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

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1 **Abstract**

2 Parents are expected to make fine-tuned decisions by weighing the benefits of caring to increase offspring
3 survival against the benefit of deserting to pursue future mating opportunities. Sex-specific costs and benefits
4 are expected to influence males' and females' parenting strategies in different ways. Mating opportunities can
5 influence parental care decisions, since the rarer sex in the population has a higher incentive to desert the
6 offspring and pursue future mating opportunities. However, in a dynamic breeding system, deserting the
7 offspring and searching for a new mate would influence mating opportunities for both males and females. We
8 investigate Chinese penduline tits *Remiz consobrinus*, which exhibit flexible parental care strategies: both males
9 and females may provide care or desert the clutch, such that uniparental care by the male or female, biparental
10 care and biparental desertion all occur in the same population. Here we show that male penduline tits change
11 parental behavior over the breeding season; they desert clutches produced early in the season although they care
12 for late clutches. The change in male parenting behavior is consistent with seasonal decline in mating
13 opportunities. In contrast, parenting by females did not change over the breeding season, nor was associated
14 with seasonal variation in mate availability. Taken together, mating opportunities have different associations
15 with parental behavior of male and female Chinese penduline tits. We suggest that to understand one of the
16 fundamental decisions in parental care evolution, i.e., caring or deserting, future studies should estimate mating
17 opportunities for both sexes simultaneously.

Keywords: parental care, offspring desertion, mating opportunity, mating system, sexual conflict

Declarations

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25 **Conflicts of interest:** Not applicable

26 **Ethics approval and consent to participate:** Our study was based on observations conducted in a nature
27 reserve located in the Liaohe Delta, China. Permission for fieldwork was obtained from the national reserve
28 administration and all research complied with local ethical guidelines and regulations. Our study did not involve
29 any housing of animals, manipulations or experiments. We monitored the behaviour of the birds with binoculars
30 10m away and using video cameras (SONY HDR-XR160E) below nesting trees; the cameras were camouflaged
31 with green cloth to match the environment in order to limit disturbance to the breeders. We caught adult
32 individuals of Chinese penduline tits using mist-net. Mist net sessions were ended when the focal individual
33 was caught, or after 40 minutes if we failed to catch the focal individual. Trapping is not harmful to the birds
34 (none of the banded adults suffered any injury) and unlikely to affect survival (the weight of rings are less than
35 5% the body mass). We caught bird solely for individually-marking them with colour rings. Males were caught
36 during nest building and female were caught after chicks hatched. We released the birds within 20 meters from
37 their nest within 10 minutes after banding.

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

45 **Consent for publication:** Not applicable

46 **Availability of data and material:** The data used to support the findings of this study are available from the
47 corresponding author upon request.

48 **Code availability:** The code used to analyze data of this study are available from the corresponding author upon
49 request.

50 **Authors' contributions:**

51 Jia Zheng: the first author, took charge of doing the fieldwork, analyzing data, and writing this manuscript.

52 Prof. Jan Komdeur: took charge of editing the manuscript, supervised the method of data analysis.

53 Prof. Tamás Székely: took charge of editing the manuscript, provided constructive comments to the structure of
54 this manuscript.

55 Dr. Maaïke A. Versteegh: took charge of editing the manuscript and helped with data analyses using the
56 software.

57 Prof. Donglai Li: Joined in the fieldwork and provided comments to the manuscript

58 Hui Wang: Joined in the fieldwork

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63

64

65 **Significance statement**

66 Divorce is a common feature of both human and nonhuman animals, and theoretical studies suggest that one of
67 the drivers of divorce is enhanced mating opportunity. Theory predicts that parents with higher mating
68 opportunities more likely abandon the family than parents with low mating opportunities. Using a small
69 songbird, the Chinese penduline tit, as model organism here we investigate parental behavior and mating
70 opportunities in a wild bird population. This species exhibits one of the most diverse avian breeding systems,
71 since the offspring can be reared by the male only, the female only, or by both parents. We show that male
72 penduline tits respond to mating opportunities by abandoning their offspring, whereas female parental behavior
73 is unrelated to mating opportunities. We propose that the relationships between mating opportunities and
74 parental care are more complex than currently acknowledged and warrant further investigation.

Introduction

75 Parental care is a behavior that often increases the survival of offspring, thereby enhancing individual fitness
76 (Clutton-Brock 1991; McGraw et al. 2010; Balshine-Earn 2012). The frequency and type of care varies across
77 major taxa: for instance, bony fishes tend to have male-only care, mammals usually exhibit female-only care,
78 whereas both parents attend the nest and look after the nestlings in most birds (Reynolds et al. 2002; Cockburn
79 2006). Nevertheless, in approximately 9% of bird species, one parent ceases to provide care and departs the
80 family before the nestlings fledge (i.e., clutch or brood desertion; termed offspring desertion Székely et al. 1996;
81 Cockburn 2006). The deserted parent has to decide to continue caring alone or give up care so that the offspring
82 are deserted by both parents (Maynard Smith 1977; Székely et al. 1996; van Dijk et al. 2012; Houston et al.
83 2013). Deserting a clutch or a brood can be beneficial by finding a new mate and producing additional young
84 with the new partner(s) (Barta et al. 2002; Olson et al. 2008; Royle et al. 2012; Halimubieke et al. 2017).
85 Understanding the circumstances that lead to care provisioning versus terminating care is one of the major
86 objectives of studies in parental care evolution (Clutton-Brock 1991; Kokko & Jennions 2008; Klug et al. 2012,
87 Royle et al. 2012).

88 Mating opportunity is one of the most important components that may affect parental care patterns (Keenleyside
89 1983; McNamara et al. 2000; Rosa et al. 2017; Feeney and Riehl 2019). Theoretical studies suggest that mating
90 opportunities can be unequal for males and females, such that the rarer sex is favored to terminate brood care
91 and seek a new mate, whereas the abundant sex tends to provide care due to the difficulties of remating
92 (McNamara et al. 2000; Székely et al. 2000; Kokko and Jennions 2008). Experimental and observational studies
93 are consistent with theoretical predictions that mating opportunities tend to predict which parent may desert the
94 brood (Keenleyside 1983; Székely et al. 1999; Pilastro et al. 2001; Griggio and Pilastro 2007; Thomson et al.
95 2014). In addition, field studies across several species have produced patterns consistent with experimental
96 works (Parra et al. 2014; Eberhart-Phillips et al. 2018), and are further supported by phylogenetic comparative
97 analyses (Olson et al. 2008; Liker et al. 2014; Remeš et al. 2015). However, some studies failed to find an
98 association between parenting and mating opportunities (Morton et al. 2010; Lehtonen et al. 2011;
99 Wojczulanis-Jakubas et al. 2012). These incongruent findings suggest that mating opportunities and parenting
100 may not have as straightforward a relationship as theoretical models tend to assume (Houston et al. 2005; Klug
101 et al. 2012). Moreover, in many species, offspring desertion is conducted largely by one of the two sexes

102 (Roulin 2002; Morton et al. 2010; Thomson et al. 2014), although males and females can be programmed to
103 carry out distinct parenting duties (Pierotti 1981; Riechert and Becker 2017). Sex-specific costs and benefits of
104 providing parental care may lead to different responses to mating opportunity in males and females (Lehtonen et
105 al. 2011; Hopwood et al. 2015; Schacht et al. 2017). Therefore, further studies are important to understand the
106 potential roles of mating opportunities in shaping one of the fundamental parenting decision whether to care for
107 the offspring or abandon them using species that exhibit flexible care types by both males and females.

108 Here we investigate mating opportunities and parental care in the Chinese penduline tits *Remiz consobrinus*, a
109 small passerine bird (body mass approximately 10 g) distributed in East Asia (Gluschenko et al. 2014; Zheng et
110 al. 2018). This species exhibits unusually variable parental care since male-only care, female-only care,
111 biparental care and biparental brood desertion may all occur in the same population (Zheng et al. 2018). The
112 breeding season of Chinese penduline tits lasts from May to August. Single male penduline tits attract females
113 by building a nest and singing melodic songs; once the pair produces a clutch, one (or both) parents may
114 abandon the nest. At uniparental nests, the full workload of incubation and chick feeding are carried out only by
115 the deserted parent. After clutch desertion, both males and females may find another partner and reneest during a
116 single breeding season (Zheng et al. 2018). This breeding system is reminiscent of the one exhibited by Eurasian
117 penduline tits *Remiz pendulinus* (Persson & Öhrström 1989; Pogány et al. 2012; van Dijk et al. 2012), although
118 the latter species exhibits strictly uniparental care and biparental brood desertion that renders the nest to fail.
119 The behavioral flexibility of Chinese penduline tits provides excellent opportunities to investigate parental
120 decisions of males and females.

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

126

127 **Methods**

128 **Study area**

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

135

136 **Nest observations, nest initiation and male pairing**

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

140 We searched for new nests every day either by seeking for new nests and tracking flight routes of single males.

141 The 'nest initiation day' was estimated from the nest building stage when the nest was found (stage A–C, see
142 Zheng et al. 2018), since the number of days spent on different nest building stages (A, B or C) were relatively
143 similar for all males (for details on the stages of nest building and the method of calculating the start day of nest
144 building see Zheng et al. 2018). On nest initiation day, males start displaying and singing to attract females (Hoi
145 et al. 1996; Pogány et al. 2012; Zheng et al. 2018). We observed each nest with binoculars from a distance of 15
146 m every other day for 20 min following Smith (1995) and Bleeker et al. (2005). The 'male pairing day' was
147 defined as the day the male became paired with a female, i.e., the first day when a male was observed copulating
148 near the nest with a female and/or when a female contributed to nest building (Szentirmai et al. 2007). The
149 'male giving up day' was defined as the day when the unpaired male abandoned his nest. During nest checks,
150 the nest stage, presence of female, male and female parental behavior (clutch desertion or care), and breeding
151 stage (egg laying, incubation, hatching) were recorded. 288 nests were found in total during the three breeding
152 seasons. For 249 nests (86.5% of all nests), the nest initiation day was known.

153 For each nest, we recorded whether the male was paired or unpaired as the pairing outcome for males. For the
154 males who became paired, we defined the 'time spent on finding a mate' as the number of days between the
155 'nest initiation date' and the 'pairing date.' For males who remained unpaired, 'time spent on finding a mate'
156 was defined as the number of days between the 'nest initiation date' and the 'giving up date.' For each clutch or
157 brood we recorded clutch size, number of hatchlings and number of fledglings.

158

159 **Patterns of care**

160 Clutch desertion usually takes place within three days after clutch completion (0.8 ± 1.3 days, Zheng et al.
161 2018). Once the fifth egg was laid (clutch size ranged from 5 to 8 eggs), we checked each clutch daily to assess
162 whether it was deserted. If one (or both) parent(s) did not show up during the daily nest checks, we filmed the
163 nest with a SONY HDR-XR160E video camera for 2 h to check whether one (or both) parents deserted the nest
164 (Szentirmai et al. 2005; Zheng et al. 2018). The day of clutch desertion was defined as the day the deserting
165 parent(s) had not been recorded at the nest based on the video recordings.

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

173

174 **Mating opportunities**

175 Male penduline tits exhibit conspicuous mate attraction displays, i.e., building a nest and singing around the nest
176 (Szentirmai et al. 2005, Zhang et al. 2018). We used three proxies of mating opportunities for males: (1) ‘pairing
177 probability’ refers to the probability of a male successfully obtaining a female at a specific day of the breeding
178 season. This variable indicates how likely a male pairs up anytime during the breeding season (Samplonius and
179 Both 2017); (2) ‘male mating time’ refers to the time a male spends on finding a mate, i.e., the number of days
180 between nest initiation and becoming paired or giving up attracting a mate. Long mating time would reflect low
181 number of unmated females relative to the number of sexually active males (Székely et al. 1999; Parra et al
182 2014). (3) We also calculated the number of single males for each day in the breeding season (we term this
183 variable ‘number of single males’), and use this variable to indicate male mating opportunity (and also, female
184 mating opportunity, see below). Thus high number of single males would reflect many competitors and thus
185 indicate low mating opportunity for males assuming that the number of available females remains invariable.

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

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

195 **Indicators of male quality**

196 Nest size and male's mask size are sexually selected traits in Eurasian penduline tits (Szentirmai et al. 2005;
197 Kingma et al. 2008), since males that build large nests and have wide masks are preferred by females (Pogány &
198 Székely 2007). Therefore, to estimate male quality in Chinese penduline tits, we (1) measured nest weight using
199 an electric scale ($\pm 0.01\text{g}$) when we collected the nests when the season completed, then assessed nest volume by
200 filling the nest with sand and measured the sand volume using 1000-ml measuring cylinder (Szentirmai et al.
201 2005). Nest volumes were only estimated in 2016. (2) Male mask size was estimated using digital photos with
202 Photoshop CS5 using background grids (0.01 cm^2) for calibration. Mask size was calculated as the average area
203 of the left and the right masks ($\pm 0.01\text{ cm}^2$, Kingma et al. 2008). (3) We also measured the body mass, tarsus
204 length, wing length and tail length with calliper to estimate body sizes of adult males.

205 **Statistical analyses**

206 Data analyses were conducted using R 3.6.3 (R Core Team 2020), and the null hypothesis was rejected at $P <$
207 0.05. If applicable, the normality of data was tested with the Shapiro test.

208 *i) Seasonal variation in nest initiation*

209 To investigate the seasonal changes in nest initiation and clutch desertion, we divided the breeding season into
210 10-day periods for each year separately. For each 10-day period, we calculated the average number of nests
211 initiated and the number of deserted clutches. Since neither the number of initiated nests nor the number of
212 deserted ones was different between years (nest initiation: $\chi^2 = 0.03$, $P = 0.87$; clutch desertion: $\chi^2 = 0.16$, $P =$
213 0.68), we used the average values of the three years for each 10 day period.

214 *ii) Parental care patterns over the season*

215 To explore the patterns of care over the breeding season, we focused on males and females separately, and split
216 the nests into two groups each. For males, we split the nests into (1) male deserting refers to clutches where
217 either the female cares alone or both parents deserted; (2) male caring refers to clutches where either the male
218 cares alone or both parents care. Consistently, for females the nests were split into (1) female deserting: the
219 clutches either with male-only care or with biparental desertion; (2) female caring: the clutches with female-only
220 care or biparental care.

221 For each sex, we constructed separate binominal Generalized Linear Models (GLM) to analyze male and female
222 parental behavior over the breeding season, with nest initiation day and year as fixed factors in the models. We
223 took sex, nest initiation day and their interaction as fixed effects and nestID as a random effect in the binominal
224 General Linear Mixed Model (GLMM) of overall parental behavior (desert vs care).

225 *iii) Mating opportunities*

226 Male pairing probability was analyzed using binominal GLM, and the male mating time was modeled with
227 quasi-poisson GLM. In these two models, nest initiation day and year were fixed effects. Female mating
228 opportunities were modeled with the number of single males on a specific day. Year, day and (day)² and the
229 interactions between year and day and year and day² were considered as fixed factors.

230 *iv) Parental behavior in relation to mating opportunities*

231 We built models to analyze the association between parental care and mating opportunities: (1) parental care in
232 males and females was analyzed separately using binominal GLMs. The number of male competitors (same as
233 the number of single males) and year were taken as fixed effects; (2) the overall parenting decision was modeled
234 with number of single males, sex and their interaction as fixed effects and nest ID as a random effect.

235 We also investigated parental behavior and mating opportunities at the individual level. Since behavior,
236 attractiveness or overall quality tend to be consistent for a given individual (Westneat et al. 2011; Pagani-Núñez
237 et al. 2014), to control for multiple records of an individual we repeated the analyses of mating opportunities
238 and their potential associations with parental care using a subset of individually marked males. In the latter
239 models, we added male ID as a random factor to correct for pseudoreplication. The individual-based analyses
240 produced consistent results with the population level-ones (S1). We calculated the mating time of the banded
241 males in their penultimate and final breeding attempts, and analyse the time differences unpaired t-test.

242 The quality of sexually selected traits such as nest size and male mask size may change over the breeding season.

243 To investigate these potential associations, we created two GLMs to analyse the change of nest quality over

244 season with nest weight and nest volume separately as response variables, and ‘nest initiation day’ as
245 explanatory variable. To control for seasonal variation in nest size and male mask size, male mating time and
246 nest initiation day were analysed using two GLMMs with male mask size as fixed factor, and the other two
247 GLMMs with male body size (body mass, tarsus length, wing length and tail length) as fixed factors. Male ID
248 was taken as random factors in these four GLMMs.

249 *v) Reproductive success and parental care strategies*

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

254

255 **Results**

256 *Seasonal variation in parental care*

257 New nests were initiated between 1 May (day 1) and 11 July (day 63): there were two peaks of nest initiations:
258 the first was in mid-May (between days 10 and 20), and the second was in early June (days 30-40, Fig. 1, Table
259 1). Parental care by males and females showed different seasonal patterns: males deserted nests early in the
260 season, whereas they cared for nests produced late in the season (Fig. 2a, Table 2, $z = 4.56$, $P < 0.001$), whereas
261 female behavior did not change over the season (Fig. 2b, Table 2, $z = -1.07$, $P = 0.28$). A significant interaction
262 term between nest initiation and sex of the parent suggests that males and females had different caring behaviors
263 during the breeding season (Table 2, $z = -4.78$, $P < 0.001$).

264

265 *Seasonal variation in mating opportunities*

266 For males, mating opportunities decreased over the breeding season, as indicated by the low probability of
267 pairing later in the season (Fig. 3a, $n = 178$; $z = -7.45$, $P < 0.001$). Consistently, males that were successful in
268 finding a mate took longer to pair up later in the season than in the early season (Fig. 3b, $n = 109$, $t = 10.16$, $P <$
269 0.001): it took 6.46 ± 4.23 days to find a mate before day 30, whereas male mating time increased to $25.74 \pm$
270 10.19 days after day 30. Mating opportunities followed a different pattern for females, since the number of
271 single males increased until day 60 and declined afterwards (Fig. 3c, Table 3, $n = 144$, $t = 16.27$, $P < 0.001$).

272 The behavior of individually banded penduline tits was consistent with the behavior at the population level (S1).
273 Of the 24 males ringed at their first nest, all deserted their first nest in the breeding season, and 16 of them
274 started a second breeding attempt; six out of the 16 males paired up, whereas 10 remained unpaired. For the six
275 successful males, it took more time to find a new mate in their second breeding attempt (24.80 ± 7.79 days) than
276 in their first attempt (7.62 ± 5.45 days, $n = 13$, $t = 11.67$, $P < 0.001$).
277 Neither volume nor weight of nests was related to nest initiation day ($n = 14$ nests, S3). Mask size of males was
278 unrelated to male mating time and nest initiation day ($\Pr(>|z|) = 0.49$ and 0.33 , respectively, S4), and we found
279 no relationship between male body size, nest initiation day and mating time (S5).

280

281 *Does mating opportunity predict parental care?*

282 The number of single males present in the population predicted male care decisions since males were more
283 inclined to care for their clutch when there were many competitors in the population. In contrast, they were
284 more inclined to desert their clutch and remate when few competitors were nearby (Fig. 4a, $n = 96$, $z = 4.62$, $P <$
285 0.001). The number of single males was unrelated to female caring decisions (Fig. 4b, Table 4, $z = 0.57$, $P =$
286 0.57). The different responses by males and females to the number of single males were indicated by a
287 significant interaction between the number of males in the population and the sex of the parent (Table 4, $z =$
288 -4.26 , $P < 0.001$).

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

293

294 *Fitness implications of caring and desertion*

295 Clutch size was not different between caring and deserting parents for either males (desert: 6.82 ± 0.81 eggs, $n =$
296 72 ; care: 6.22 ± 0.71 eggs, $n = 9$, $z = -0.18$, $P = 0.86$) or females (desert: 6.38 ± 0.96 eggs, $n = 13$; care: $6.84 \pm$
297 0.77 eggs, $n = 68$, $z = 0.40$, $P = 0.62$). Furthermore, neither hatching success nor fledgling success was different
298 between parental strategies, suggesting that the fitness rewards for caring and deserting are similar (Table 5).

299

300 **Discussion**

301 Mating opportunity is emerging as a major predictor of breeding system variation, and our study contributed to
302 this research field by showing sex difference in mating opportunities in a songbird species that exhibit flexible
303 mating systems and parenting strategies. First, we show that males desert their clutches early in the breeding
304 season when mating opportunities are high, whereas they care for the clutches late in the season when mating
305 opportunities are low. Second, female caring/deserting behavior does not change over the breeding season
306 although female mating opportunities also varied during the breeding season. These findings suggest that mating
307 opportunities have a different influence on parental care decisions of males versus female Chinese penduline
308 tits.

309

310 *Seasonal variation in male parental care and mating opportunity*

311 Males uniformly desert clutches in the early season consistently with the proposition that males attempt to seize
312 the breeding opportunities to increase their reproductive fitness (Maynard Smith 1977, Székely and Lessells
313 1993). We found lots of male Chinese penduline tits arrived at the breeding ground and initiated their first nest,
314 which raised the first peak of nest initiation around day 20. We cannot determine whether all males who
315 initiated a new nest in the second peak (30-40) had already deserted a clutch or were newcomers to the
316 population. However, we observed that most (66.7%) of the banded males started a new nest a few days before
317 or right after the desertion day: they started the first nest from day 1-20 (day 10.3 ± 9.1) and the second nest
318 from day 30-50 (day 39.8 ± 9.6), which were correspondent with the nest initiation peaks. These observations
319 indicate that deserting males rejoined the mating pool and by pairing up they reduced the decline of male mating
320 opportunities as the season progressed. Male Chinese penduline tits still put their stake on clutch desertion in the
321 early season, although the overall remating success was only 37.5% (6 out of 16 banded males). This is contrary
322 to species, such as rock sparrow *Petronia petronia* and barn owl *Tyto alba*, where the female deserters usually
323 have high remating success after brood desertion (Pilastro 2001; Roulin 2002). However, our finding is
324 consistent with Kentish plovers (*Charadrius alexandrinus*), where males desert in the early season, even when
325 the ASR is female biased (Székely and Lessells 1993; Székely et al. 1996). Further, the same reproductive
326 rewards of a single nest with different parental care indicate that one parent is able to efficiently overtake the
327 workload of chick feeding (fledging success: 80.6%, Zheng et al. 2018). Although the mating opportunity is
328 declining in early season, a male can still desert the clutch and pursue for an additional reproductive fitness by
329 re-mating with a new female and produce additional offspring.

330 We found that male Chinese penduline tits switched their parenting role from a deserter to a care giver at their
331 last nest, when more single males were advertising in the population. We suggest two explanations for this
332 phenomenon. First, male penduline tits may detect the declined mating opportunity by experiencing the
333 increased male-male competition and extended time of acquiring a mate. The large effort of mate acquisition
334 indicates that males will not get more reproductive benefits from a sequential clutch desertion than from feeding
335 and protecting the current brood under low remating opportunities (Kokko and Jennions 2008; Béziers and
336 Roulin 2015). Empirical studies have shown that males increase their parental investments when the sex ratio is
337 male-biased (Liker et al. 2013; Rosa et al. 2017), and the rate of brood desertion decreases when mating
338 opportunity is less biased (Pilastro 2001; Eberhart-Phillips et al. 2018). This pattern also have been proven in
339 insects and fish, where males extend the duration of parental care when they are experiencing intensive
340 competition (Hopwood et al. 2015; Grüter 2005). Second, in a migratory species with a short breeding season,
341 such as rock sparrow *Petronia petronia*, individual parental care decisions may be restricted by the amount of
342 time remaining in the season (Griggio 2015). In this study, we found the number of males in the mating pool
343 was found declining after day 60. Excepted for a few males successfully paired up and left the mating pool,
344 79.2% of the unpaired nests (61 of 77 nests) were given up by the single males after day 60. The late pairing day
345 in the last breeding attempt indicates that males likely do not have enough time to finish a new breeding round
346 before migration. This may also induce male care provisioning in the late season.

347

348 *Female parental care and mating opportunities*

349 Female Chinese penduline tits did not show any seasonal changes in parental care. We suggest that mating
350 opportunity might not be a determinant factor for female parenting decisions. This result is consistent with that
351 found in Eurasian penduline tits that males followed similar pattern to the behavior of male Chinese penduline
352 tits (ie, desert early clutches and care for late clutches), whereas females behavior was not seasonally varied;
353 rather, some females Eurasian penduline tits consistently deserted their clutches both early and late in the season
354 whereas other females consistently cared for their clutches both early and late in the season (Pogány et al. 2008).
355 A lack of variation in female parenting strategy was also observed in Nicaraguan cichlid fish (*Amphilophus spp.*
356 and *Amatitlania spp.*), where the mating opportunities increased in the late season (Lehtonen et al. 2011), and in
357 blue-headed vireos (*Vireo solitarius*), where female mating opportunities varied over the breeding seasons
358 (Morton et al. 2010). However, the frequency of female desertion increased with male availability in rock

359 sparrow (Pilastro 2001) and black coucal (*Centropus grillii*, Goymann 2015). These discordant results imply
360 that there is no general pattern of the influence of mating opportunities on female parental care strategy. Other
361 physiological or ecological factors, such as body condition and food abundance, should also be taken into
362 consideration (Eldegard and Sonerud 2009; Bleeker et al. 2005).

363

364 *Why parental care patterns vary within a species?*

365 Variation in breeding systems within species is common across the animal kingdom (Vagi et al. 2018, Jaeggi et
366 al. 2020), although research has conventionally focused on species that exhibit a “typical” mating system or
367 parenting pattern. Understanding the existence of variable parenting patterns is challenging, and studies focusing
368 on species with variable care patterns are especially important in these endeavor (McGraw et al. 2010, Balshine
369 2012). Specifically, variable care patterns have been reported from several bird species, fish and amphibians
370 (Székely 1999; Pilastro et al. 2001; Roulin 2002; Pogány et al. 2008; Lehtonen et al. 2011; Schulte and Lötters
371 2013, Pike et al. 2016). First, sex-different mating opportunities is a possible predictor for these intra-specific
372 variations (van Dijk et al. 2012): as we show in Chinese penduline tits, mating opportunities may have temporal
373 dynamics favoring desertion in one part of the breeding season but not in the other part. Second, the benefits
374 from caring may differ between males and females, if one parent provides better care than the other
375 (Clutton-Brock 1991, Szentirmai et al. 2007). For instance, the presence of mammary glands and thus the ability
376 of females to feed the young in mammals have been thought to generate a strong difference in offspring survival
377 raised by male-only versus female-only families, putting a strong selective pressure on females to provide care
378 (Clutton-Brock 1991, Royle et al. 2012). In Chinese penduline tits the similar reproductive success of male-only
379 and female-only broods suggest that males and females can provide qualitatively similar care (Zheng et al. 2018,
380 this study), consistently with findings in Eurasian penduline tits (Pogány et al. 2012). Third, since parenting
381 takes time and energy, and the parents often develop dedicated organs and structures for caring their young
382 (such as nests, brood pouches), the mortality costs of these behaviors and/or specific adaptations may be
383 different for males and females during and/or after breeding season (Liker and Székely 2005, Santos et al. 2012,
384 Royle et al. 2016). For instance, male-biased predation decrease occurrence of polyandry in frog (Lodé et al.
385 2004), sexual-specific mortality increased during predation peak while protecting offspring in rodent and
386 incubating in Mallards (Sommer 1999, Arnold et al. 2012), and the sex with lower mortality rate in birds has
387 lower recruitment rates, future fecundity or less likelihood of offspring desertion (Jeschke and Kokko 2008,

388 Descamps et al. 2009, Fowler and Williams 2017). However, we can not evaluate the different mortality costs
389 for males and females in Chinese penduline tits, since less than 5% of adults returned to breed in our study area
390 (Zheng et al. unpubl data). Whilst the jury is still out whether sex different mating opportunities, parental
391 abilities and or mortality costs drive parenting evolution in most taxa, we argue that studies need to consider
392 these processes.

393

394 Mating opportunities, however, may not be uniform for all males or all females in a population. A male
395 penduline tits who build large nest and has large mask size were claimed with better sexual quality to quickly
396 paired up with a female (Szentirmai et al. 2005; Kingma et al. 2008). High-quality males have been proved
397 spend less time acquiring a mate in some species (Houde 1987; Kingma et al. 2008) and are expected to feed
398 more if they are less attractive (DeMory et al. 2010; Horváthová et al. 2012). Therefore, the male care pattern
399 we observed could also be explained as attractive males desert early nests and less attractive ones provide care
400 to late nests. However, our study showed that male attractiveness cannot explain this pattern in Chinese
401 penduline tits because (1) the same banded males were observed shifting their parental care from deserting to
402 caring over different breeding attempts within one season. (2) Nest and male mask size were indicator of sexual
403 selection in Eurasian penduline tits (Kingma et al. 2008; Szentirmai et al. 2005). However, we found the nest
404 quality (volume and weight) has not decline over season and mask size has no difference between males. (3)
405 Males body parameters and eye mask size do not related to the time a male spent on mate attraction. These
406 evidences indicate that the males who paired up in the late season was not per se with low quality (S3).

407 Extra-paired paternity (EPP) was suggested associated with the parental care pattern in Remizidae (Ball et al.
408 2017) and the amount of parental investment in animals (Kvarnemo 2018; Gao et al. 2020; Schrader et al. 2020).
409 However, according to our microsatellite analyses, EPP is relatively low (around 6%, 36 nests, 198 nestlings) in
410 Chinese penduline tits (Wang H et al. unpublished data), which is similar as the Cape penduline tits
411 *Anthoscopus minutus* (5.4%, Ball et al. 2017) that obligate biparental care; There is no seasonal effect on EPP
412 (logistic regression: start date -- $z = -0.28$, $p = 0.778$; year -- $z = -0.90$, $p = 0.37$), indicating males do not leave
413 earlier in the season to obtain EPP. Therefore, we do not suppose male Chinese penduline tits uniformly desert
414 the clutch in order to pursuit for a extra-paired copulation in the early season.

415

416 **Conclusion**

417 To understand parental care evolution, it is important to investigate species that exhibit multiple care patterns.
418 Here we investigated such a species, the Chinese penduline tits that exhibit all four major types of care within a
419 single population. We show that male parental behavior (care/desert) was associated with mating opportunities
420 whereas female behavior was unrelated to mating opportunities. We also show that the fitness rewards from
421 male-only and female-only care are similar. Ultimately, our study provides more support for a sex different
422 mating opportunities driving variable care patterns rather than for sex difference in parental abilities rearing the
423 young. We call for further investigations of species with variable breeding systems including relatives of
424 Chinese penduline tits *Remiz spp.* that appear to exhibit different patterns in caring and mating (Bot et al. 2011).

References

- Arnold T, Roche E, Devries J, Howerter D (2012) Costs of reproduction in breeding female mallards: predation risk during incubation drives annual mortality. *Avian Conserv Ecol* 1:7(1)
- Barta Z, Houston AI, McNamara JM, Székely T (2002) Sexual conflict about parental care: the role of reserves. *Am Nat* 159:687-705
- Balshine, S 2012. Patterns of parental care in vertebrates. In: Royle NJ, Smiseth PT, M. Kölliker (eds) *The evolution of parental care*. Oxford University Press, Oxford, pp 62-88
- Bleeker M, Kingma SA, Szentirmai I, Székely T, Komdeur J (2005) Body condition and clutch desertion in penduline tit *Remiz pendulinus*. *Behavior* 142:1465-1478
- Béziers Paul, Roulin Alexandre (2015) Double brooding and offspring desertion in the barn owl (*Tyto alba*). *J Avian Biol* 46:001-010
- 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 M C, 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 Roy Soc 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, Buttlar 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 Letters* 5:278-81

- Eberhart-Phillips LJ, Küpper C, Carmona-Isunza MC, Vincze O, Zefania S, Cruz-López M, Burke T (2018) Demographic causes of adult sex ratio variation and their consequences for parental cooperation. *Nature Comm* 9:1-8
- Eldegard K, Sonerud 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. *Phil Trans R Soc Lond 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. *Achievements in the Life Sciences* 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, Pilastro A (2007) Sexual conflict over parental care in a species with female and male brood desertion. *Anim Behav* 74:779-785
- Griggio M (2015) An experimental test on time constraint and sexual conflict over parental care. *Ecol Evol* 5:3622-3627
- 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 P E, 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
- 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
- Horváthová T, Nakagawa S, Uller T (2012) Strategic female reproductive investment in response to male attractiveness in birds. *Proc Roy Soc B* 279:163-170
- 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 Roy 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

- Kokko H, Jennions MD (2008) Parental investment, sexual selection and sex ratios. *J Evolution Biol* 21:919-948
- 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
- Kvarnemo C (2018) Why do some animals mate with one partner rather than many? A review of causes and consequences of monogamy. *Biol Rev* 93:1795-812
- 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* 59:890-7
- Liker A, Freckleton RP, Székely T (2013). The evolution of sex roles in birds is related to adult sex ratio. *Nature Comm* 4:67-88.
- 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 Roy Soc B* 271:S399-401.
- 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 Wildlife 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 Roy Soc 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 Scandinavica* 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/>

- Remeš V, Freckleton RP, Tökölyi J, Liker A, Székely T (2015) The evolution of parental cooperation in birds. *PNAS* 112:13603-13608
- Reynolds JD, Goodwin NB, Freckleton RP (2002) Evolutionary transitions in parental care and live-bearing in vertebrates. *Phil Trans Roy Soc* 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 behaviours? *Curr Opin Behav Sci* 12:30-6
- 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 P M (2017) Adult sex ratios and reproductive strategies: a critical re-examination of sex differences in human and animal societies. *Philos T 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* 27:711-723
- Shuster, S.M, 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, VJr and Ketterson ED (eds), *Current Ornithology*, Chapter 6: 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: *Vertebrate mating systems*, Apollonio M, Festa-Bianchet M, Mainardi D (eds), 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
- Trivers R (1972) Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man*. Campbell B (ed) Aldine Press, Chicago, pp 139–179
- Vági B, Végvári Z, Liker A, Freckleton RP, Székely T (2019) Parental care and the evolution of terrestriality in frogs. *Proc Roy 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

van Dijk R, 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 Roy Soc B* 279:1927

Végvári 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* 3:1-10

425 **Figure legends**

426 **Fig. 1** Number of Chinese penduline tit nests initiated over the breeding season (mean \pm S.D. for each 10 day
427 period). Day 1 = 1 May. Data were combined for 2016, 2017 and 2019.

428 **Fig. 2** Caring and deserting behavior in Chinese penduline tits in relation to the date of nest initiation. Each dot
429 refers to a nest; darker dots refer to overlapping data. For statistics, see Table 2.

430 **Fig. 3** Pair formation in Chinese penduline tits. (a) Male's probability of finding a mate: each dot refers to a nest
431 (n = 178 nests). (b) Mating time (days, mean \pm SD) of males over the breeding season (n = 109 nests). (c)
432 Number of single males over the breeding season (n = 144 nests). For statistics, see Table 3.

433 **Fig. 4** Mean number of single males in the mating pool in relation to caring and deserting decisions of (a) male
434 and (b) female Chinese penduline tits. Thick lines indicate the medians, whereas the bottom and top of boxes are
435 the 25 quartiles and 75 quartiles, respectively. *refers to significant difference between groups. For statistics, see
436 Table 4.

437

Fig. 1

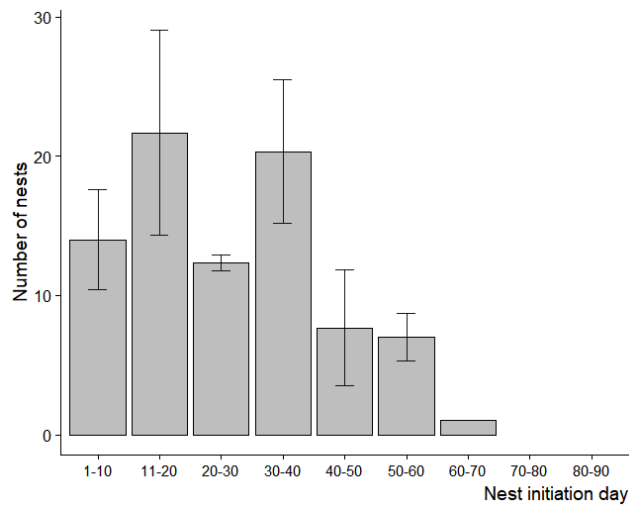
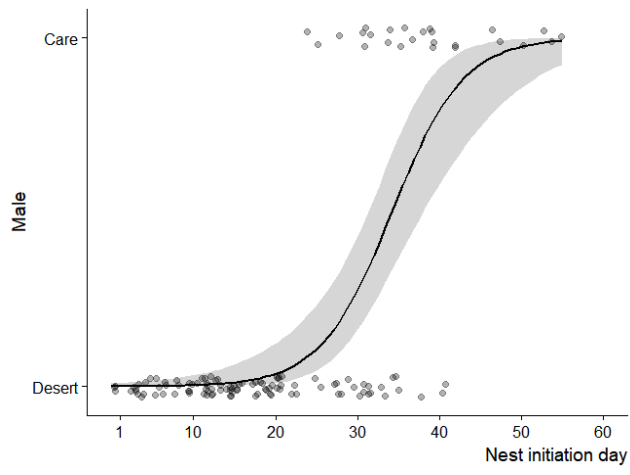


Fig. 2

(a)



(b)

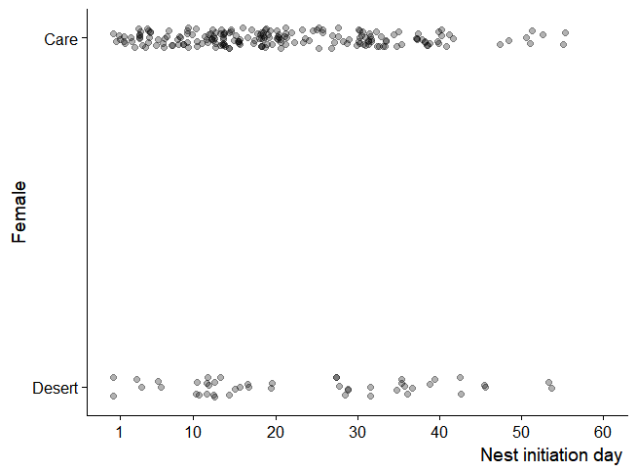
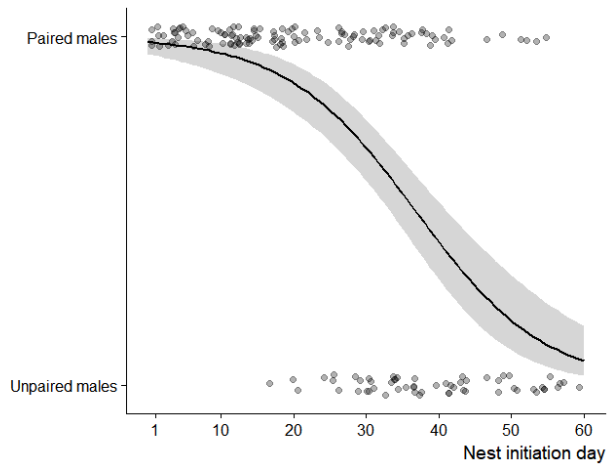
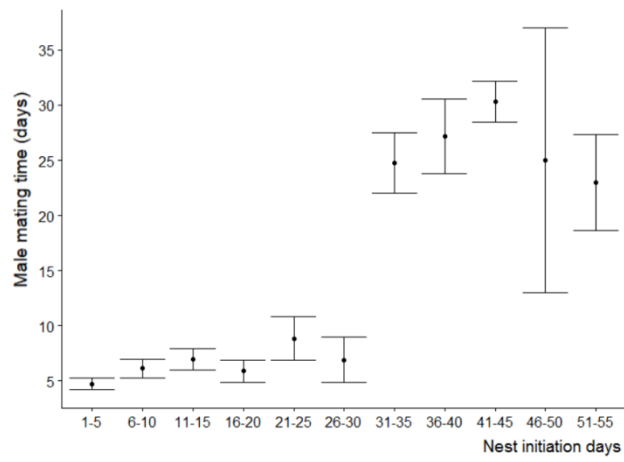


Fig. 3

(a)



(b)



(c)

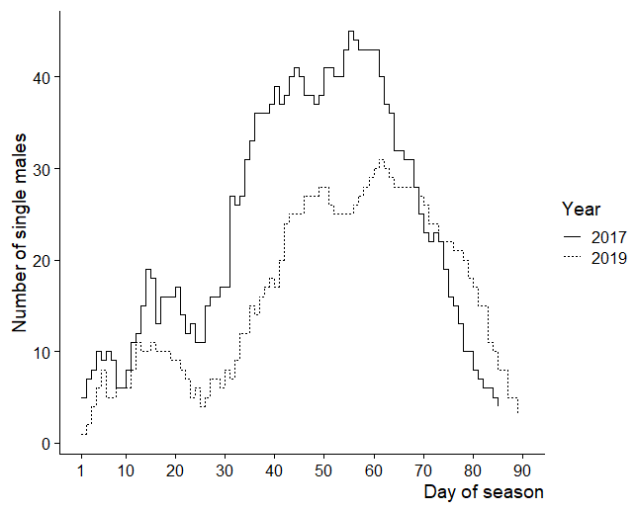
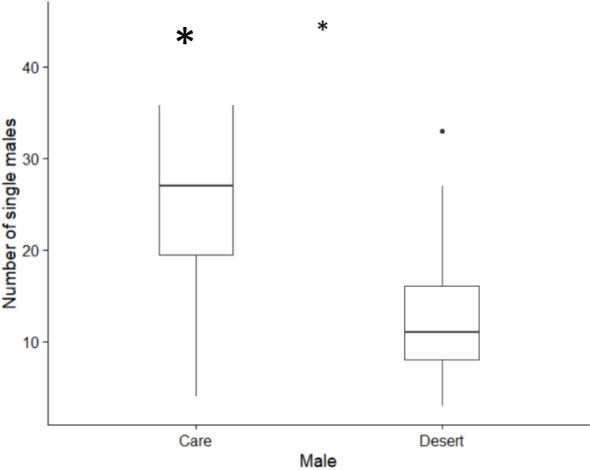


Fig. 4

(a)



(b)

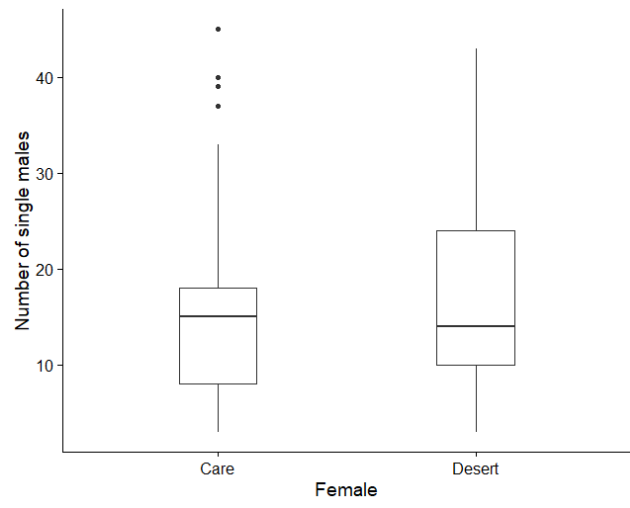


Table 1 Dates of egg laying, clutch size and parental care behavior in Chinese penduline tits. Day 1 = 1 May.

Year	First egg laying day	Last egg laying day	Average egg laying day	Clutch size (mean \pm S.D.)	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)

Table 2 Seasonal variation in parental care of Chinese penduline tits. Generalized linear models (GLM) with binomial error for male behavior and female behavior (n = 109 nests), or Generalized linear mixed model with binomial error for parental behavior using nestID as a random factor (n = 218 nests). The response variable in all three models is Care or Desert. Nest initiation date is given as number of days since 1 May (see Fig. 1). R²: McFadden pseudo-R².

Response variable	Explanatory variables	Estimate	SE	Z-value	Pr(> z)	R ²
Male behavior	Intercept	484.52	601.33	0.81	0.42	0.60
	Nest initiation	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	-0.02	0.02	-1.07	0.28	
	Year	0.11	0.21	0.54	0.59	
Parental behavior	Intercept	-1.87	0.45	-4.13	<0.001	0.75
	Nest initiation	0.02	0.02	0.99	0.32	
	Sex	9.74	1.65	5.90	<0.001	
	Nest initiation × Sex	-0.25	0.05	-4.78	<0.001	

Table 3 Male and female mating opportunities over the breeding season in Chinese penduline tits. Male pairing probability was analyzed using GLM with binomial error (n = 178 nests), whereas the time males spent finding a mate and the number of available 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 value	Pr(> z) or Pr(> t)	R ²
Male	Male pairing probability	Intercept	-889.82	332.66	-2.71	0.01	0.35
		Nest initiation	-0.12	0.02	-7.45	<0.001	
		Year	0.45	0.16	2.71	0.01	
	Male mating time	Intercept	106.32	107.87	0.99	0.33	0.38
		Nest initiation	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) ²	-0.001	6.6e-05	-16.20	<0.001	
		Nest initiation	0.10	0.006	16.72	<0.001	
		Year	0.57	0.22	-2.53	0.01	
		(Nest initiation) ² × Year	2.6e-04	1.0e-04	2.52	0.01	
		Nest initiation × Year	0.01	0.01	-1.10	0.27	

Table 4 Parental care in relation to mating opportunities in male and female Chinese penduline tits. Male parental care and female parental care (Care or Desert) was separately analyzed using GLM with binomial error (n = 96 nests), and the overall parenting decision (Care or Desert) was analyzed using GLM with binomial error using nestID as a random factor (n = 192 nests). Nest initiation refers to the date when the nest was initiated (see Fig. 4). R²: McFadden pseudo-R².

Response variable	Explanatory variables	Estimate	SE	Z-value	Pr(> z)	R ²
Male parental care	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 care	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	
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	

1 **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
2 models, respectively. Generalized linear mixed model with Poisson error distribution using nestID as a random factor (n = 81 nests); male and female decision is Care or
3 Desert. Nest initiation refers to days after 1 May. R2: McFadden pseudo-R2.

Response variable	Explanatory variables	Estimate	SE	Z-value	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	-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	-0.01	0.01	-1.41	0.16	
Fledgling number	Year	-0.05	0.06	-0.86	0.39	0.35
	Intercept	-49.50	159.28	-0.31	0.76	
	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	0.01	0.01	1.85	0.06	
	Year	0.02	0.08	0.31	0.76	

4

5 **Supplementary materials**

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

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6

7 **S1** Comparing the behavior of individually banded male penduline tits to population behavior. Models are the same as those analyzed in population scales with individual ID

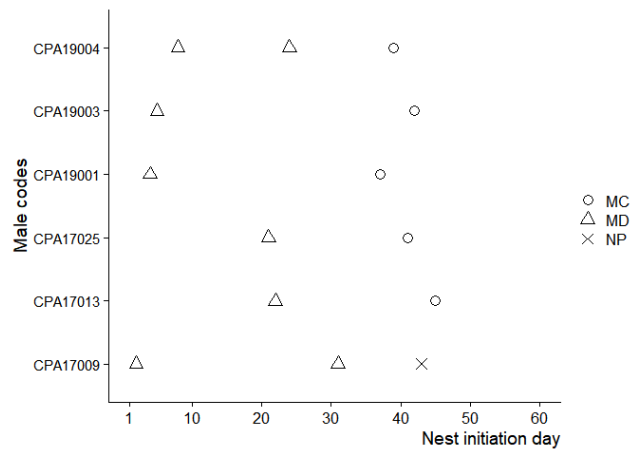
8 included as a random factor. All the analyses with banded individuals are consistent with the results obtained at the population scale.

model	Response variable	Model	Explanatory variables	Estimate	SE	Z-value	Pr(> z)	
Mating opportunities	Pairing probability	GLM	Intercept	103.42	0.002	42784.9	<0.001	
		Binomial (logistic)	Nest initiation day	-2.33	0.003	-729.7	<0.001	
	Time male spent on finding a mate	GLM	Intercept	1.20	0.17	7.07	<0.001	
		poisson	Nest initiation day	0.04	0.005	7.61	<0.001	
	Number of single males		GLM	Intercept	1.62	0.20	8.14	<0.001
				(Nest initiation day) ²	-0.0004	0.0004	-1.07	0.27
			poisson	Nest initiation day	0.06	0.02	2.90	0.004

Parental care & mating opportunities	Male parental care	GLMM	Intercept	-4.67	1.63	-2.87	0.004
		Binomial (logistic)	Number of available males	0.23	0.10	2.34	0.02
	Female parental care	GLMM	Intercept	2.21	1.11	1.98	0.05
		Binomial (logistic)	Number of available males	-0.08	0.05	-1.48	0.13

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- 10 **S2** Nest initiation days of 6 banded males who were successfully remated within a season. Male parental care strategies and pairing outcomes in each breeding attempt are
 11 shown with different shaped symbols. All males deserted their first clutch, and 5 of them provided care to their final clutch. Male care (MC): male provided care to the
 12 current clutch; Male desert (MD): male deserted the current clutch; Not paired (NP): male did not succeed in pairing up with a female at the nest.



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15 S3. Seasonal variation in nest size in Chinese penduline tits. Nest weight and nest volume were analyzed using GLMs (n = 14 nests).

Response variable	Explanatory variables	Estimate	SE	t-value	Pr(> z)	R ²
Nest weight	Intercept	47.40	7.14	6.64	0.00	
	Nest initiation day	-0.49	0.43	-1.13	0.29	0.42
Nest volume	Intercept	226.68	23.21	9.77	0.00	
	Nest initiation day	1.35	1.42	0.95	0.36	0.16

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22 S4. Mask size in relation to male mating time and nest initiation date (n = 16 nests). Male mating time and Nest initiation day were analyzed using GLMMs.

Response variable	Explanatory variables	Estimate	SE	Z-value	Pr(> z)	R ²
Male mating time	Intercept	37.16	24.94	1.06	0.31	
	Mask size	-25.77	36.10	-0.71	0.49	0.04
Nest initiation day	Intercept	53.09	34.75	1.53	0.15	
	Mask size	-36.07	35.91	-1.00	0.33	0.16

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33 S5 Male body size in relation to mating time and nest initiation day (n = 42 nests). Male mating time and Nest initiation day were analyzed using GLMMs.

Response variable	Explanatory variables	Estimate	SE	t-value	Pr(> z)	R ² ³⁴
Male mating time	Intercept	112.50	139.44	0.81	0.43	0.16
	Body mass	6.55	5.23	1.25	0.22	
	Tarsus length	-11.87	7.02	-1.69	0.11	
	Wing length	-1.00	1.93	-0.52	0.61	
	Tail length	1.22	1.25	0.98	0.34	
	Year	8.75	6.29	1.39	0.18	
Nest initiation day	Intercept	363.77	175.76	2.07	0.05	0.21
	Body mass	5.24	6.60	0.79	0.44	
	Tarsus length	-8.60	8.85	-0.97	0.34	
	Wing length	-4.61	2.43	-1.90	0.07	
	Tail length	-0.24	1.57	-0.15	0.88	
	Year	10.67	7.93	1.35	0.19	