



Males and females of a polygamous songbird respond differently to mating opportunities

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Abstract

Parents are expected to make fine-tuned decisions by weighing the benefits of providing care to increase offspring survival against that of deserting to pursue future mating opportunities. A higher incentive for the rarer sex in the population indicates an impact of mating opportunities on parental care decisions. However, in a dynamic breeding system, deserting the offspring and searching for a new mate would influence mating opportunities for both sexes. Sex-specific costs and benefits are expected to influence males' and females' parenting strategies in different ways. Here, we investigated Chinese penduline tits, *Remiz consobrinus*, which exhibit flexible parental care strategies: uniparental care by the male or female, biparental care, and biparental desertion occur in the same population. We show that male penduline tits change their parental behavior over the breeding season; they desert clutches produced early in the season but care for the late season clutches. The change in male parenting behavior is consistent with the seasonal decline in mating opportunities. In contrast, parenting by females did not change over the breeding season, nor was it associated with seasonal variation in mate availability. Taken together, mating opportunities have different associations with parental behavior of male and female Chinese penduline tits. We recommend an inclusion of mating opportunities for both sexes simultaneously in order to understand one of the fundamental decisions in parental care evolution—care or desert.

Significance statement

Divorce is a common feature of both human and nonhuman animal societies. Theoretical studies suggest that one of the drivers of divorce is enhanced mating opportunity, i.e., parents with higher mating opportunities are more likely to abandon their family than those with low mating opportunities. Here, we investigate the dynamics of parental behavior and mating opportunities in a wild population of a small songbird, the Chinese penduline tit *Remiz consobrinus*. This species exhibits one of the most diverse avian breeding systems wherein both uniparental (male or female) and biparental rearing can be seen in a single population. We show that male penduline tits abandon their offspring in response to enhanced mating opportunities while the female parental

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behavior remains unaffected. This implies the relationship between mating opportunities and parental care is more complex than currently acknowledged and requires further investigation.

Keywords Offspring desertion · Parental care · Mating opportunity · Mating system · Sexual conflict

Introduction

Parental care is a behavior that often increases the survival of offspring, thereby enhancing individual fitness (Clutton-Brock 1991; McGraw et al. 2010; Balshine 2012). The frequency and type of care vary across major taxa: for instance, bony fishes tend to have male-only care, mammals usually exhibit female-only care, whereas both parents attend to and look after the nestlings in most birds (Reynolds et al. 2002; Cockburn 2006). Nevertheless, in approximately 9% of bird species, one parent ceases to provide care and departs from the family before the nestlings fledge (i.e., clutch or brood desertion; termed offspring desertion Székely et al. 1996; Cockburn 2006). The deserted parent has to decide whether to continue caring alone or give up leaving the offspring deserted by both parents (Maynard Smith 1977; Székely et al. 1996; van Dijk et al. 2012; Houston et al. 2013). Deserting a clutch or a brood can be beneficial in case of finding a new mate and producing additional young ones with the new partner(s) (Barta et al. 2002; Olson et al. 2008; Royle et al. 2012; Halimubieke et al. 2019). Understanding the circumstances that lead to care provisioning versus terminating care is one of the major objectives of studies in parental care evolution (Clutton-Brock 1991; Kokko and Jennions 2008; Klug et al. 2012; Royle et al. 2012).

Mating opportunity is one of the most important components that affect parental care patterns (Keenleyside 1983; McNamara et al. 2000; Rosa et al. 2017; Feeney and Riehl 2019). Theoretical studies suggest that mating opportunities can be unequal for the sexes, such that the rarer sex can terminate brood care and seek a new mate, whereas the abundant sex tends to provide care due to reduced chances of remating (McNamara et al. 2000; Székely et al. 2000; Kokko and Jennions 2008). Experimental and observational studies are consistent with theoretical predictions in that mating opportunities can predict which parent is likely to desert the brood (Keenleyside 1983; Székely et al. 1999; Pilastro et al. 2001; Griggio and Pilastro 2007; Thomson et al. 2014). In addition, field studies across several species have produced patterns consistent with experimental evidence (Parra et al. 2014; Eberhart-Phillips et al. 2018), and are further supported by phylogenetic comparative analyses (Olson et al. 2008; Liker et al. 2014; Remeš et al. 2015). However, some studies failed to find an association between parenting and mating opportunities (Morton et al. 2010; Lehtonen et al. 2011; Wojczulanis-Jakubas and Jakubas 2012). These incongruent findings suggest that mating opportunities and parenting may not have as

straightforward a relationship as theoretical models tend to assume (Houston et al. 2005; Klug et al. 2012). Moreover, in many species, offspring are deserted largely by one of the two sexes (Roulin 2002; Morton et al. 2010; Thomson et al. 2014) despite males and females carrying out distinct parenting duties (Pierotti 1981; Schacht et al. 2017). Sex-specific costs and benefits of providing parental care may lead to different responses to mating opportunity in males and females (Lehtonen et al. 2011; Hopwood et al. 2015; Schacht et al. 2017). Therefore, further studies are important to understand the potential role of mating opportunities in shaping one of the fundamental parenting decisions, whether to care for the offspring or abandon them, using species that exhibit flexible care types by both males and females.

Here, we investigate mating opportunities and parental care in Chinese penduline tits, *Remiz consobrinus*, a small passerine bird (body mass approximately 10 g) distributed across East Asia (Gluschenko et al. 2014; Zheng et al. 2018). This species exhibits unusually diverse parental care strategies since male-only care, female-only care, biparental care, and biparental brood desertion may all occur in the same population (Zheng et al. 2018). The breeding season of Chinese penduline tits lasts from May to August. Single male penduline tits attract females by building a nest and singing melodious songs; once the pair produces a clutch, one (or both) parents may abandon the nest. At uniparental nests, the full workload (incubation and chick feeding) befalls the deserted parent. After clutch desertion, both males and females may find another partner and rebreed during a single breeding season (Zheng et al. 2018). This breeding system is reminiscent of the one exhibited by Eurasian penduline tits, *Remiz pendulinus* (Persson and Öhrström 1989; Pogány et al. 2012; van Dijk et al. 2012), although the latter exhibits strictly uniparental care and biparental brood desertion rendering the nest a failure. The behavioral flexibility of Chinese penduline tits provides excellent opportunities to investigate parental decisions of males and females.

We have four aims in this study: first, to investigate parental care patterns over the breeding season and report the parenting decisions of both male and female Chinese penduline tits. Second, to quantify mating opportunities for male and female penduline tits and investigate how it varies over the breeding season. Third, to explore the associations between mating opportunities and parental care by males and females; and finally, to examine the fitness implications of caring and deserting for both sexes.

Methods

Study area

We studied the Chinese penduline tit in an area located in the Liaohekou National Nature Reserve of Liaoning Province, Northeast China (40° 45′–41° 05′ N, 120° 28′–121° 58′ E; for further details, see Zheng et al. 2018). The study area (approximately 44 km²) is covered by natural reed beds, separated into nine reed ponds by several roads. Trees (such as Siberian elm *Ulmus pumila*, black locust *Robinia pseudoacacia*, weeping willow *Salix babylonica* and Chinese white poplar *Populus tomentosa*) are intermittently distributed along both sides of the roads inside the study area.

Nest observations, nest initiation, and male pairing

Fieldwork was conducted during three breeding seasons: from May 15 to July 30, 2016, and from May 1 to July 30, 2017 and 2019. During each study period, all nests were initiated after May 1. Therefore, we used May 1 as day 1 and relatively converted each date of the season into day number.

We searched for new nests every day by tracking songs or flight routes of single males. The “nest initiation day” was estimated from the building stage when the nest was found (stages A–C, see Zheng et al. 2018), since the number of days spent on different nest-building stages (A, B, or C) were relatively similar for all males (for details on the method of calculating the start day and stages of nest building, see Zheng et al. 2018). On nest initiation day, males start displaying and singing to attract females (Hoi et al. 1996; Pogány et al. 2012; Zheng et al. 2018). We observed each nest with binoculars from a distance of ~15 m every 2 days for 20 min as mentioned in Smith (1995) and Bleeker et al. (2005). The “male pairing day” was defined as the day a male paired with a female, i.e., the first day when a male was observed copulating near the nest with a female and/or when a female contributed to nest building (Szentirmai et al. 2007). The “male giving up day” was defined as the day when an unpaired male abandoned its nest. During nest checks, the nest stage, presence of a female, parental behavior of both sexes (clutch desertion or care), and breeding stage (egg laying, incubation, hatching) were recorded. Two hundred and eighty-eight nests were found in total during the three breeding seasons. For 249 nests (86.5% of all nests), the nest initiation day could be determined. It was not possible to record data blind as our study involved focal nests and breeding pairs in the field.

For each nest, we recorded whether the male was paired or unpaired. For the paired males, we defined the “male mating time” as the number of days between the “nest initiation date” and the “pairing date.” For males who remained unpaired, “male mating time” was defined as the number of days

between the “nest initiation date” and the “giving up day.” For each clutch or brood, we recorded clutch size, number of hatchlings, and number of fledglings.

Patterns of care

Clutch desertion usually takes place within three days after clutch completion (mean \pm SD, 0.8 ± 1.3 days, Zheng et al. 2018). Once the fifth egg was laid (clutch size ranged from 5 to 8 eggs), we checked each clutch daily to assess whether it was deserted. If one (or both) parent(s) did not show up during a daily nest check, we filmed the nest with a SONY HDR-XR160E video camera for 2 h to confirm whether one (or both) parent(s) had deserted the nest (Szentirmai et al. 2005; Zheng et al. 2018). The day of clutch desertion was defined as the day the deserting parent(s) had not been recorded at the nest.

We caught adult males using a mist net, playback of male songs, and by presenting a male dummy and an old nest near the mist net (van Dijk et al. 2006). Because many males (87%) deserted the clutch, we aimed to capture males before egg laying. Females were caught after the eggs hatched using a tuck net (Zheng et al. 2018). Adults were ringed with a uniquely numbered metal ring and three-colored rings to enable identification of individuals and to monitor their behavior during the entire season (41 males, 47 females). At 15 days of age, the nestlings were ringed (237 nestlings, $n = 50$ nests). The local recruitment rate appears to be low: only 2.1% of ringed chicks and adults were resighted locally during the study.

Mating opportunities

Male penduline tits exhibit conspicuous mate attraction displays, i.e., building a nest and singing around the nest (Szentirmai et al. 2005; Zheng et al. 2018). We used three proxies of mating opportunities for males: (1) “pairing probability”—refers to the probability of a male successfully obtained a female on a specific day of the breeding season. This variable indicates the likelihood of a male pairing up anytime during the breeding season (Samplonius and Both 2017); (2) “male mating time”—refers to the time a male spent on finding a mate, i.e., the number of days between nest initiation, and pairing up with (or giving up attracting) a mate. Long male mating time would reflect a low number of unmated females relative to the number of sexually active males (Székely et al. 1999; Parra et al. 2014); (3) “number of single males”—number of single males encountered each day during the breeding season. We used the third variable to indicate male mating opportunity (and also, female mating opportunity, see below). Thus, a high number of single males would reflect many competitors and thus indicate low mating opportunity for males.

Unlike males, that exhibit conspicuous mating displays, the sexual activities of female penduline tits are inconspicuous, similar to females of most passerine birds (Shuster and Wade 2003; Mészáros et al. 2006; Végvári et al. 2018). To estimate female mating opportunity, we used the number of single males present in the mating pool on a specific day (Carmona-Isunza et al. 2017). Note that a high number of single males would indicate high mating opportunity for females (Carmona-Isunza et al. 2017).

Out of 3 years of study, we recorded the nest initiation day for nearly all nests in both 2017 (105 out of 107 nests (98.1%)) and 2019 (72 out of 74 nests (97.3%)), whereas in 2016 our data were less precise since we only knew the nest initiation day for 41 out of 68 nests (60.3%). Therefore, to estimate mating opportunities we only used data from 2017 and 2019.

Indicators of male quality

In Eurasian penduline tits, males that build large nests and have wider masks are preferred by females (Pogány and Székely 2007). Consequently, nest size and male's mask size are considered sexually selected traits (Szentirmai et al. 2005; Kingma et al. 2008). In order to assess male quality along similar lines in Chinese penduline tits, we (1) measured nest weight using an electronic scale (± 0.01 g) after collecting the nests on season completion, and assessed nest volume by filling it with sand and measuring the sand volume using a 1000-ml measuring cylinder (Szentirmai et al. 2005). Nest volumes were only estimated for 2016; (2) estimated male mask size with the help of digital photos on Photoshop CS5 using background grids (0.01 cm²) for calibration. Mask size was calculated as the average area of the left and right masks (± 0.01 cm², Kingma et al. 2008). Additionally, we measured the body mass, tarsus length, wing length, and tail length with calipers to estimate body sizes of adult males.

Statistical analyses

Data analyses were conducted using R 3.6.3 (R Core Team 2020), and the null hypothesis was rejected at $P < 0.05$. If applicable, the normality of data was assessed with the Shapiro test.

i. Seasonal variation in nest initiation

To investigate the seasonal changes in nest initiation and clutch desertion, we divided the breeding season into 10-day periods for each year separately. For each 10-day period, we calculated the average number of nests initiated and the number of deserted clutches. Since neither the number of initiated nests nor the number of deserted ones were different between years (nest initiation: $\chi^2 = 0.03$, $P = 0.87$; clutch desertion: $\chi^2 = 0.16$, $P = 0.68$), we used the average values of the three years for each 10-day period.

ii. Parental care patterns over the season

To investigate overall parental behavior (desert vs care), we constructed a binomial generalized linear mixed model (GLMM) with sex, nest initiation day, and their interaction as fixed effects, and nestID as a random effect.

To explore the sex-specific patterns of parental care decisions over the breeding season, we focused on males and females separately and split the nests into two groups each. For males, we split the nests into two groups: (1) "male deserting": the clutches either with "female-only care" or with "biparental desertion"; (2) "male caring": the clutches with "male-only care" or "biparental care." For females, the nests were split into two similar groups: (1) "female deserting": the clutches either with "male-only care" or with "biparental desertion"; (2) "female caring": the clutches with "female-only care" or "biparental care."

For each sex, we constructed separate binomial generalized linear models (GLM) to analyze male and female parental behavior over the breeding season, with nest initiation day and year as fixed factors in the models.

iii. Mating opportunities

Male pairing probability was analyzed using binomial GLM, and the male mating time was modeled with quasi-Poisson GLM. In both the models, nest initiation day and year were fixed effects—the number of single males on a specific day with quasi-Poisson GLM. Year, nest initiation day, (nest initiation day)², and the interactions between year and nest initiation day, and year and (nest initiation day)², were considered as fixed factors.

iv. Parental behavior in relation to mating opportunities

We analyzed the association between parental care and mating opportunities in two ways: (1) the overall parenting decision (i.e., care or desert) was modeled with number of single males, sex and their interaction as fixed effects, and nest ID as a random effect. (2) Parental decisions in males and females were analyzed separately using binomial GLMs. The number of single males (i.e., the number of male competitors) and year were taken as fixed effects. We also investigated male behavior and mating opportunities at the individual level. Behavior, attractiveness, or overall quality tends to be consistent for a given individual (Westneat et al. 2011; Pagani-Núñez and Senar 2014). To control for multiple records of an individual, we repeated the analyses of mating opportunities and their potential associations with parental care using a subset of individually marked males to control for multiple records of an individual. In the latter models, we added male ID as a random factor to correct for pseudoreplication. We found the individual-based analyses produced consistent results with the population level ones (S1). We calculated the mating time of the

banded males in their penultimate and final breeding attempts, and analyzed the time differences using an unpaired *t*-test.

The quality of sexually selected traits such as nest size and male mask size may change over the breeding season. To investigate these potential associations, we created two GLMs to analyze the change of nest quality over the season, with nest weight and nest volume separately as response variables, and “nest initiation day” as an explanatory variable. To control for seasonal variation in nest size and male mask size, and their influence on the mating opportunity, we created GLMMs with male mating time and nest initiation day as response variables and male mask size as a fixed factor. We also created GLMMs with the same response variables and body size (body mass, tarsus length, wing length, and tail length) as fixed factors. Male ID was taken as random factors in these four GLMMs.

v. Reproductive success and parental care strategies

We used three proxies for reproductive success: clutch size, hatchling number, and fledgling number. We analyzed these proxies using Poisson error distribution in GLMs. Female parental decision (desert vs. care), male parental decision (desert vs. care), and nest initiation days were fixed effects in the three models. Clutch size was added as a fixed effect to the models of hatchling number and fledgling number.

Results

Seasonal variation in parental care

New nests were initiated between May 1 (day 1) and July 11 (day 63). There were two peaks of nest initiations: the first was in mid-May (between days 11 and 20), and the second was in early June (days 31–40) (Fig. 1, Table 1). A significant interaction term between nest initiation and sex of the parent suggests that males and females showed different parental decisions during the breeding season (Table 2, $z = -4.78$, $P < 0.001$). The analyses on the two sexes separately showed that males deserted nests produced early in the season, and cared for nests produced late in the season (Fig. 2a, Table 2, $z = 4.56$, $P < 0.001$), whereas female behavior did not change over the season (Fig. 2b, Table 2, $z = -1.07$, $P = 0.28$).

Seasonal variation in mating opportunities

For males, mating opportunities decreased over the breeding season, as indicated by the low probability of pairing later in the season (Fig. 3a, $n = 178$; $z = -7.45$, $P < 0.001$). Consistently, males that were successful in finding a mate took longer to pair

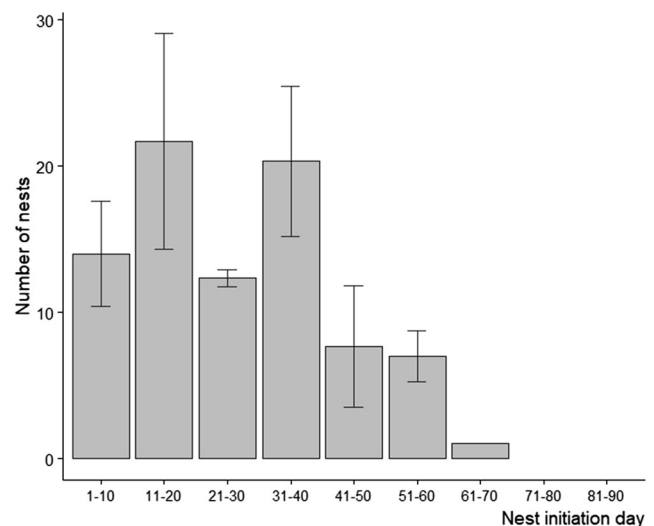


Fig. 1 Number of Chinese penduline tit nests initiated over the breeding season for each 10-day period (mean ± SD). Day 1 = May 1. Data were combined for 2016, 2017 and 2019

up later in the season than in the early season (Fig. 3b, $n = 109$, $t = 10.16$, $P < 0.001$). It took (mean ± SD) 6.46 ± 4.23 days for males to find a mate before day 30, and (mean ± SD) 25.74 ± 10.19 days after day 30. Mating opportunities followed a different pattern for females, since the number of single males increased until day 60 and declined afterward (Fig. 3c, Table 3, $n = 144$, $t = 16.27$, $P < 0.001$).

The behavior of individually banded penduline tits was consistent with the behavior at the population level (supplementary material S1). Of the 24 males ringed at their first nest, all deserted their first nest during the breeding season. Of those, 16 males started a second breeding attempt and six out of the 16 males paired up, whereas 10 remained unpaired. For the six successful males, it took more time to find a new mate in their second breeding attempt (mean ± SD: 24.80 ± 7.79 days) than their first attempt (mean ± SD, 7.62 ± 5.45 days, $n = 13$, $t = 11.67$, $P < 0.001$).

Neither volume nor weight of nests was related to nest initiation day ($n = 14$ nests, S3). Mask size of males was unrelated to male mating time and nest initiation day ($P = 0.49$ and 0.33 , respectively, S4), and we found no relationship between male body size, nest initiation day and mating time (S5).

Does mating opportunity predict parental care?

The different response by males and females to the number of single males was indicated by a significant interaction between the number of males in the population and the sex of the parent (Table 4, $z = -4.26$, $P < 0.001$). The number of single males present in the population predicted male care decisions since males were more inclined to care for their clutch when there were many competitors in the population. In contrast, they

Table 1 Period of egg laying, clutch size and parental care behavior in Chinese penduline tits. Day 1 = May 1

Year	First day of egg laying	Last day of egg laying	Average egg laying days	Clutch size (mean \pm SD)	Parental care (no. of nests)			
					Female-only care	Male-only care	Biparental care	Biparental desertion
2016	24	50	33.9 \pm 6.3	6.8 \pm 0.8	69.6% (32)	6.5% (3)	15.2% (7)	8.7% (4)
2017	11	63	32.7 \pm 9.8	6.8 \pm 0.7	69.0% (49)	5.6% (4)	14.1% (10)	11.3% (8)
2019	24	73	37.1 \pm 10.4	6.7 \pm 0.9	69.6% (32)	6.5% (3)	15.2% (7)	8.7% (4)

were more inclined to desert their clutch and remate when fewer competitors were nearby (Fig. 4a, $n = 96$, $z = 4.62$, $P < 0.001$). The number of single males was unrelated to female care decisions (Fig. 4b, Table 4, $z = 0.57$, $P = 0.57$).

All of the six successfully re-paired males that we had banded deserted their first clutch. Five out of six males changed parental behavior from deserting to providing care for their subsequent clutch(s), when experiencing low mating opportunities in the late season. The sixth male deserted its first and second clutch but remained unpaired during its third breeding attempt (S2).

Fitness implications of caring and desertion

Clutch size was not different between caring and deserting parents for either males (desert: mean \pm SD 6.82 \pm 0.81 eggs, $n = 72$; care: mean \pm SD 6.22 \pm 0.71 eggs, $n = 9$, $z = -0.18$, $P = 0.86$) or females (desert: mean \pm SD 6.38 \pm 0.96 eggs, $n = 13$; care: mean \pm SD 6.84 \pm 0.77 eggs, $n = 68$, $z = 0.40$, $P = 0.62$). Furthermore, neither hatching success nor fledgling success was different between parental strategies, suggesting that the fitness rewards for caring and deserting are similar (Table 5). Although hatching and fledgling success did not differ between parental decisions, deserting males that successfully paired up second and/or third time could sire more offspring in a single breeding season lending them higher reproductive success.

Discussion

Mating opportunity is a major predictor of breeding system variation. Our study contributes to the advancement of this field by showing the impacts of sex differences in mating opportunities in a songbird species that exhibit flexible mating systems and parenting strategies. First, we show that males desert their clutches early in the breeding season when mating opportunities are high, whereas they care for the clutches late in the season when mating opportunities are low. Second, female caring/deserting behavior does not change over the breeding season although female mating opportunities also varied throughout. These findings suggest that mating opportunities have a different influence on parental care decisions of male versus female Chinese penduline tits.

Seasonal variation in male parental care and mating opportunity

Males uniformly desert clutches in the early season, consistent with the proposition that males attempt to seize breeding opportunities to increase their reproductive fitness (Maynard Smith 1977; Székely and Lessells 1993). We found many male Chinese penduline tits arrived at the breeding ground and initiated their first nest resulting in the first peak of nest initiation around day 20. We could not determine whether all males who initiated a new nest during the second peak (31–40) had already deserted a clutch or were newcomers to the population. However, we observed that most (66.7%) of the

Table 2 Seasonal variation in parental care of Chinese penduline tits. Generalized linear mixed model (GLMM) with binomial error for parental behavior using nestID as a random factor ($n = 218$ nests), and generalized linear models (GLM) with binomial error for male and female behavior ($n = 109$ nests). The response variable in all three models is care or desert. R^2 : McFadden pseudo- R^2

Response variable	Explanatory variables	Estimate	SE	Z	Pr(> z)	R^2
Parental behavior	Intercept	-1.87	0.45	-4.13	<0.001	0.75
	Nest initiation day	0.02	0.02	0.99	0.32	
	Sex	9.74	1.65	5.90	<0.001	
	Nest initiation day \times sex	-0.25	0.05	-4.78	<0.001	
Male behavior	Intercept	484.52	601.33	0.81	0.42	0.60
	Nest initiation day	0.24	0.05	4.56	<0.001	
	Year	-0.24	0.30	-0.82	0.41	
Female behavior	Intercept	-228.19	428.83	-0.53	0.60	0.15
	Nest initiation day	-0.02	0.02	-1.07	0.28	
	Year	0.11	0.21	0.54	0.59	

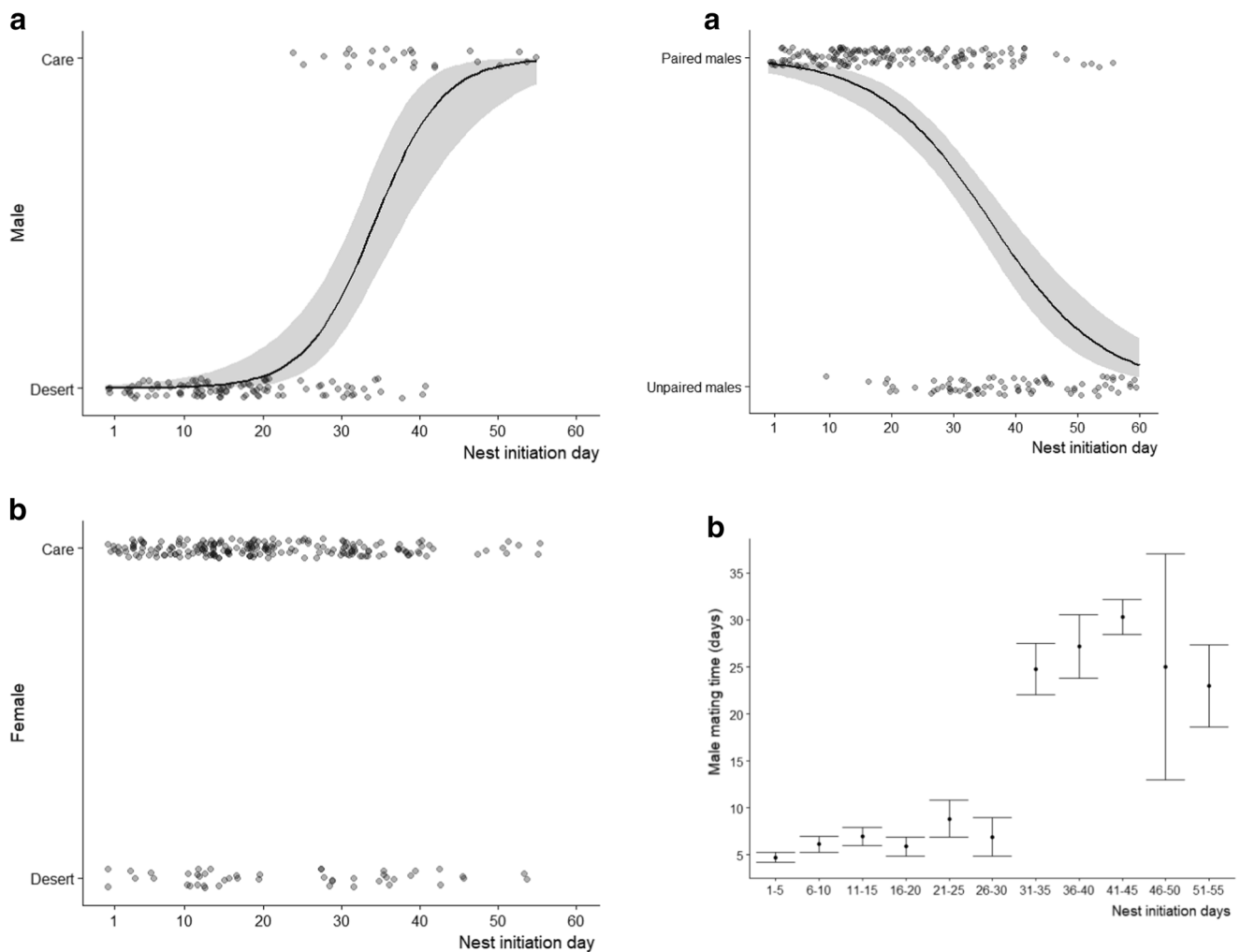


Fig. 2 Caring and deserting behavior in **a** male and **b** female Chinese penduline tits in relation to the day of nest initiation. Each dot refers to a nest. The gray areas indicate the 95% confidence level interval for predictions from the logistic regressions. Day 1 = May 1. Data were combined for 2016, 2017 and 2019. For statistics, see Table 2

banded males started a new nest a few days before or right after the desertion day: they started the first nest between days 1–20 (mean \pm SD: day 10.3 ± 9.1) and the second nest between days 31–50 (mean \pm SD: day 39.8 ± 9.6), which corresponded with the nest initiation peaks. These observations indicate that deserting males rejoined the mating pool and caused the decline of male mating opportunities as the season progressed. Male Chinese penduline tits still put their stake on clutch desertion in the early season, although the overall remating success was only 37.5% (6 out of 16 banded males). This finding is contrary to species, such as rock sparrow *Petronia petronia* and barn owl *Tyto alba*, where the female deserters usually have high remating success after brood desertion (Pilastro et al. 2001; Roulin 2002). However, our finding is consistent with Kentish plovers (*Charadrius alexandrinus*), where males desert in the early season, even when the adult sex ratio is female-biased

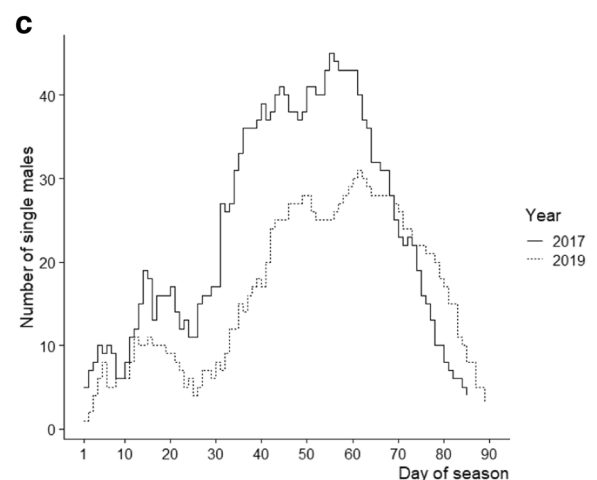


Fig. 3 Pair formation in Chinese penduline tits. **a** Male pairing probability: each dot represents a nest ($n = 178$ nests). Day 1 = May 1. Data were combined for 2016, 2017 and 2019. **b** Mating time (days, mean \pm SD) of males over the breeding season ($n = 109$ nests). The gray area indicates the 95% confidence level interval for predictions from the logistic regressions. Day 1 = May 1. Data were combined for 2016, 2017 and 2019. **c** Number of single males over the breeding season of 2017 and 2019 ($n = 144$ nests). For statistics, see Table 3

Table 3 Male and female mating opportunities of Chinese penduline tits over the breeding season. Male pairing probability was analyzed using GLM with binomial error ($n = 178$ nests). Male mating time and the number of single males were analyzed using GLM with quasi-Poisson error, $n = 109$ and 144 nests, respectively (see Fig. 3)

Mating opportunity for	Response variable	Explanatory variables	Estimate	SE	Z or t	Pr(> z) or Pr(> t)	R ²
Male	Male pairing probability	Intercept	- 889.82	332.66	- 2.71	0.01	0.35
		Nest initiation day	- 0.12	0.02	- 7.45	<0.001	
		Year	0.45	0.16	2.71	0.01	
Male	Male mating time	Intercept	106.32	107.87	0.99	0.33	0.38
		Nest initiation day	0.04	0.004	10.16	<0.001	
		Year	- 0.05	0.05	- 0.97	0.33	
Female	Number of single males	Intercept	1.23	0.13	9.39	<0.001	0.87
		(Nest initiation day) ²	- 0.001	6.6e-05	- 16.20	<0.001	
		Nest initiation day	0.10	0.006	16.72	<0.001	
		Year	0.57	0.22	- 2.53	0.01	
		(Nest initiation day) ²	(Nest initiation day) ² × year	2.6e-04	1.0e-04	2.52	
	Nest initiation day × year	0.01	0.01	- 1.10	0.27		

(Székely and Lessells 1993; Székely et al. 1996). Furthermore, the same reproductive rewards of a single nest with different parental care indicate that one parent is able to efficiently take up the workload of chick feeding (fledging success: 80.6%, Zheng et al. 2018). Despite a decline in mating opportunities during the early season, males are still seen to prefer desertion of the first clutch in pursue of additional reproductive success by remating and producing more offspring.

We found that male Chinese penduline tits switched their parenting decision from a deserter to a care giver at their last nest, when more single males were advertising in the population. We present two explanations for this phenomenon. First, male penduline tits may have detected the decline in mating opportunity due to increased male-male competition and the extended time needed to acquire a mate. A large effort on mate acquisition indicates that males will not get more reproductive benefits from a sequential clutch desertion than from feeding and protecting the current brood under low remating

opportunities (Kokko and Jennions 2008; Béziers and Roulin 2016). Empirical studies have shown that males increase their parental investments when the sex ratio is male-biased (Liker et al. 2013; Rosa et al. 2017), and the rate of brood desertion decreases when the mating opportunity is less biased (Pilastro et al. 2001; Eberhart-Phillips et al. 2018). This pattern also has been proven in insects and fish, where males extend the duration of parental care when they are experiencing intensive competition (Grüter and Taborsky 2005; Hopwood et al. 2015). Second, in a migratory species with a short breeding season, such as rock sparrow, individual parental care decisions may be restricted by the amount of time remaining in the season (Griggio 2015). In this study, we found the number of males in the mating pool declined after day 60. Except for a few males that successfully paired up and left the mating pool, 79.2% of the unpaired nests (61 of 77 nests) were given up by the single males after day 60. A late pairing day in the last breeding attempt indicates that males likely do not have enough time to finish a new breeding round

Table 4 Parental decisions (care or desert) with respect to mating opportunities in male and female Chinese penduline tits. The overall parenting decision was analyzed using GLMM with binomial error distribution, using nest ID as a random factor ($n = 192$ nests). Male and female parental decisions were separately analyzed using GLM with binomial error ($n = 96$ nests). R²: McFadden pseudo-R²

Response variable	Explanatory variables	Estimate	SE	Z	Pr(> z)	R ²
Parenting decision	Intercept	- 1.80	0.52	- 3.48	<0.001	0.58
	Number of single males	0.02	0.03	0.61	0.54	
	Sex	6.70	1.04	6.47	<0.001	
	Number of single males × sex	- 0.22	0.05	- 4.26	<0.001	
Male parental decision	Intercept	- 2967	1011	- 2.93	0.003	0.51
	Number of single males	0.28	0.06	4.62	<0.001	
	Year	1.47	0.5	- 2.93	0.003	
Female parental decision	Intercept	4.71	599.54	0.11	0.99	0.004
	Number of single males	0.02	0.03	0.57	0.57	
	Year	- 0.003	0.30	- 0.01	0.99	

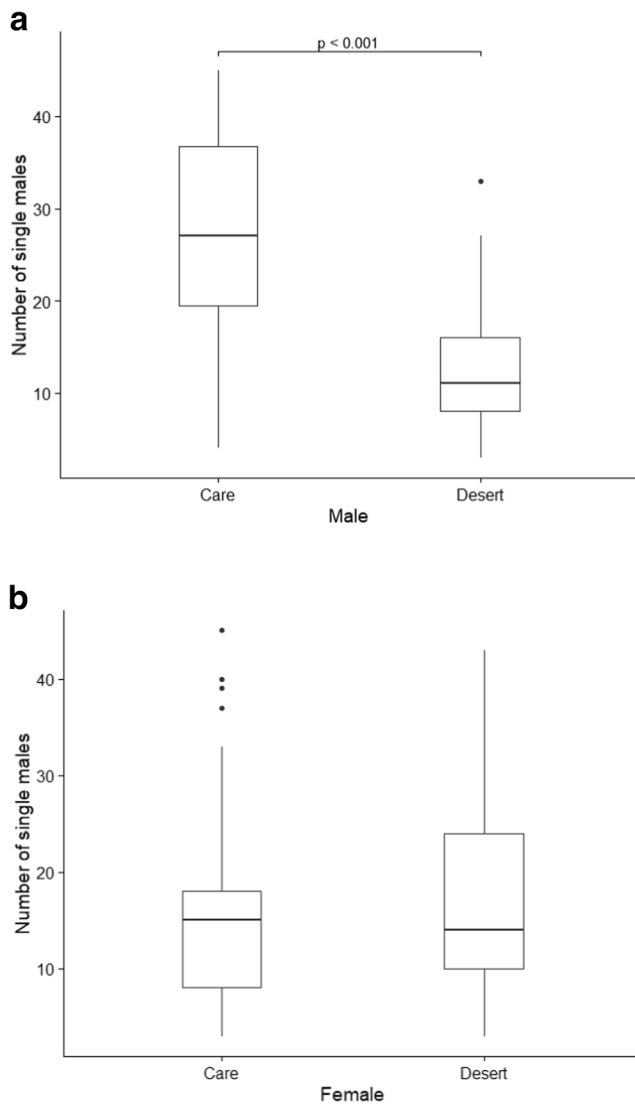


Fig. 4 Mean number of single males in the mating pool with respect to caring and deserting decisions of **a** male and **b** female Chinese penduline tits. Thick lines indicate the medians. The bottom and top of the boxes are 25th and 75th quartiles. The whiskers are the lower and upper range values within 1.5 times the interquartile range and the outliers are the data points outside 1.5 times the interquartile range. The P value indicate significant differences between groups. For statistics, see Table 4

before migration. This may also induce male care provisioning during the late season.

Female parental care and mating opportunities

Female Chinese penduline tits did not show a seasonal change in parental care decisions. We suggest that mating opportunity might not be a determinant factor for female parenting decisions. This result is consistent with Eurasian penduline tits where some females consistently deserted while others consistently cared for their clutches both early and late in the season (Pogány et al. 2008). A lack of variation in female parenting decision was also observed in Nicaraguan cichlid

fish (*Amphilophus* spp. and *Amatitlania* spp.), where mating opportunities increased during the late season (Lehtonen et al. 2011), and in blue-headed vireos (*Vireo solitarius*), where female mating opportunities varied over the breeding season (Morton et al. 2010). However, the frequency of female desertion increased with male availability in rock sparrow (Pilastro et al. 2001) and black coucal (*Centropus grillii*, Goymann et al. 2015). These discordant results imply that the influence of mating opportunities on female parental care decisions shows no general pattern. Other physiological or ecological factors, such as body condition and food abundance, should also be taken into consideration (Bleeker et al. 2005; Eldegard and Sonerud 2009).

Why do parental care patterns vary within a species?

Variation in breeding systems within species is common across the animal kingdom (Vági et al. 2018; Jaeggi et al. 2020). Unfortunately, research has conventionally focused on species that exhibit a “typical” mating system or parenting pattern. Understanding the existence of variable parenting patterns is challenging, and studies focusing on species with variable care patterns are especially important in these endeavors (McGraw et al. 2010; Balshine 2012). Specifically, variable care patterns have been reported from several birds, fish, and amphibian species (Székely et al. 1999; Pilastro et al. 2001; Roulin 2002; Pogány et al. 2008; Lehtonen et al. 2011; Schulte and Lötters 2013; Pike et al. 2016). First, sex different mating opportunities are a possible predictor for these intraspecific variations (van Dijk et al. 2012); as we show in Chinese penduline tits, mating opportunities may have temporal dynamics favoring desertion in one part of the breeding season but not in the other part. Second, the benefits from caring may differ between males and females, i.e., when one parent provides better care than the other (Clutton-Brock 1991; Szentirmai et al. 2007). For instance, the presence of mammary glands and thus the ability of females to feed the young in mammals has been thought to generate a strong difference in offspring survival raised by male-only versus female-only families, putting a strong selective pressure on females to provide care (Clutton-Brock 1991; Royle et al. 2012). In Chinese penduline tits, the similar reproductive success of male-only and female-only broods suggests that males and females can provide qualitatively similar care (Zheng et al. 2018, this study) which is consistent with findings in Eurasian penduline tits (Pogány et al. 2012). Third, since parenting takes time and energy, and the parents often develop dedicated organs and structures to care for their young (such as nests, brood pouches), the mortality costs of these behaviors and/or specific adaptations may be different for males and females during and/or after the breeding season (Liker and Székely 2005; Santos and Nakagawa 2012; Royle et al. 2016). For instance, male-biased predation decreases the

Table 5 Reproductive success of caring and deserting Chinese penduline tits. Clutch size, hatchling number, and fledgling number are the response variables in the three models. GLMM with Poisson error distribution using nest ID as a random factor ($n = 81$ nests). Male decision and female decision are care or desert. R^2 : McFadden pseudo- R^2

Response variable	Explanatory variables	Estimate	SE	Z	Pr(> z)	R^2
Clutch size	Intercept	8.31	90.20	0.09	0.93	0.34
	Male decision	-0.03	0.18	-0.18	0.86	
	Female decision	0.07	0.14	0.4	0.62	
	Nest initiation day	-0.002	0.01	-0.37	0.71	
	Year	-0.003	0.04	-0.07	0.94	
Hatchling number	Intercept	106.04	122.68	0.86	0.39	0.38
	Male decision	0.26	0.27	0.98	0.33	
	Female decision	-0.17	0.37	-0.47	0.64	
	Clutch size	0.09	0.10	0.96	0.34	
	Nest initiation day	-0.01	0.01	-1.41	0.16	
	Year	-0.05	0.06	-0.86	0.39	
Fledgling number	Intercept	-49.50	159.28	-0.31	0.76	0.35
	Male decision	0.19	0.11	1.61	0.11	
	Female decision	0.08	0.27	0.31	0.76	
	Clutch size	0.33	0.41	0.81	0.42	
	Nest initiation day	0.01	0.01	1.85	0.06	
	Year	0.02	0.08	0.31	0.76	

occurrence of polyandry in frogs (Lodé et al. 2004), sex-specific mortality increases during predation peaks while protecting offspring in rodent (Sommer 2000), and in birds, the sex with a lower mortality rate has lower recruitment rates, lower future fecundity or less likelihood of offspring desertion (Jeschke and Kokko 2008; Descamps et al. 2009; Fowler and Williams 2017). However, we cannot evaluate the different mortality costs for males and females in Chinese penduline tits, since less than 5% of adults returned to breed in our study area (JZ et al. unpublished data). While the jury is still out whether sex different mating opportunities, parental abilities and or mortality costs drive parenting evolution in most taxa, we argue that studies need to comprehensively consider these processes in a wide range of animals.

Mating opportunities, however, may not be uniform for all males or all females in a population. A male penduline tit who builds a large nest and has a large mask size is considered to be of “better” sexual quality and pairs up with a female faster (Szentirmai et al. 2005; Kingma et al. 2008). High-quality males have been proven to spend less time acquiring a mate in some species (Houde 1987; Kingma et al. 2008) and are expected to feed less compared to less attractive males (DeMory et al. 2010; Horváthová et al. 2012). Consequently, the male care pattern we observed could be interpreted as attractive males deserting early nests and less attractive ones providing care to the late nests. However, our study showed that male attractiveness is incapable of explaining this pattern in Chinese penduline tits because (1) the same banded males were observed shifting their parental care from deserting to caring over different breeding attempts within one season; (2) nest and male mask size, which were indicators of sexual selection in Eurasian penduline tits

(Szentirmai et al. 2005; Kingma et al. 2008), did not differ here. That is to say, nest quality (volume and weight) did not decline over the season and mask size was not different between males; (3) male body parameters and eye mask size were not related to the time a male spent on mate attraction. These observations conclude that the males who paired up in the late season were not per se of low quality (S3).

Extra-pair paternity (EPP) is suggested to be associated with the parental care in Remizidae (Ball et al. 2017) and the amount of parental investment in animals in general (Kvarnemo 2018; Gao et al. 2020; Schrader et al. 2020). However, according to our microsatellite analyses, EPP is relatively low in Chinese penduline tits (around 6%, 36 nests, 198 nestlings, HW et al. unpublished data), which is similar to Cape penduline tits *Anthoscopus minutus* (5.4%, Ball et al. 2017) that obligate biparental care. There is no seasonal effect on EPP (logistic regression: start date— $z = -0.28$, $p = 0.778$; year— $z = -0.90$, $p = 0.37$), indicating males do not leave earlier in the season to obtain EPP. Therefore, we do not suppose that extra-pair copulation is the causation of male Chinese penduline tits uniformly desert the clutch in early season.

Conclusion

To understand parental care evolution, it is important to investigate species that exhibit multiple care patterns. Here, we investigated such a species, the Chinese penduline tits, that exhibit all four major types of care within a single population. We showed that male parental decision (care/desert) was associated with mating opportunities whereas female behavior was unrelated to mating opportunities. We also showed that the fitness

rewards from male-only and female-only care nests are similar. Concisely, our study provides more support for a sex-dependent response to mating opportunities as an explanation for variable care patterns rather than sex-specific parental abilities to rear the young. Further investigation of species with variable breeding systems including relatives of Chinese penduline tits, *Remiz* spp., that appear to exhibit different patterns in caring and mating (Bot et al. 2011), are mandatory to attain a clearer understanding of their relationship.

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Authors' contributions JZ: the first author, took charge of doing the fieldwork, analyzing data, and writing this manuscript.

JK: took charge of editing the manuscript, supervised the method of data analysis.

TS: took charge of editing the manuscript, provided constructive comments to the structure of this manuscript.

MAV: took charge of editing the manuscript and helped with data analyses using the R studio

DL: joined in the fieldwork and provided comments to the manuscript.

HW: joined in the fieldwork.

ZZ: took charge of editing the manuscript and provided primary financial support.

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Data availability The data sets supporting the results of this article will be available in the Dryad repository :

https://datadryad.org/stash/share/s14wBXNPchw_Gt7UWKulX0aDZGxkN-CQYOA4GILfwRw

Code availability All code for data cleaning and analysis pertaining to this study are available from the corresponding author upon request.

Declarations

Ethics approval and consent to participate Our study was based on observations conducted in a nature reserve located in the Liaohe Delta, China. Permission for fieldwork was obtained from the national reserve administration and all aspects of the study complied with local ethical

guidelines and regulations. Our study did not involve any housing of animals, manipulations or experiments. We monitored the behavior of the birds with binoculars from ~15 m away using video cameras (SONY HDR-XR160E) placed below nesting trees. The cameras were camouflaged with green cloth to match the environment in order to limit disturbance to the breeders. We caught adult individuals of Chinese penduline tits using mist-net. Mist net sessions ended when the focal individual was caught, or after 40 min in case of failure. Trapping was neither harmful to the birds (none of the banded adults suffered any injury) nor was it likely to affect their survival (the weight of rings are less than 5% the body mass). We caught birds solely for (individually) marking them with color rings. Males were caught during nest building and females were caught after chicks hatched. Less than 10 min after banding, we released the birds within 20 m from their nest.

All applicable international, national, and/or institutional guidelines for the use of animals were followed. The research complies with the current laws of China. Our study was approved by the Institutional animal care and use committee of Beijing Normal University and MOE KEY laboratory for biodiversity science and ecology engineer, Beijing Normal University. Fieldwork was carried out with permission from Liaohokou National Nature Reserve, Liaoning, China. The bird banding was approved by the Forestry Department of Liaoning Province, China. This research (observational study) was under an agreement with the Animal Management Committee at the College of Life Sciences, Beijing Normal University (permit no. CLS-EAW-2020-002).

Conflict of interest The authors declare that they have no conflicts of interest.

References

- Balshine S (2012) Patterns of parental care in vertebrates. In: Royle NJ, Smiseth PT, Kölliker M (eds) The evolution of parental care. Oxford University Press, Oxford, pp 62–88
- Ball AD, van Dijk RE, Lloyd P, Pogány Á, Dawson DA, Dorus S et al (2017) Levels of extra-pair paternity are associated with parental care in penduline tits (*Remizidae*). *Ibis* 159:449–455
- Barta Z, Houston AI, McNamara JM, Székely T (2002) Sexual conflict about parental care: the role of reserves. *Am Nat* 159:687–705
- Béziers P, Roulin A (2016) Double brooding and offspring desertion in the barn owl (*Tyto alba*). *J Avian Biol* 47:235–244
- Bleeker M, Kingma SA, Szentirmai I, Székely T, Komdeur J (2005) Body condition and clutch desertion in penduline tit *Remiz pendulinus*. *Behaviour* 142:1465–1478
- Bot S, Brinkhuizen D, Pogány Á, Székely T, van Dijk R (2011) Penduline tits in Eurasia: distribution, identification and systematic. *Dutch Birding* 33:177–187
- Carmona-Isunza MC, Ancona S, Székely T, Ramallo-González AP, Cruz-López M, Serrano-Meneses MA, Küpper C (2017) Adult sex ratio and operational sex ratio exhibit different temporal dynamics in the wild. *Behav Ecol* 28:523–532
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton
- Cockburn A (2006) Prevalence of different modes of parental care in birds. *Proc R Soc Lond B* 273:1375–1383
- DeMory ML, Thompson CF, Sakaluk SK (2010) Male quality influences male provisioning in house wrens independent of attractiveness. *Behav Ecol* 21:1156–1164
- Descamps S, Gilchrist HG, Bêty J, Buttler EI, Forbes MR (2009) Costs of reproduction in a long-lived bird: large clutch size is associated with low survival in the presence of a highly virulent disease. *Biol Lett* 5: 278–281

- Eberhart-Phillips LJ, Küpper C, Carmona-Isunza MC, Vincze O, Zefania S, Cruz-López M, Kosztolányi A, Miller TEX, Barta Z, Cuthill IC, Burke T, Székely T, Hoffman JL, Krüger O (2018) Demographic causes of adult sex ratio variation and their consequences for parental cooperation. *Nat Commun* 9:1651
- Eldegard K, Sonnerud GA (2009) Female offspring desertion and male-only care increase with natural and experimental increase in food abundance. *Proc R Soc Lond B* 276:1713–1721
- Feeney WE, Riehl CP (2019) Monogamy without parental care? Social and genetic mating systems of avian brood parasites. *Philos Trans R Soc B* 374:20180201
- Fowler MA, Williams TD (2017) A physiological signature of the cost of reproduction associated with parental care. *Am Nat* 190:762–773
- Gao LF, Zhang HY, Zhang W, Sun YH, Liang MJ, Du B (2020) Effects of extra-pair paternity and maternity on the provisioning strategies of the Azure-winged Magpie *Cyanopica cyanus*. *Ibis* 162:627–636
- Gluschenko YN, Burkovskiy OA, Tiunov IM (2014) The history of the settling of the Chinese penduline tit *Remiz consobrinus* (Remizidae, Passeriformes, Aves) in the Primorsky Krai Territory. *Achiev Life Sci* 8:133–136
- Goymann W, Makomba M, Urasa F, Schwabl I (2015) Social monogamy vs. polyandry: ecological factors associated with sex roles in two closely related birds within the same habitat. *J Evol Biol* 28:1335–1353
- Griggio M (2015) An experimental test on time constraint and sexual conflict over parental care. *Ecol Evol* 5:3622–3627
- Griggio M, Pilastro A (2007) Sexual conflict over parental care in a species with female and male brood desertion. *Anim Behav* 74:779–785
- Grüter C, Taborsky B (2005) Sex ratio and the sexual conflict about brood care in a biparental mouthbrooder. *Behav Ecol Sociobiol* 58:44–52
- Halimubieke NJ, Valdebenito O, Harding P, Cruz-López M, Serrano-Meneses MA, James R, Kupán K, Székely T (2019) Mate fidelity in a polygamous shorebird, the snowy plover (*Charadrius nivosus*). *Ecol Evol* 9:10734–10745
- Hoi H, Schleicher B, Valera F (1996) Nest size variation and its importance for mate choice in penduline tits, *Remiz pendulinus*. *Anim Behav* 51:464–466
- Hopwood PE, Moore AJ, Tregenza T, Royle NJ (2015) Male burying beetles extend, not reduce, parental care duration when reproductive competition is high. *J Evol Biol* 28:1394–1402
- Horváthová T, Nakagawa S, Uller T (2012) Strategic female reproductive investment in response to male attractiveness in birds. *Proc R Soc Lond B* 279:163–170
- Houde AE (1987) Mate choice based upon naturally occurring color-pattern variation in a guppy population. *Evolution* 41:1–10
- Houston AI, Székely T, McNamara JM (2005) Conflict between parents over care. *Trends Ecol Evol* 20:33–38
- Houston AI, Székely T, McNamara JM (2013) The parental investment models of Maynard Smith: a retrospective and prospective view. *Anim Behav* 86:667–674
- Jaeggi AV, Miles MI, Festa-Bianchet M, Schradin C, Hayes LD (2020) Variable social organization is ubiquitous in Artiodactyla and probably evolved from pair-living ancestors. *Proc R Soc B* 287:20200035
- Jeschke JM, Kokko H (2008) Mortality and other determinants of bird divorce rate. *Behav Ecol Sociobiol* 63:1–9
- Keenleyside MH (1983) Mate desertion in relation to adult sex ratio in the biparental cichlid fish *Herotilapia multispinosa*. *Anim Behav* 31:683–688
- Kingma SA, Szentirmai I, Székely T, Bókony V, Bleeker M, Liker A, Komdeur J (2008) Sexual selection and the function of a melanin-based plumage ornament in polygamous penduline tits *Remiz pendulinus*. *Behav Ecol Sociobiol* 62:1277–1288
- Klug H, Alonzo SH, Bonsall MB (2012) Theoretical foundations of parental care. In: Royle NJ, Smiseth PT, Kölliker M (eds) *The evolution of parental care*. Oxford University Press, Oxford, pp 21–39
- Kokko H, Jennions MD (2008) Parental investment, sexual selection and sex ratios. *J Evol Biol* 21:919–948
- Kvarnemo C (2018) Why do some animals mate with one partner rather than many? A review of causes and consequences of monogamy. *Biol Rev* 93:1795–1812
- Lehtonen TK, Wong BB, Lindström K, Meyer A (2011) Species divergence and seasonal succession in rates of mate desertion in closely related Neotropical cichlid fishes. *Behav Ecol Sociobiol* 65:607–612
- Liker A, Székely T (2005) Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution* 59:890–897
- Liker A, Freckleton RP, Székely T (2013) The evolution of sex roles in birds is related to adult sex ratio. *Nat Commun* 4:1587
- Liker A, Freckleton RP, Székely T (2014) Divorce and infidelity are associated with skewed adult sex ratios in birds. *Curr Biol* 24:880–884
- Lodé T, Holveck MJ, Lesbarreres D, Pagano A (2004) Sex-biased predation by polecats influences the mating system of frogs. *Proc R Soc B* 271:S399–S401
- Maynard Smith J (1977) Parental investment: prospective analysis. *Anim Behav* 25:1–9
- McGraw L, Székely T, Young LJ (2010) Pair bonds and parental behavior. In: Székely T, Moore A, Komdeur J (eds) *Social behavior: genes, ecology and evolution*. Cambridge University Press, Cambridge, pp 271–301
- McNamara JM, Székely T, Webb JN, Houston AI (2000) A dynamic game-theoretic model of parental care. *J Theor Biol* 205:605–623
- Mészáros AL, Kajdócsi S, Szentirmai I, Komdeur J, Székely T (2006) Breeding site fidelity in penduline tit *Remiz pendulinus*, in Southern Hungary. *Eur J Wildl Res* 52:39–42
- Morton ES, Stutchbury BJ, Chiver I (2010) Parental conflict and brood desertion by females in blue-headed vireos. *Behav Ecol Sociobiol* 64:947–954
- Olson VA, Liker A, Freckleton RP, Székely T (2008) Parental conflict in birds: comparative analyses of offspring development, ecology and mating opportunities. *Proc R Soc Lond B* 275:301–307
- Pagani-Núñez E, Senar JC (2014) Are colorful males of great tits *Parus major* better parents? Parental investment is a matter of quality. *Acta Oecol* 55:23–28
- Parra JE, Beltrán M, Zefania S, Dos Remedios N, Székely T (2014) Experimental assessment of mating opportunities in three shorebird species. *Anim Behav* 90:83–90
- Persson O, Öhrström P (1989) A new avian mating system: ambisexual polygamy in the penduline tit *Remiz pendulinus*. *Ornis Scand* 20:105–111
- Pierotti R (1981) Male and female parental roles in the Western Gull under different environmental conditions. *Auk* 98:532–549
- Pike DA, Clark RW, Manica A, Tseng HY, Hsu JY, Huang WS (2016) Surf and turf: predation by egg-eating snakes has led to the evolution of parental care in a terrestrial lizard. *Sci Rep* 6:22207
- Pilastro A, Biddau L, Marin G, Mingozzi T (2001) Female brood desertion increases with number of available mates in the rock sparrow. *J Avian Biol* 32:68–72
- Pogány Á, Székely T (2007) Female choice in the penduline tit *Remiz pendulinus*: the effects of nest size and male mask size. *Behaviour* 144:411–427
- Pogány Á, Szentirmai I, Komdeur J, Székely T (2008) Sexual conflict and consistency of offspring desertion in Eurasian penduline tit *Remiz pendulinus*. *BMC Evol Biol* 8:242
- Pogány Á, van Dijk R, Horváth P, Székely T (2012) Parental behavior and reproductive output in male-only cared and female-only cared clutches in the Eurasian penduline tit (*Remiz pendulinus*). *Auk* 129:773–781

- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed April 2015
- Remeš V, Freckleton RP, Tökölyi J, Liker A, Székely T (2015) The evolution of parental cooperation in birds. *Proc Natl Acad Sci U S A* 112:13603–13608
- Reynolds JD, Goodwin NB, Freckleton RP (2002) Evolutionary transitions in parental care and live-bearing in vertebrates. *Philos Trans R Soc B* 357:269–281
- Rosa ME, Barta Z, Fülöp A, Székely T, Kosztolányi A (2017) The effects of adult sex ratio and density on parental care in *Lethrus apterus* (Coleoptera, Geotrupidae). *Anim Behav* 132:181–188
- Roulin A (2002) Offspring desertion by double-brooded female barn owls (*Tyto alba*). *Auk* 119:515–519
- Royle NJ, Smiseth PT, Kölliker M (2012) The evolution of parental care. Oxford University Press, Oxford
- Royle NJ, Alonzo SH, Moore AJ (2016) Co-evolution, conflict and complexity: what have we learned about the evolution of parental care behaviors? *Curr Opin Behav Sci* 12:30–36
- Samplonius JM, Both C (2017) Competitor phenology as a social cue in breeding site selection. *J Anim Ecol* 86:615–623
- Santos ESA, Nakagawa S (2012) The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. *J Evol Biol* 25:1911–1917
- Schacht R, Kramer KL, Székely T, Kappeler PM (2017) Adult sex ratios and reproductive strategies: a critical re-examination of sex differences in human and animal societies. *Philos Trans R Soc B* 372: 20160309
- Schrader M, Keller MK, Lucey GF (2020) Adaptation to monogamy influences parental care but not mating behavior in the burying beetle, *Nicrophorus vespilloides*. *Ecol Evol* 10:6525–6535
- Schulte LM, Lötters S (2013) The power of the seasons: rainfall triggers parental care in poison frogs. *Ecol Evol* 27:711–723
- Shuster SM, Wade MJ (2003) Mating systems and strategies. Princeton University Press, Princeton
- Smith HG (1995) Experimental demonstration of a trade-off between mate attraction and paternal care. *Proc R Soc Lond B* 260:45–51
- Sommer S (2000) Sex-specific predation on a monogamous rat, *Hypogeomys antimena* (Muridae: Nesomyinae). *Anim Behav* 59: 1087–1094
- Székely T, Lessells CM (1993) Mate change by Kentish plovers *Charadrius alexandrinus*. *Ornis Scand* 24:317–322
- Székely T, Webb JN, Houston AI, McNamara JM (1996) An evolutionary approach to offspring desertion in birds. In: Nolan V Jr, Ketterson ED (eds) *Current ornithology*. Plenum Press, New York, pp 271–330
- Székely T, Cuthill IC, Kis J (1999) Brood desertion in Kentish plover sex differences in remating opportunities. *Behav Ecol* 10:185–190
- Székely T, Webb JN, Cuthill IC (2000) Mating patterns, sexual selection and parental care: an integrative approach. In: Apollonio M, Festa-Bianchet M, Mainardi D (eds) *Vertebrate mating systems*. World Scientific Press, Singapore, pp 194–223
- Szentirmai I, Komdeur J, Székely T (2005) What makes a nest-building male successful? Male behavior and female care in penduline tits. *Behav Ecol* 16:994–1000
- Szentirmai I, Székely T, Komdeur J (2007) Sexual conflict over care: antagonistic effects of clutch desertion on reproductive success of male and female penduline tits. *J Evol Biol* 20:1739–1744
- Thomson RL, Pakanen VM, Tracy DM, Kvist L, Lank DB, Rönkä A, Koivula K (2014) Providing parental care entails variable mating opportunity costs for male Temminck's stints. *Behav Ecol Sociobiol* 68:1261–1272
- Vági B, Végyvári Z, Liker A, Freckleton RP, Székely T (2019) Parental care and the evolution of terrestriality in frogs. *Proc R Soc B* 286: 20182737
- van Dijk RE, Szentirmai I, Székely T (2006) Practical field guide for investigating breeding ecology of penduline tits *Remiz pendulinus*. Unpublished Field Guide, Version 1.2, University of Bath. https://www.researchgate.net/publication/228708374_Practical_field_guide_for_investigating_breeding_ecology_of_penduline_tits_Remiz_pendulinus. Accessed April 2015
- van Dijk RE, Székely T, Komdeur J, Pogány A, Fawcett TW, Weissing FJ (2012) Individual variation and the resolution of conflict over parental care in penduline tits. *Proc R Soc Lond B* 279:1927–1936
- Végyvári Z, Katona G, Vági B, Freckleton RP, Gaillard JM, Székely T, Liker A (2018) Sex-biased breeding dispersal is predicted by social environment in birds. *Ecol Evol* 8:6483–6491
- Westneat DF, Hatch MI, Wetzel DP, Ensminger AL (2011) Individual variation in parental care reaction norms: integration of personality and plasticity. *Am Nat* 178:652–667
- Wojczulanis-Jakubas K, Jakubas D (2012) When and why does my mother leave me? The question of brood desertion in the Dovekie (*Alle alle*). *Auk* 129:632–637
- Zheng J, Li D, Zhang Z (2018) Breeding biology and parental care strategy of the little-known Chinese Penduline Tit (*Remiz consobrinus*). *J Ornithol* 159:657–666

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