *Eremophila alpestris*

Chang-Jing Liu, Bo Du, Nai-Fa Liu, Shi-Jie Bao, and Shengxiang Zhang*

Gansu Key Laboratory of Biomonitoring and Bioremediation for Environmental Pollution, School of Life Sciences, Lanzhou University, 222 South Tianshui Road, Lanzhou 730000, P.R. China

In many species, nestling demands vary continuously during early development and both parents have different parental care strategies at each nestling age. Sexual conflict arises when each parent expects its partner investing more in parental care. It is largely unknown how the two parents respond to the dynamics of nestling demands and resolve the sexual conflict during nestling period, especially on Qinghai-Tibetan Plateau. To address this question, we monitored parental care behaviors of horned larks (*Eremophila alpestris*) using video-recording systems. We found that male horned larks invested less in parental care, but had a larger body size than females, which is consistent with the parental investment hypothesis. Only the female brooded nestlings, but both parents contributed to feeding efforts. Feeding rates of males and females were negatively correlated, indicating that they used evolutionarily stable strategies. Strategies of parental care via nestling age were sex-specific. Females continuously adjusted care behaviors to follow the dynamics of nestling demands as nestling age increased, such as decreasing brood attentiveness and increasing feeding rate. By contrast, male feeding rate showed no significant correlation with nestling age, but increased with the synchrony feeding rate. We suggest the synchrony feeding behavior may act as a control measure for females to promote and assess the males' contribution. We consider low mating opportunities drive males to act as assistants for females, and correspondingly cause males to pay less attention to nestling demands than females.

Key words: sexual conflict, nestling demands, synchrony feeding rate, Qinghai-Tibetan Plateau, ESS

INTRODUCTION

Nestlings of altricial birds need to be cared until they fledge out of nests, and bi-parental care can increase the fledging success of nestlings (Houston et al., 2005). Nevertheless, parental care is energy-consuming, and each sex prefers for its partner to invest more in parental care (Trivers, 1972; Olson et al., 2009). Previous studies determine the male generally invest less in taking care of nestlings than the female (Trivers, 1972; Queller, 1997). Parental investment hypothesis suggests that the male focus less on caring but more on mating, and the energy saved from less care can be used to develop secondary sexual characters and compete for females (Trivers, 1974; Ketterson and Nolan, 1994). Therefore, parental care disparity drives sexual selection intensity, and the male experiences higher selective pressure on body size (Olson et al., 2009). In addition, these studies also suggest that the male reduces its parental care due to uncertain paternity. Sexual size dimorphism has been widely studied in many bird species (Trivers, 1974; Berry and Shine, 1980; Li et al., 2010). However, the relationship between the parental investment and sexual size dimorphism remains unclear for monogamous and bi-parental species (Owens and Hartley, 1998; Székely et al., 2000; Palestis et al., 2012).

Nestling demands, including brooding and food demands, vary continuously during the nestling period. The brooding demands decrease but the food demands increase with nestling age (Sanz and Tinbergen, 1999; Steen et al., 2012). Parents need to decrease brood attentiveness but increase feeding rate as nestling age increases. However, not every parent continuously adjusts its care behaviors to follow the dynamics of nestling demands, and responses of the two parents are sometimes sex-specific (Cézilly et al., 1994; Sanz and Tinbergen, 1999; Rossmanith et al., 2009; Steen et al., 2012). Evolutionarily stable strategies (ESS) predict one of the two parents may compensate for the reduced efforts of its partner. However, most studies on ESS have been theoretical or conducted through experimental manipulations (such as removing or handicapping one parent) (Wright and Cuthill, 1989; Sanz et al., 2001; Harrison et al., 2009; Rossmanith et al., 2009). What leads to sex-specific parental care strategies and whether the ESS could be verified in natural environment has not been elucidated (Houston et al., 2005; Harrison et al., 2009; Rossmanith et al., 2009).

Here, we explored parental care strategies of a monog-

* Corresponding author. Tel. : +86-931-8915607;
Fax : +86-931-8915607;
E-mail: sxzhang@lzu.edu.cn
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amous species, the horned lark (*Eremophila alpestris*) in natural environment on Qinghai-Tibetan Plateau. The horned lark has a short nestling period (~9 days) and multiple nest attempts per year. Adult males and females can be distinguished by their external appearances, and their open-cup nests are easy to observe. We compared parental care efforts between the two sexes, and tested whether the parent investing less in parental care has a biased body size. Using video-recording systems, we monitored parental care behaviors of the two parents for each nestling age, and investigated how they responded to the dynamics of nestling demands during the entire nestling period.

METHODS AND MATERIALS

Study area

Fieldwork was conducted in 2010 in Gahai-Zecha National Natural Reserve (34°14′N, 102°20′E), which is located on the northeastern Qinghai-Tibetan Plateau. It has an annual average temperature of 1.2°C, and annual total precipitation of 782 mm (Liu and Ma, 1997). The Gahai Lake lies in the center of the region, and is surrounded by mountains (average elevation = ~3400 m, gradient < 30°), which are covered by alpine Kobersia steppe meadow. Our study area is located between the Gahai Lake and northern mountains, covering approximately 400-ha alpine meadow.

Nest monitoring using video-recording system

To avoid the effects of brood size on parental care, only the nests having the same number of nestlings (n = 3) were monitored (Sanz and Tinbergen, 1999). We systematically searched for horned lark nests by walking transect lines, ~2 m apart within the plots, and then positioned them by a GPS handset (Garmin eTrex Summit). We conducted daily checks on each nest, and recorded parental behaviors after all the three eggs had hatched.

The video-recording system included a digital camcorder (Zx1 Pocket Video Camera, Eastman Kodak Company) and a tripod. The camcorder was placed on the tripod, ~0.3 m above the ground and ~1.8 m away from the nest (Supplementary Figure S1 online). Parental care behaviors were recorded from 10:00 to 15:00 for each nestling age.

Body measurements and behavioral parameters extraction

To measure body size of adult horned larks, we captured them when they flocked together. Horned larks are resident species on Qinghai-Tibetan Plateau, and they flock together before the breeding reason. We placed mist nets throughout the study area and captured as many of them as possible, while they were flocking together. Body mass was recorded using an electronic balance, to the nearest 0.01 g. The length of culmen, tarsus, wing and tail were measured with a digital caliper, to the nearest 0.01 mm (Supplementary Table S1 online) (Zhou and Jiang, 2008).

We extracted three common behavioral parameters, including male feeding rate, female feeding rate and brood attentiveness, from the videos. Feeding rate refers to the number of feeding trips per hour per nestling (Martin et al., 2000). Female brood attentiveness refers to the percentage of total observation time the female spends in brooding nestlings. Particularly, recent studies suggest that the coordination of breeding activities, for example synchrony feeding behavior, can partly counterbalance the sexual conflict (Shen et al., 2010; Mariette and Griffith, 2012). Therefore, we extracted synchrony feeding rate as the fourth parameter to assess parental care behaviors of horned larks. We defined synchrony feeding behaviors as events in which both parents fed nestlings within 90 s, because field videos showed that the duration of single male/female feeding behavior was less than 30 s and then an average of ~60 s was used to clean nestling droppings, tidy nest and look around (Supplementary Videos).

Statistical analysis

First, we performed one-sample Kolmogorov-Smirnov tests to check the normality of dataset, and found all the parameters were normally distributed (P > 0.05). To compare body sizes between the two sexes, we determined the differences in body mass and length of culmen, tarsus, wing and tail by independent-sample t tests (Li et al., 2010). To compare parental care efforts between the two sexes, we examined the differences in parental care behaviors using paired-sample t tests.

To determine how parental care behaviors varied with nestling ages, we first analyzed the correlation effects among independent parameters (nestling age, male feeding rate, female feeding rate, synchrony feeding rate and female brood attentiveness) using Spearman's correlation method.

We performed linear mixed models for repeated measurements to investigate the effects of potential explanatory factors (male/female/synchrony feeding rate, female brood attentiveness, nestling age, and interactions of two strongly correlated parameters) on parental care behaviors (female brood attentiveness and female/male feeding rate), and the nest ID was included as a random factor. We incorporated the interaction of two strongly correlated parameters (r > 0.6 and P < 0.05) as an independent parameter during model building process, because cross correlation could compromise the effects of multiple independent parameters (Zhou and Chu, 2012). The model which has the smallest value of Hurvich and Tsai's criterion (AIC_c) was selected as the best model (Hurvich and Tsai, 1989; Burnham and Anderson, 2002). All data analyses were performed using SPSS 19.0, and significance level was set at P < 0.05 (two-tailed). Data are presented as mean ± SE.

RESULTS

Comparisons of body sizes and parental care behaviors

We measured body weight and the length of culmen, wing, tail and tarsus for 81 adult horned larks (49 males and 32 females). We found the breeding population had a male-biased sex ratio (1.5:1). The t tests showed these body measurements of the male were significantly larger than those of the female (Table 1), indicating a significantly male-bias toward larger body size. The two sexes provided similar contributions in feeding efforts. The male feeding efforts were slightly lower than the female, but this difference was not statistically significant (t = –1.261, P = 0.218; Table 1). Only the female brooded the nestlings, and the male invested less than the female in parental care (Table 1).

Parental care strategies for different nestling ages

We obtained a total of 134.82-h videos from eight nests, which covered 31 observation days (4.35 ± 0.36 h/d), and 3–4 observation days for each nestling age (Table 2). Correlation analyses (Table 3) showed that there was a strong neg-

Table 1. Comparisons of body size and parental care behaviors between male and female horned larks, *Eremophila alpestris*.

Parameters	Male	Female	t	P
Mass (g)	33.56 ± 0.35	31.71 ± 0.34	3.622	**0.001**
Culmen (mm)	9.75 ± 0.09	9.25 ± 0.10	3.475	**0.001**
Wing (mm)	115.94 ± 0.42	107.25 ± 0.69	11.432	**<0.001**
Tail (mm)	84.56 ± 0.54	77.53 ± 0.84	7.353	**<0.001**
Tarsus (mm)	24.91 ± 0.16	24.12 ± 0.19	3.123	**0.003**
Brood attentiveness (%)	0.00 ± 0.00	29.07 ± 4.44	–6.550	**<0.001**
Feeding rate (trips/nestling/h)	4.96 ± 0.36	6.29 ± 0.80	–1.261	0.218

Notes: Independent-sample t tests are used for five parameters of body size (n_{male} = 49, n_{female} = 32); Paired-sample t tests are used for brood attentiveness and feeding rate (n = 28).

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ative correlation between the two types of parental care behaviors (feeding rate and brood attentiveness) in females (r = –0.606, P = 0.001). The males and females yield a significant negative correlation in feeding rates, (r = –0.560, P = 0.002). In addition, female brood attentiveness (r = –0.905, P < 0.001) and female feeding rate (r = 0.720, P < 0.001) significantly correlated with nestling age, but not male feeding rate (r = –0.231, P = 0.237). Synchrony feeding rate showed no significant correlation with any other parameters. However, when synchrony feeding rate was subtracted from feeding rate, female-only feeding rate still showed a significant positive correlation with nestling age (r = 0.678, P < 0.001), but male-only feeding rate showed a weak negative correlation with nestling age (r = –0.355, P = 0.064) (Fig. 1).

The linear mixed model showed that the variation of female feeding rate correlated significantly with nestling age (F = 7.137, t = 2.672, P = 0.014), male feeding rate (F = 12.239, t = –3.498, P = 0.002) and the interaction of nestling age × female brood attentiveness (F = 5.481, t = –2.341, P = 0.029) (Table 4). Nestling age was the only main factor explaining the variation of female brood attentiveness (F = 22.636, t = –4.758, P < 0.001) (Table 4). Synchrony feeding rate was the only main factor explaining the variation of male feeding rate (F = 4.374, t = 2.091, P = 0.049) (Table 4).

Table 2. Nest ID, recording time and sample size for each nestling age in horned larks, *Eremophila alpestris*.

Nestling age (d)	Nest ID	Recording time (h)	Sample size	Total recording time (h)
1	a, b, c	6.16 ± 1.58	3	18.48
2	a, b, d, e	5.37 ± 0.69	4	21.49
3	a, d, e, f	3.35 ± 1.05	4	13.39
4	b, d, e	5.88 ± 1.37	3	17.63
5	b, d, e, f	3.19 ± 0.63	4	12.75
6	b, d, e	4.56 ± 0.23	3	13.69
7	b, d, g	3.79 ± 1.14	3	11.36
8	b, d, g	4.15 ± 1.73	3	12.43
9	d, f, g, h	3.40 ± 1.02	4	13.60
Total			31	134.82

Notes: There is no significant difference in recording time among different nestling ages (ANOVA; $F_{8,22}$ = 1.084, P = 0.410).

Table 3. Spearman's correlation matrix among parameters of nestling age, male feeding rate, female feeding rate, synchrony feeding rate and female brood attentiveness in horned larks, *Eremophila alpestris*.

Parameters	Male feeding rate	Female feeding rate	Synchrony feeding rate	Female brood attentiveness
Nestling age	–0.231	**0.720****	0.280	**–0.905****
Male feeding rate		**–0.560****	0.256	0.104
Female feeding rate			0.182	**–0.606****
Synchrony feeding rate				–0.217

Notes: Significant parameters are highlighted using bold type. ** P < 0.01

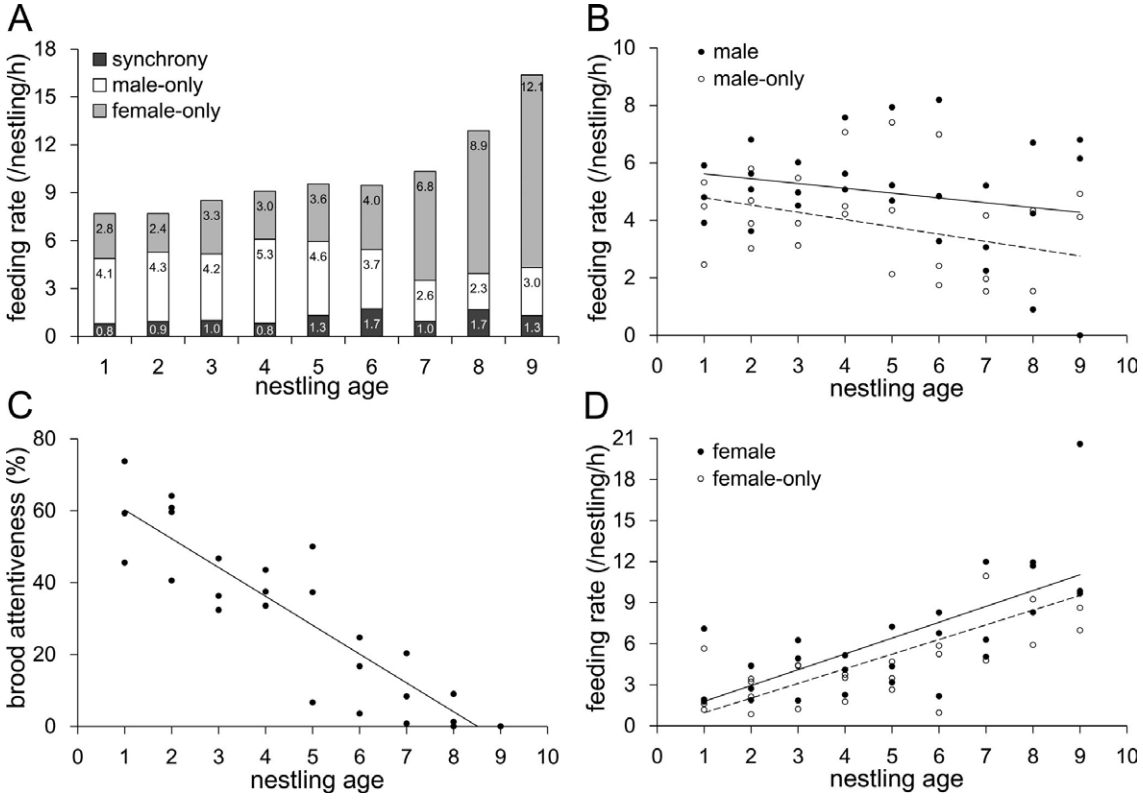


Fig. 1. Male, female and synchrony feeding rates in horned larks, *Eremophila alpestris* for each nestling age. **(A)** Male-only feeding rate, female-only feeding rate and synchrony feeding rate for each nestling age. **(B)** Male feeding rate (male-only feeding rate + synchrony feeding rate; solid circle and solid line) and male-only feeding rate (empty circle and broken line) show no significant correlation with nestling age (r = –0.231, P = 0.237; r = –0.355, P = 0.064). **(C)** Female brood attentiveness shows a significant negative correlation with nestling age (r = –0.905, P < 0.001). **(D)** Female feeding rate (female-only feeding rate + synchrony feeding rate; solid circle and solid line) and female-only feeding rate (empty circle and broken line) show significant positive correlation with nestling age (r = 0.720, P < 0.001; r = 0.678, P < 0.001).

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Table 4. Results of linear mixed models for the interpretation of the variation of female brood attentiveness and female/male feeding rate in horned larks, *Eremophila alpestris*.

Dependent parameter	AIC_c of the best model	Potential explanatory factors	Type III tests of fixed effects		Estimates of fixed effects		
			F	*P*	Estimate ± SE	*t*	*P*
Female brood attentiveness	−6.651	**Nestling age**	**22.636**	**<0.001**	**−0.084 ± 0.018**	**−4.758**	**<0.001**
		Female feeding rate	0.006	0.937	−0.002 ± 0.022	−0.080	0.937
		Synchrony feeding rate	0.717	0.406	0.028 ± 0.033	0.846	0.406
		Male feeding rate	1.736	0.201	−0.020 ± 0.015	−1.318	0.201
		Nestling age × Female feeding rate	0.996	0.996	0.000 ± 0.003	0.005	0.996
Female feeding rate	117.608	**Nestling age**	**7.137**	**0.014**	**1.291 ± 0.483**	**2.672**	**0.014**
		Male feeding rate	**12.239**	**0.002**	**−0.947 ± 0.271**	**−3.498**	**0.002**
		Nestling age × Female brood attentiveness	**5.481**	**0.029**	**−2.243 ± 0.958**	**−2.341**	**0.029**
		Synchrony feeding rate	1.815	0.192	0.848 ± 0.629	1.347	0.192
		Female brood attentiveness	1.614	0.217	0.756 ± 0.596	1.271	0.217
Male feeding rate	100.195	**Synchrony feeding rate**	**4.374**	**0.049**	**0.951 ± 0.455**	**2.091**	**0.049**
		Female feeding rate	1.002	0.329	−0.728 ± 0.728	−1.001	0.329
		Nestling age	0.216	0.647	−0.242 ± 0.521	−0.465	0.647
		Female brood attentiveness	0.401	0.534	−3.720 ± 5.872	−0.633	0.534
		Nestling age × Female feeding rate	0.278	0.604	0.044 ± 0.084	0.527	0.604
		Nestling age × Female brood attentiveness	0.232	0.635	−0.392 ± 0.814	−0.482	0.635
		Female feeding rate × Female brood attentiveness	0.082	0.778	0.353 ± 1.234	0.286	0.778

Notes: Significant parameters are highlighted using bold type.

DISCUSSION

In this study, we compared parental care behaviors between male and female horned larks. We found that male horned larks invested less in parental care. Lower investments in parental care make competitiveness and extra-pair fertilizations a more profitable strategy for males, which probably lead the male to be the competitive sex (Ramírez et al., 2010). According to parental investment hypothesis, sexual selection on the competitive sex was strengthened and led to a biased body size. Our finding that horned lark has a male-biased body size was consistent with the prediction of parental investment hypothesis. In addition, we have not observed extra-pair copulation (EPC) during field investigation in our studied area and EPC was also barely reported in horned larks in other studies (Beason, 1995). However, we could not rule out the possibility that uncertain paternity was the reason for less male investment (Queller, 1997). DNA fingerprinting studies are warranted to ascertain the impacts of uncertain paternity on male investment of horned larks.

We found both sexes of horned larks undertook the feeding efforts, and there was no significant difference between them. Feeding rates of males and females were negatively correlated, which fit the prediction of ESS models, i.e. bi-parental care is evolutionarily stable when any shortfall in one parent's effort is partially compensated for by its partner (Schwagmeyer et al., 2002; Harrison et al., 2009). Previous studies by removing or handicapping one parent indicate that the unmanipulated parent increases its effort when its partner is removed or handicapped (Wright and Cuthill, 1989; Harrison et al., 2009). However, the responses of unmanipulated partner were sex-specific in the great tit *Parus major*, i.e. females fully compensated for the decreasing effort of their handicapped partners', while males did not compensated and even tended to decrease the feeding effort when females were handicapped (Sanz et al., 2001). In this study, although we did not control the observed subjects and their breeding behaviors, we verified that the two parents of horned larks also used ESS to feed nestlings on the Qinghai-Tibetan Plateau.

Parental care patterns of horned larks differed between the two sexes at different nestling ages. Female horned larks continuously adjusted care behaviors to follow the dynamics of nestling demands. As predicted by the development of nestling endothermy (Sanz and Tinbergen, 1999), females reduced their brood attentiveness as nestling age increased, but correspondingly increased their feeding rate to fulfill the increase of nestlings' food demands (Steen et al., 2012). However, males did not change their feeding rate with nestling age. The sex-specific parental care strategies of horned larks were consistent with typical bi-parental care pattern (caring females vs. competitive males) (Ramírez et al., 2010). The female had the responsibility of brooding and feeding nestlings and our data indicated that female brood attentiveness was negatively correlated with female feeding rate. But the male did not brood nestlings and its major responsibility in parental care was nestlings feeding. This single responsibility in parental care may account for the age-independent feeding behavior in males. In addition, age-independent feeding behavior in males could also be associated with the relatively constant tasks for territories defense during nestlings breeding and feeding period. Furthermore, nestling begging behavior may have an effect on parental care and may be responsible for the differences between the male and the female (MacGregor and Cockburn, 2002; Mock et al., 2005; Dor and Lotem, 2010). Parental responses are different in response to nestling behaviors in some species (e.g., Schwagmeyer and Mock, 2003). Female horned larks may be more attentive and respond more to nestling begging, which yet needs to be further studied.

Our results showed that the variation of male feeding rate could only be explained by the synchrony feeding rate. We speculated that synchrony feeding behaviors may partly counterbalance sexual conflicts and benefit both parents from 'more eyes' effects, which help them reduce predation risk and enhance feeding efficiency (Pulliam, 1973; Shen et al., 2010). Furthermore, synchrony feeding rate may help female horned larks assess their partners' contribution to parental care and

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then act as a control measure for the female to promote male feeding rate (Mariette and Griffith, 2012). Regarding male parental care strategies, re-mating opportunities may play a key role in determining male parental care strategies, because multiple brood attempts per year and male-biased sex ratio (1.5:1) result in low mating opportunities and high replacements for male horned larks. Accordingly, reducing the possibility of being replaced could be the best way to obtain re-mating opportunities for the male. Therefore, we suggest male horned larks may increase their feeding rates with synchrony feeding rates to meet the evaluation criteria of females and thus increase re-mating opportunities.

In this study, we systematically recorded parental care behaviors of an open-cup nesting bird, the horned lark, for the first time on Qinghai-Tibetan Plateau, and determined both parents provided feeding efforts in sex-specific patterns. The female focused on the development of nestlings and kept responding to the dynamics of nestling demands. Unlike the female, the male mainly provided assistance for the female, and fed the nestlings regardless of nestling age. Sex differences lead to sexual conflicts, but sexual cooperation will correspondingly reduce the conflicts. We suggest that long-term studies on pair bonds and parentage in horned larks, or even in other open-cup nesting birds, should be performed, to confirm the costs and benefits of male investment in parental care.

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REFERENCES

Beason RC (1995) Horned Lark. American Ornithologists' Union

Berry JF, Shine R (1980) Sexual size dimorphism and sexual selection in turtles (Order Testudines). Oecologia. 44: 185–191Cézilly F, Tourenq C, Johnson A (1994) Variation in parental care with offspring age in the Greater Flamingo. Condor 96: 809–812

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed.). Springer-Verlag

Dor R, Lotem A (2010) Parental effort and response to nestling begging in the house sparrow: repeatability, heritability and parent-offspring co-evolution. J Evol Biol 23: 1605–1612

Harrison F, Barta Z, Cuthill I, Szekely T (2009) How is sexual conflict over parental care resolved? A meta-analysis. J Evol Biol 22: 1800–1812

Houston AI, Székely T, McNamara JM (2005) Conflict between parents over care. Trends Ecol Evol 20: 33–38

Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples, Biometrika 76: 297–307

Ketterson ED, Nolan V (1994) Male parental behavior in birds. Annu Rev Ecol Syst 25: 601–628

Li J, Wang N, Wang Y, Lin S, Li Q, Liu YY, et al. (2010) Sexual size dimorphism and sex identification using morphological traits of two Aegithalidae species. Zool Sci 27: 946–951

Liu NF, Ma CY (1997) Gahai-Zecha National Natural Reserve. China Forestry Publishing House, Beijing

MacGregor NA, Cockburn A (2002) Sex differences in parental response to begging nestlings in superb fairy-wrens. Anim Behav 63: 923–932

Mariette MM, Griffith SC (2012) Nest visit synchrony is high and correlates with reproductive success in the wild Zebra finch *Taeniopygia guttata*. J Avian Biol 43: 131–140

Martin TE, Martin PR, Olson CR, Heidinger BJ, Fontaine JJ (2000) Parental care and clutch sizes in North and South American birds. Science 287: 1482–1485

Mock DW, Schwagmeyer P, Parker G (2005) Male house sparrows deliver more food to experimentally subsidized offspring. Anim Behav 70: 225–236

Olson V, Webb T, Freckleton R, Szekely T (2009) Are parental care trade-offs in shorebirds driven by parental investment or sexual selection? J Evol Biol 22: 672–682

Owens IP, Hartley IR (1998) Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proc R Soc Lond B Biol Sci 265: 397–407

Palestis BG, Nisbet IC, Hatch JJ, Arnold JM, Szczys P (2012) Tail length and sexual selection in a monogamous, monomorphic species, the Roseate Tern *Sterna dougallii*. J Ornithol 153: 1153–1163

Pulliam R (1973) On the advantages of flocking. J Theor Biol 38: 419–422

Queller DC (1997) Why do females care more than males? Proc R Soc Lond B Biol Sci 264: 1555–1557

Ramírez F, Hobson KA, Wangensteen OS, Genovart M, Viscor G, Sanpera C, et al. (2010) A physiological marker for quantifying differential reproductive investment between the sexes in Yellow-legged gulls (*Larus michahellis*). J Exp Mar Biol Ecol 396: 48–52

Rossmanith E, Blaum N, Höntsch K, Jeltsch F (2009) Sex-related parental care strategies in the lesser spotted woodpecker *Picoides minor*: of flexible mothers and dependable fathers. J Avian Biol 40: 28–33

Sanz JJ, Tinbergen JM (1999) Energy expenditure, nestling age, and brood size: an experimental study of parental behavior in the great tit *Parus major*. Behav Ecol 10: 598–606

Sanz JJ, Kranenbarg S, Tinbergen JM (2001) Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). J Anim Ecol 69: 74–84

Schwagmeyer P, Mock DW (2003) How consistently are good parents good parents? Repeatability of parental care in the house sparrow, *Passer domesticus*. Ethology 109: 303–313

Schwagmeyer P, Mock DW, Parker GA (2002) Biparental care in house sparrows: negotiation or sealed bid? Behav Ecol 13: 713–721

Shen SF, Chen HC, Vehrencamp SL, Yuan HW (2010) Group provisioning limits sharing conflict among nestlings in joint-nesting Taiwan yuhinas. Biol Lett 6: 318–321

Steen R, Sonerud GA, Slagsvold T (2012) Parents adjust feeding effort in relation to nestling age in the Eurasian Kestrel (*Falco tinnunculus*). J Ornithol 153: 1087–1099

Székely T, Reynolds JD, Figuerola J (2000) Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. Evolution 54: 1404–1413

Trivers RL (1972) Parental investment and sexual selection. In "Sexual Selection and the Descent of Man" Ed by B Campbell, Aldinc, Chicago, pp 136–179

Trivers RL (1974) Parent-offspring conflict. Am Zool 14: 249–264

Wright J, Cuthill I (1989) Manipulation of sex differences in parental care. Behav Ecol Sociobiol 25: 171–181

Zhou D, Chu L (2012) How would size, age, human disturbance, and vegetation structure affect bird communities of urban parks in different seasons? J Ornithol 153: 1101–1112

Zhou F, Jiang A (2008) A new species of babbler (Timaliidae: Stachyris) from the Sino-Vietnamese border region of China. Auk 125: 420–424

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