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

Jia Zheng[a,b], Jan Komdeur[a], Tamás Székely[c], Maaike A. Versteegh[a], Donglai Li[d], Hui Wang[b], Zhengwang Zhang[b]

[a] Behavioral and Physiological Ecology, Groningen Institute for Evolutionary Life Sciences, University of Groningen, 9712 CP Groningen, The Netherland

[b] Ministry of Education Key Laboratory for Biodiversity Sciences and Ecological Engineering, College of Life Sciences, Beijing Normal University, No.19 Xinjiekouwai Street, Beijing 100875, China

[c] Milner Centre for Evolution, Department of Biology and Biochemistry, University of Bath, Claverton Down, Bath BA2 7AY, UK

[d] College of Life Sciences, Liaoning University, Shenyang 110036, China

Corresponding author:

Zhengwang Zhang

MOE Key Lab for BSEE, College of Life Sciences, Beijing Normal University

No.19 Xinjiekouwai Street, Haidian District，Beijing 100875, China

Phone: +86 58809666

e-mail: zzw@bnu.edu.cn

Authors' information

Jia Zheng   jia.zheng@rug.nl

Jan Komdeur   j.komdeur@rug.nl

Tamás Székely   t.szekely@bath.ac.uk

Maaike A. Versteegh   m.a.versteegh@rug.nl

Donglai Li   lidonglai@lnu.edu.cn

Hui Wang   201931200041@mail.bnu.edu.cn

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

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-nest. 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

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 renest 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 km^2) 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

Patterns of care

Clutch desertion usually takes place within three days after clutch completion (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 the daily nest checks, we filmed the nest with a SONY HDR-XR160E video camera for 2 h to check whether one (or both) parents 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 based on the video recordings.

We caught adult males using a mist net, playback of male songs, and 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 color 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, Zhang et al. 2018). We used three proxies of mating opportunities for males: (1) 'pairing probability' refers to the probability of a male successfully obtaining a female at a specific day of the breeding season. This variable indicates how likely a male pairs up anytime during the breeding season (Samplonius and Both 2017); (2) 'male mating time' refers to the time a male spends on finding a mate, i.e., the number of days between nest initiation and becoming paired or giving up attracting a mate. Long mating time would reflect low number of unmated females relative to the number of sexually active males (Székely et al. 1999; Parra et al 2014). (3) We also calculated the number of single males for each day in the breeding season (we term this variable 'number of single males'), and use this variable to indicate male mating opportunity (and also, female mating opportunity, see below). Thus high number of single males would reflect many competitors and thus 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 (±0.01g) 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 (±0.01 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 day^2 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, wind 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 ±

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 endavor (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), consistent 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).

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425   **Figure legends**

426   **Fig. 1** Number of Chinese penduline tit nests initiated over the breeding season (mean ± 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 ± 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
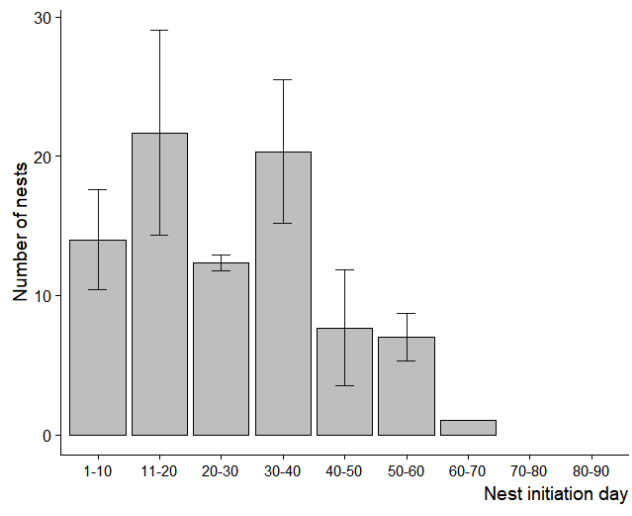436   Table 4.

437

Fig. 1

Fig. 2

（a)
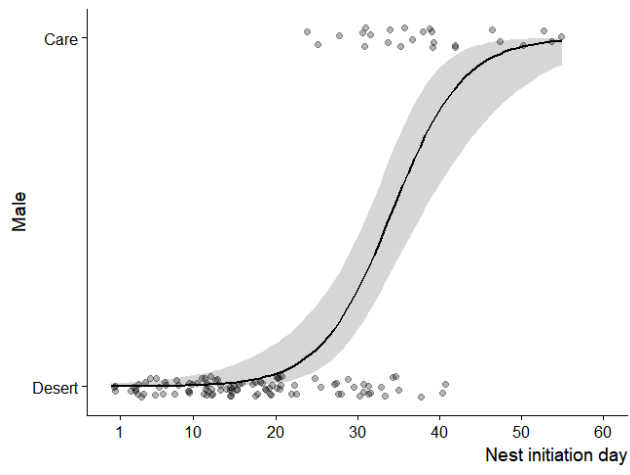
(b)
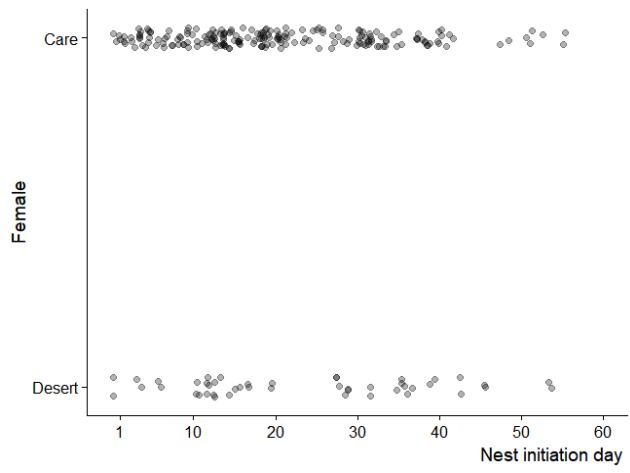
Fig. 3

(a)
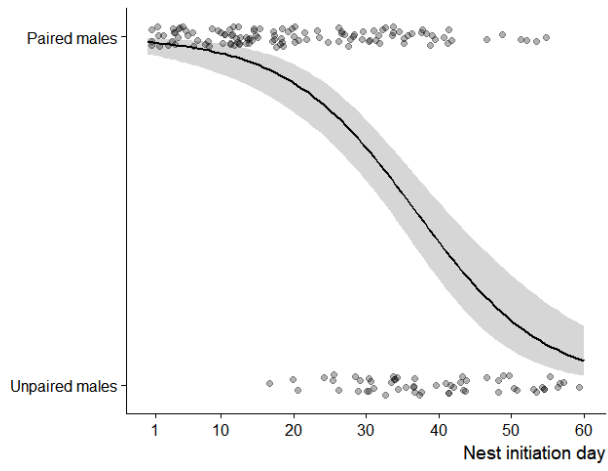
(b)
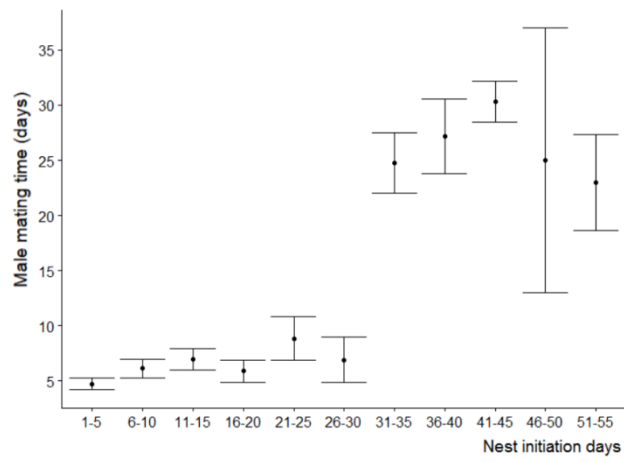
(c)
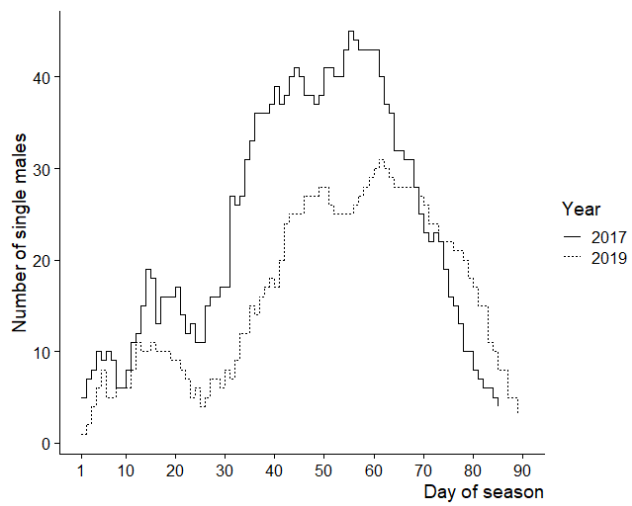
Fig. 4

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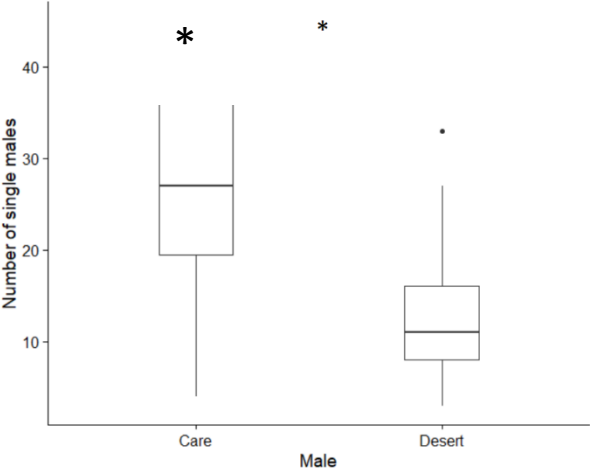
(b)
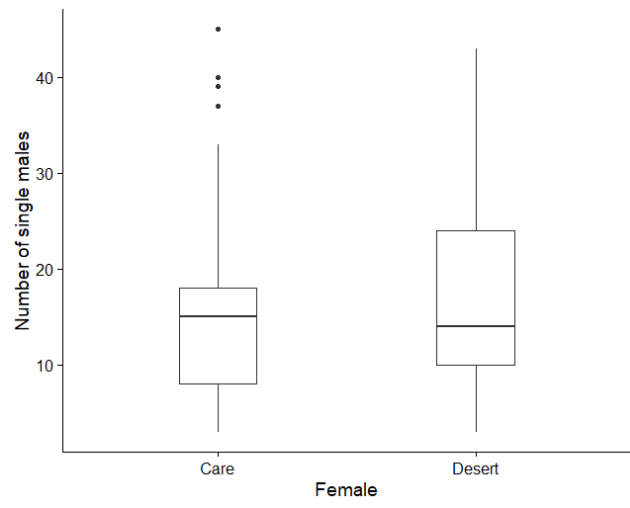
Table 1 Dates of egg laying, clutch size and parental care behavior in Chinese penduline tits. Day 1 = 1 May.

Year	First egg laying day	Last egg laying day	Average egg laying day	Clutch size (mean ± S.D.)	Parental care (no. of nests)			
					Female-only care	Male-only care	Biparental care	Biparental desertion
2016	24	50	33.9 ± 6.3	6.8 ± 0.8	69.6% (32)	6.5% (3)	15.2% (7)	8.7% (4)
2017	11	63	32.7 ± 9.8	6.8 ± 0.7	69.0% (49)	5.6% (4)	14.1% (10)	11.3% (8)
2019	24	73	37.1 ± 10.4	6.7 ± 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). R^2: McFadden pseudo-R^2.

Response variable	Explanatory variables	Estimate	SE	Z-value	Pr(>|z|)	R^2
Male behavior	Intercept	484.52	601.33	0.81	0.42	
	Nest initiation	0.24	0.05	4.56	<0.001	0.60
	Year	-0.24	0.30	-0.82	0.41	
Female behavior	Intercept	-228.19	428.83	-0.53	0.60	
	Nest initiation	-0.02	0.02	-1.07	0.28	0.15
	Year	0.11	0.21	0.54	0.59	
Parental behavior	Intercept	-1.87	0.45	-4.13	<0.001	
	Nest initiation	0.02	0.02	0.99	0.32	0.75
	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	
		Nest initiation	-0.12	0.02	-7.45	<0.001	0.35
		Year	0.45	0.16	2.71	0.01	
	Male mating time	Intercept	106.32	107.87	0.99	0.33	
		Nest initiation	0.04	0.004	10.16	<0.001	0.38
		Year	-0.05	0.05	-0.97	0.33	
Female	Number of singe males	Intercept	1.23	0.13	9.39	<0.001	
		(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	0.87
		(Nest initiation)$^2 \times$ Year	2.6e-04	1.0e-04	2.52	0.01	
		Nest initiation $\times$ 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). R^2: McFadden pseudo-R^2.

Response variable	Explanatory variables	Estimate	SE	Z-value	Pr(>|z|)	R^2
Male parental care	Intercept	-2967	1011	-2.93	0.003	
	Number of single males	0.28	0.06	4.62	<0.001	0.51
	Year	1.47	0.5	-2.93	0.003	
Female parental care	Intercept	4.71	599.54	0.11	0.99	
	Number of single males	0.02	0.03	0.57	0.57	0.004
	Year	-0.003	0.30	-0.01	0.99	
Parenting decision	Intercept	-1.80	0.52	-3.48	<0.001	
	Number of single males	0.02	0.03	0.61	0.54	0.58
	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	
	Male decision	-0.03	0.18	-0.18	0.86	
	Female decision	0.07	0.14	0.4	0.62	0.34
	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	
	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	0.38
	Nest initiation	-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	
	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	0.35
	Nest initiation	0.01	0.01	1.85	0.06	
	Year	0.02	0.08	0.31	0.76	

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5   **Supplementary materials**

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

Jia Zheng[a,b], Jan Komdeur[a], Tamás Székely[c], Maaike A. Versteegh[a], Donglai Li[d], Hui Wang[b], Zhengwang Zhang[b]

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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
			$(\text{Nest initiation day})^2$	-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.
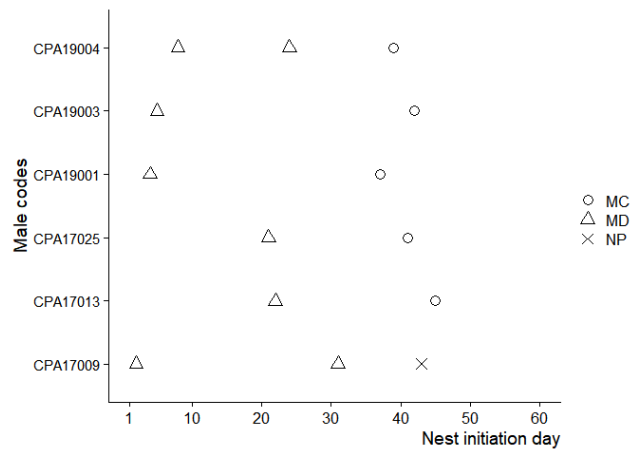
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15   S3. Seasonal variation in nest size in Chinese penduline tits. Nest weight and nest volume were analyzed using GLMs (n = 14 nests).

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
Male mating time	Intercept	112.50	139.44	0.81	0.43	
	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	0.16
	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	
	Body mass	5.24	6.60	0.79	0.44	
	Tarsus length	-8.60	8.85	-0.97	0.34	0.21
	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	