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1 **Individual variation and the resolution of conflict**  
2 **over parental care in penduline tits**

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24 Eurasian penduline tits (*Remiz pendulinus*) have an unusually diverse breeding system  
25 consisting of frequent male and female polygamy, and uniparental care by the male or the  
26 female. Intriguingly, 30–40% of all nests are deserted by both parents. To understand the  
27 evolution of this diverse breeding system and frequent clutch desertion, we use six years of  
28 field data to derive fitness expectations for males and females depending on whether or not  
29 they care for their offspring. The resulting payoff matrix corresponds to an asymmetric  
30 Snowdrift Game with two alternative evolutionarily stable strategies (ESSs): female-only and  
31 male-only care. This, however, does not explain the polymorphism in care strategies and frequent  
32 biparental desertion, since theory predicts that one of the two ESSs should have spread to fixation.  
33 We argue that the average population payoff matrix gives a poor representation of individual  
34 conflicts. If individuals differ in their payoff matrices, their decisions may depend on their own  
35 fitness prospects rather than on the population average. Using bootstrapping, we demonstrate  
36 that taking account of individual variation in payoffs explains the patterns of care better than a  
37 model based on population payoffs. Our work highlights the need for a new generation of  
38 individual-based evolutionary game-theoretic models.

39

40 **Keywords:** cooperation, Snowdrift Game, evolutionary game theory, evolutionarily stable  
41 strategy, nest desertion, sexual conflict

## 42 1. INTRODUCTION

43 Decisions about parental care are among the most important life-history decisions that  
44 animals face. Across vertebrates a diversity of parental care systems exists, ranging from  
45 cooperative breeding with biparental care and helpers, such as in meerkats (*Suricata suricatta*  
46 [1] and long-tailed tits (*Aegithalos caudatus* [2]), to limited (or no) parental care, such as in  
47 precocial birds and many fish species [3-5]. The fitness consequences of parental care decisions  
48 depend on the social and non-social environment [3,5-7] and strongly reflect the trade-off  
49 between investment in the current brood and investment in future survival and reproduction [3;  
50 8; 9]. Although both parents have a shared interest in their current brood, there is conflict  
51 between them because each individual would prefer its mate to provide the majority of  
52 parental care [5,9,10].

53 Evolutionary game theory is a powerful approach for studying cooperation and conflict in a  
54 coherent framework [11,12], and it has often been used to model parental care decisions (*e.g.*  
55 [13-18]). With a few notable exceptions [19,20], most published parental care models are  
56 conceptual and not directly tailored to a specific empirical system. Attempts to test  
57 theoretical predictions have focused primarily on biparental care, examining how a parent  
58 responds to its local circumstances and the parental effort of its mate (*e.g.* [21-23]).  
59 Realistic game-theory models for the interactions between parents involved in biparental  
60 care have to consider how such behavioural interactions may depend on individual traits  
61 and environmental variables, and how the outcome of the interactions may change over  
62 time. This makes the models and their solutions inherently intricate [13,16]. Furthermore,  
63 model predictions are often sensitive to their specific assumptions (*e.g.* [13]), so for  
64 accurate tests of care models it is particularly important to validate the underlying  
65 theoretical assumptions.

66 Testing models of parental care might be easier in systems that are not restricted to  
67 biparental care, but have a polymorphic pattern of care. Several species of vertebrates

68 exhibit a combination of male-only, female-only and biparental care within the same population  
69 (*e.g.* [24-26]). Here we focus on the Eurasian penduline tit (*Remiz pendulinus*), in which male-  
70 only care, female-only care and biparental desertion all occur within the same population [27, 28].  
71 Full incubation and feeding of nestlings is carried out by one parent only. In our study population  
72 in southern Hungary, 45.0% of all nests are cared for by the female alone, 16.7% are cared for by  
73 the male alone and 38.3% are deserted by both parents [29]. Biparental care is never observed.  
74 Despite large geographic distances and substantial variation in breeding density and other  
75 ecological variables, this pattern of care is consistent across five populations of penduline tits in  
76 distant locations in Europe [29] (Electronic Supplementary Information [ESM] S1).

77         The diverse care pattern in penduline tits, in particular the high frequency of nest  
78 desertion, is likely the result of sexual conflict between the two parents [28,30,31]. One  
79 parent is able by itself to incubate the clutch and feed all the nestlings until independence  
80 [32,Pogány *et al.* in prep.], giving each parent an incentive to desert the nest. Nest desertion  
81 puts the deserted partner in a difficult situation (a “cruel bind” [33]): even if uniparental care  
82 is costly, the deserted partner has a strong incentive to stay, since deserting as well would  
83 condemn the offspring to death. Nevertheless, the deserted partner may also leave the nest if  
84 desertion is associated with higher fitness expectations than continuing to care for the current  
85 brood [34]. Game-theory models show that sexual conflict over parental care can indeed  
86 result in biparental desertion, or in uniparental care and an associated arms race for being the  
87 first to desert [35].

88         Our objective here is to apply these game-theoretic concepts to a particularly well-  
89 studied wild population of Eurasian penduline tits, in which males and females may have up  
90 to six mates in a single breeding season [28]. Based on six years of data from this population,  
91 we estimate the fitness consequences for both males and females of caring for the offspring or  
92 deserting the nest. Using these estimates we calculate a payoff matrix, from which we derive  
93 the evolutionarily stable strategy (ESS) for each sex. We show that the resulting ESS

94 predictions do not explain the variation in parental care observed in the field. We argue that  
95 this is because the average payoff matrix for the population gives a poor representation of the  
96 conflict faced by each pair of penduline tits, which is likely to depend on their individual  
97 characteristics. We therefore investigate the possibility that the variation in care patterns is  
98 caused by individual variation in payoffs [36]. By incorporating individual variation we can  
99 account better for population-level patterns of parental care. Throughout, we discuss the  
100 difficulties of applying simple payoff matrices to real populations with substantial individual  
101 variation, and argue that evolutionary models should aim to take a more realistic approach by  
102 modelling individual variation.

103

## 104 **2. ESTIMATING PAYOFFS**

### 105 **(a) *Study site and data collection***

106 We studied Eurasian penduline tits during the breeding season between April and August in  
107 six consecutive years (2002–2007) at a 1,321 ha fishpond system, Fehértó, in southern Hungary  
108 (46°19'N 20°6'E). Each year, 41–116 ringed males and 15–51 ringed females bred at this site  
109 [28]. The male bias in the number of ringed individuals reflects the fact that females are more  
110 difficult to trap than males, rather than a genuine bias in population sex ratio. Males were  
111 usually trapped before incubation using mist nets, whereas females were usually trapped at the  
112 nest during incubation. We searched for nest-building penduline tits and then visited each  
113 nest roughly every two days [37] to determine the date of nest initiation, date of pair  
114 formation, number of eggs (between the sixth and the ninth (median = eighth) day after the  
115 start of incubation), date of desertion, identity of the parent attending the nest and the number  
116 of nestlings (ten days after hatching of the first egg; the number of nestlings on the tenth day  
117 after hatching is highly correlated with the number of fledglings [37,38]). Adults were  
118 trapped and ringed with one metal ring and a unique combination of three colour rings (A.C.  
119 Hughes, Middlesex, UK). Standard biometric measurements were taken, as well as digital

120 photographs of each side of the bird's head to quantify the size of the 'mask', signalling  
121 attractiveness (see [38,39] for details). The pattern of nest desertion in our population did not  
122 differ between nests where neither parents was trapped and those where at least one of the  
123 parents was trapped (multinomial logistic regression;  $\chi^2 = 3.932$ ,  $df = 2$ ,  $P = 0.140$ ,  $n = 389$   
124 nests), suggesting that trapping did not influence the probability of desertion. Adult return rates  
125 between years are low (5% for males, 2% for females [40]). To avoid pseudoreplication, we  
126 randomly selected data from only one season per colour-ringed individual, giving a total  
127 sample of 337 nests from 172 individuals). The composition of pairs was nearly always  
128 different between subsequent clutches: out of 194 colour-ringed pairs that produced a clutch  
129 between 2002 and 2007, only six pairs (3.1%) kept the same mate between successive nests  
130 (for further details on fieldwork see [28]). The pattern of parental care for these six pairs (50%  
131 female-only care, 10% male-only care, and 40% biparental desertion) did not appear to differ from  
132 that observed at the population level.

133

#### 134 **(b) *Fitness consequences of care and desertion***

135 Throughout this paper, we focus on parental care or desertion decisions concerning each  
136 individual's first breeding attempt in the season. Since incubation and nestling feeding  
137 take about 34 days [41], caring for the first brood severely constrains the opportunities for  
138 subsequent breeding (Table 1a). To estimate the contribution of the first clutch to parental  
139 fitness, we calculated the average number of eggs and nestlings for all nests that were  
140 initiated before 6 June, depending on the parental care category (female-only care, male-  
141 only care, biparental desertion) of the nest (Table 1a). The cut-off date corresponds to the  
142 midpoint of the interval between the nest initiation date of the first and second nest of  
143 ringed males (mean  $\pm$  SD between males: 3 June  $\pm$  22.7 days ( $n = 267$  males), 8 June  $\pm$   
144 21.1 days ( $n = 101$  males), respectively). If a given individual had more than one nest  
145 before 6 June, we only selected the earliest nest in the season as its first nest.

146 Our data on first clutches are in line with previous studies of penduline tits [28,29].  
147 Nest desertion takes place during the egg-laying phase. If the male deserts first, the female  
148 often lays two or three additional eggs, so that female-only cared clutches are  
149 significantly larger than those cared for by males and those deserted by both parents  
150 (Table 1a). In biparentally deserted nests all offspring die, whereas offspring survival (*i.e.*  
151 survival from hatching until 10 days after hatching) does not differ between male-only and  
152 female-only cared clutches (binary logistic regression including parental care category, clutch  
153 size, egg-laying date, year and the interaction between parental care category and clutch size  
154 as fixed effects;  $\chi^2 = 1.458$ ,  $P = 0.227$ ,  $n = 142$  nests; Pogány, Á. *et al.* unpublished data). The  
155 reproductive success of males may be inflated (or deflated) by the occurrence of extra-pair  
156 young; in this system, about 24% of all offspring are sired by an extra-pair male [42].  
157 However, the percentage of extra-pair young does not differ between nests cared for by the  
158 male and those deserted by him, nor between nests cared for by the female and those  
159 deserted by her [42]. Therefore, extra-pair paternity is unlikely to bias our results.

160 The data on first broods within a season were based on 115 nests for which the  
161 parental care category was known. For 172 ringed birds (111 males and 61 females)  
162 involved in successful breeding attempts at these nests, the parental care category of their  
163 first nest of the season could be determined ('successful' meaning that pair formation and  
164 egg laying took place). For each combination of sex (male, female) and parental care  
165 category (male-only care, female-only care, biparental desertion), we calculated the  
166 percentage of birds involved in a second successful breeding attempt and the mean number  
167 of subsequent nests established by those birds. Males may only care for one brood in a  
168 breeding season, whereas females may care for up to two broods. The difference between males  
169 and females in the probability of having a subsequent successful nest after providing parental care  
170 (0.06 for males versus 0.38 for females; Table 1a) is largely due to the fact that males often care  
171 near the end of the breeding season [28,43]. Additionally, males who deserted their first nest were



172 less likely to have a subsequent successful nest if the female had also deserted (probability = 0.34)  
173 than if she had stayed behind to provide care (0.74; Table 1a). This might suggest that males at  
174 nests that are biparentally deserted are of lower quality and/or less attractive. Previously we  
175 showed that the size of a male's eye-stripe or 'mask' indicates his attractiveness [38,39], but mask  
176 size was not different between males whose nest was deserted by both parents and males at nests  
177 where either the male or the female provided care (binary logistic regression; model effect  
178 estimate  $\pm$  SE = 1.025  $\pm$  0.912, Wald statistic = 1.262,  $df$  = 1,  $P$  = 0.261,  $n$  = 88 males). Tarsus  
179 length, wing length, and body mass of males were also not different between these two categories  
180 of nests ( $P$  > 0.331). Additionally, at the second nest in a season the pattern of parental care for  
181 males was not different from that observed at the population level (Table 3b) if his first nest was  
182 cared for by the female ( $\chi^2$  = 0.211,  $P$  = 0.900,  $n$  = 34 males) or was biparentally deserted ( $\chi^2$  =  
183 1.186,  $P$  = 0.553,  $n$  = 31 males). This suggests that the breeding experience of males did not  
184 predict the likelihood of biparental desertion of a subsequent nest.

185         Based on all penduline tits within a category (i.e., including those birds that did not  
186 establish a second nest), we calculated the average number of eggs and nestlings produced  
187 during subsequent breeding attempts (Table 1a). If the number of eggs and/or nestlings could  
188 not be determined, it was estimated as the population mean of nests with the corresponding  
189 parental care category (male-only care: 3.67 eggs and 2.22 nestlings; female-only care: 5.80  
190 eggs and 3.07 nestlings; biparental desertion: 2.93 eggs and 0 nestlings;  $n_{\text{eggs}}$  = 371 nests and  
191  $n_{\text{nestlings}}$  = 194 nests). Overall, we estimated reproductive success for 77 out of a total of 339  
192 clutches (22.7%) and for 33 out of 336 broods (9.8%).

193         Finally, we calculated the seasonal reproductive output for each parental category,  
194 by adding up the average number of nestlings in the first and subsequent nests (Table 1a).  
195 To check the consistency of our calculations of parental strategy-dependent seasonal  
196 reproductive output, we also determined the total number of nestlings produced over the  
197 season by the 172 ringed penduline tits, separately for males and females in each care

198 category of their first nest. For all six categories, the reproductive output of the colour-  
199 ringed penduline tits we followed throughout the breeding season was almost identical to  
200 that in Table 1a.

201

### 202 **3. GAME-THEORETIC ANALYSIS**

#### 203 **(a) *No individual variation in payoffs***

204 The seasonal reproductive output given in the penultimate row of Table 1a corresponds to the  
205 total number of nestlings shown in the payoff matrix for the parental care categories in Table 1b.

206 A male who cared for the offspring in his first nest produced more nestlings over the course  
207 of the season ( $2.20 \pm 1.40$ ) than a male whose first nest was biparentally deserted ( $1.54 \pm 2.54$ ;  
208 Mann-Whitney  $U$  test:  $U = 257.5$ ,  $P = 0.009$ ,  $n = 65$ , Cohen's  $d = 0.878$ ,  $1-\beta = 0.88$ ). In  
209 contrast, a female who cared for the offspring in her first nest did not produce significantly  
210 more nestlings over the course of the season ( $4.58 \pm 2.62$ ) than a female whose first nest was  
211 biparentally deserted ( $2.35 \pm 2.90$ ;  $U = 93.5$ ,  $P = 0.108$ ,  $n = 58$ ,  $d = 1.120$ ,  $1-\beta = 0.70$ ). Note,  
212 however, that we only had six females in the latter category.

213 Pairs rarely produced multiple clutches together (see § 2(a); [39]). We therefore  
214 assume that penduline tits play a single-shot game with two alternative actions: care or  
215 desert. An influential single-shot game from the game-theoretic literature is the Prisoner's  
216 Dilemma. In this game, each player may either cooperate or defect, but the best response to any  
217 action by the opponent is to defect [44-47]. Thus the Prisoner's Dilemma characterises a  
218 situation in which cooperative behaviour is vulnerable to exploitation by non-cooperators,  
219 eventually leading to an equilibrium in which no one cooperates. Despite the high frequency of  
220 nest desertion in penduline tits, Table 1b suggests that desertion is not the dominant strategy: if  
221 the male deserts, the female does best by caring, whereas if the female deserts, the male does  
222 best by caring. Thus, penduline tits do not appear to be playing a Prisoner's Dilemma at the  
223 population level. An alternative possibility is the Snowdrift Game, in which cooperation is

224 beneficial for both players but the costs of cooperating depend on the opponent's strategy [48-  
225 50]. This is also true for parental care. Since parental care is an asymmetric game between  
226 two types of players, namely males and females, the game in Table 1b may reflect an  
227 asymmetric Snowdrift Game (cf. 'Battle of the Sexes' [51]). Although in asymmetric games an  
228 ESS can never be a mixed strategy [52], the asymmetry (male versus female) may be used to  
229 settle the conflict: each of the ESSs, corresponding to the two forms of unilateral cooperation  
230 (i.e. male-only care and female-only care), may be viewed as a convention. Although either  
231 convention is evolutionarily stable once it is adopted by the whole population, the problem  
232 remains which one will be reached in the course of evolution. Both players agree that  
233 unilateral cooperation would be best, but they differ in which of the two ESSs they prefer.

234         If one of the ESSs is payoff dominant [53]—in that the payoff to each player is at  
235 least as great as the payoff it would get at the alternative ESS—then an obvious solution is to  
236 adopt that ESS. In terms of the average reproductive payoffs in our dataset, female-only care is  
237 more profitable for both sexes than male-only care (Table 1b), and thus female-only care is the  
238 payoff-dominant ESS. However, the predicted outcome of female-only care is inconsistent with  
239 the observed behaviour. Why is it that some pairs exhibit male-only care, when female-only care  
240 apparently gives a higher payoff for both sexes? And if the parents coordinate their actions, why  
241 do we still observe such a high frequency of biparental desertion (28–44%; ESM S1)?

242

#### 243 **(b) *Individual variation in payoffs***

244 Since individuals vary in their fitness prospects, a payoff matrix based on reproductive outputs  
245 averaged across the whole population may provide a poor framework for understanding  
246 conflict resolution within individual pairs. Although at a population level penduline tits appear  
247 to be playing a Snowdrift Game, individual pairs of birds may differ in their payoffs from  
248 particular actions and may bargain an outcome depending on their individual traits (and  
249 their particular environmental circumstances). Within each pair, individual characteristics

250 such as attractiveness or condition are likely to affect the payoff for a given parental  
251 category. If a male is attractive, for instance, his female partner may be more willing to  
252 care for his offspring [54], whilst the male may benefit more from desertion by finding a  
253 new mate more rapidly than a less attractive male. Similarly, males may be more willing to  
254 care for the offspring of fecund females, while those females may be better at producing  
255 additional clutches. But accounting for such individual differences is to generate precise,  
256 pair-specific predictions of the outcome of individual conflicts over parental care is a very  
257 difficult task.

258         Nevertheless, using the available field data on reproductive output for three of  
259 the categories (though never biparental care) for some of the birds may allow us to  
260 generate more accurate predictions than when we only consider the population average  
261 payoff matrix. Here we use an approach based on bootstrapping. The game played by  
262 each pair is represented by the general payoff matrix shown in Table 2a and Table 3a.  
263 Note that in our study population not a single case of biparental care was observed at the 534  
264 nests we investigated, so the payoffs  $A$  and  $a$  cannot be estimated for any individual. Instead,  
265 we assume that unilaterally deserting a caring partner always yields a higher fitness payoff  
266 than caring (i.e.  $b > a$  and  $B > A$ ). For all other outcomes (male-only care, female-only  
267 care and biparental desertion) we allow the expected payoffs to vary between individuals.

268         For most pairs we lack individual payoffs for both the male and the female, so as an  
269 approximation we used a bootstrapping approach to generate a large sample of payoff matrices  
270 from the field data. This involved randomly drawing (with replacement) from the observed  
271 individual payoff values (seasonal number of nestlings) for each parental care category for males  
272 and females. Each bootstrapped matrix was composed of the following values randomly drawn  
273 from the corresponding observed payoffs: one  $b$  value drawn from the  $n = 46$  observed male  
274 payoffs under female-only care; one  $c$  value from the  $n = 18$  male payoffs under male-only care;  
275 one  $d$  value from the  $n = 47$  male payoffs under biparental desertion; one  $B$  value from the  $n = 3$

276 female payoffs under male-only care; one  $C$  value from the  $n = 52$  female payoffs under female-  
277 only care; and one  $D$  value from the  $n = 6$  female payoffs under biparental desertion. To each of  
278 these values we added a small amount drawn from a random normal distribution with mean 0  
279 and standard deviation 0.01. This was to preclude the occurrence of tied payoffs, which would  
280 otherwise be common in the biparental desertion category since many of these individuals  
281 produced no offspring in the breeding season. We repeated this process until we had generated  
282 5,000 unique bootstrapped matrices from the field data.

283         There are four possibilities (Table 2b–e) for the type of parental care game being  
284 played by a pair, determined by the particular values of  $c$ ,  $d$ ,  $C$  and  $D$ :

- 285 (i)  $c < d$  and  $C > D$ : a game in which female-only care is the only ESS;  
286 (ii)  $c > d$  and  $C < D$ : a game in which male-only care is the only ESS;  
287 (iii)  $c < d$  and  $C < D$ : a Prisoner’s Dilemma where biparental desertion is the only ESS; or  
288 (iv)  $c > d$  and  $C > D$ : a Snowdrift Game with two ESSs (male-only care and female-only care).

289 On the basis of our bootstrapped matrices, 21.4% of nests are predicted to have female-only care  
290 (case (i)), 20.1% male-only care (case (ii)) and 9% biparental desertion (case (iii)), while the  
291 remaining 49.5% of pairs will be involved in a Snowdrift Game (case (iv)) from which any of the  
292 three outcomes may result (Table 3a). In the Snowdrift Game we assume that if one of the two  
293 ESSs is payoff dominant, this is the one the pair will adopt. Thus we assume that female-only  
294 care results when  $b > c$  and  $C > B$  (26.4% of the bootstrapped matrices, in addition to those  
295 from case (i)) and that male-only care results when  $b < c$  and  $C < B$  (3.4% of the bootstrapped  
296 matrices, in addition to those from case (ii); Table 3a). For 19.7% of the bootstrapped  
297 matrices, the male and female are involved in a Snowdrift Game in which neither equilibrium  
298 is payoff dominant. We consider three possible scenarios for how the conflict is resolved at  
299 these nests:

- 300 (1) Both parents desert the nest. This scenario predicts an additional 19.7% of nests with  
301 biparental desertion (Table 3b).

302 (2) The parents adopt the solution that is payoff dominant at the population level, namely  
303 female-only care (Table 1b). This scenario predicts an additional 19.7% of nests with  
304 female-only care (Table 3b).

305 (3) The two ESSs are adopted with equal probability, resulting in female-only care at half of  
306 these nests and male-only care at the remaining half [37]. This scenario predicts an  
307 additional 9.9% of nests with female-only care and an additional 9.9% of nests with  
308 male-only care (Table 3b).

309 Of these three scenarios for resolving the Snowdrift Game in the absence of payoff  
310 dominance, the first (biparental desertion) best predicts the observed patterns of care, as  
311 this provides the closest match to the pattern of parental care observed in our study  
312 population (Table 3b). The predicted frequencies of female-only care (47.8%) and  
313 biparental desertion (28.7%) are within the natural ranges (ESM S1), although it  
314 overestimates the frequency of male-only care (23.5%, Table 3b). This model, based on  
315 individual variation, is therefore broadly consistent with the observed patterns of care in  
316 our study population, and provides a better fit than the earlier model based on the average  
317 payoff matrix for the population (Section 3a), which predicted female-only care at all nests.

318 To test how individual variation may influence the resolution of conflict over care, we ran  
319 our bootstrapped model again, now only including the reproductive payoffs of males of whom we  
320 knew the size of the 'mask' ( $n = 30$ ,  $n = 10$ ,  $n = 40$  males whose first nest in the season was cared  
321 for by the female, cared for by the male, or biparentally deserted, respectively). From previous  
322 studies we know that the area of the mask is associated with attractiveness of males [38] and with  
323 the parental care decision of males, but not of females [39]: males with larger masks are more  
324 likely to desert, whereas the female's decision to care or desert does not appear to be influenced  
325 by the size of the male's mask [39]. We therefore assumed that all males with a larger than  
326 average mask (i.e.  $> 1.30 \text{ cm}^2$ ,  $n = 120$  males) would desert, whereas for those males whose mask  
327 was  $< 1.30 \text{ cm}^2$  and for the females we assumed that payoff dominance and the Snowdrift Game

328 determine parental care as outlined in Table 3a. The predictions of parental care from this model  
329 accounting for individual variation in attractiveness closely resemble the observed pattern of  
330 parental care in penduline tits (Table 3b).

331

#### 332 **4. DISCUSSION**

333 We found no evidence that penduline tits are playing a Prisoner's Dilemma, despite the high  
334 frequency of biparental desertion. At the population level, the payoff matrix based on seasonal  
335 reproductive success is most consistent with an asymmetric Snowdrift Game with two  
336 alternative ESSs, female-only care and male-only care. Female-only care is the payoff-  
337 dominant ESS, but this fails to predict the patterns of care in the wild, where more than half of  
338 the nests are either cared for by the male (13.5%) or deserted by both parents (39.1%). We  
339 argue that the population payoff matrix is of little use in explaining observed patterns of care  
340 because expected reproductive payoffs are likely to vary between individuals, and therefore  
341 different pairs may be playing very different games when deciding whether to care or desert.

342 Our individual-based approach predicts a mixture of parental care strategies, with  
343 frequencies of female-only care and biparental desertion that fall within the observed range in  
344 natural populations (Table 3b, ESM S1). Though largely consistent with observed frequencies of  
345 parental care, our first model overestimates the frequency of male-only care and underestimates the  
346 occurrence of biparental desertion compared to the empirical dataset (Table 3b). In many ways this  
347 mismatch is not surprising, given that we have payoffs only for a subset of individuals in specific  
348 situations. Furthermore, we lack information on the extent to which an individual's expected  
349 payoffs are correlated across the three different situations (male-only care, female-only care and  
350 biparental desertion), and on the correlation between the male and female payoffs of each pair.  
351 Such information is largely beyond our reach, even for such an intensively studied field system as  
352 this penduline tit population. Nevertheless, our approach based on bootstrapped individual payoffs  
353 highlights the importance of considering individual variation when predicting the behaviour of

354 individual pairs instead of applying more conceptual models like the Prisoner's Dilemma.

355         The significant deviation of our initial model from the empirically observed pattern  
356 of care could be partly due to stochastic factors affecting some of the payoffs based on  
357 small sample sizes. This may, for example, have been responsible for the overestimate of  
358 the occurrence of male-only care, which was derived from only  $n = 18$  payoffs for males  
359 and  $n = 3$  for females. But the fact that males are more likely to provide care nearer the end  
360 of the breeding season (yet without entailing biparental care [27,42]), for instance, suggests  
361 that there are other factors besides just the strategy-dependent payoffs that are important in  
362 determining which parent will provide care and which will desert.

363         The discrepancy between predicted and observed patterns of care may be partly  
364 ascribed to individual differences, such as individual quality or environment [36]. To some  
365 extent we took these individual-specific effects into account by replacing the average  
366 fitness payoffs at a population level with individual payoffs. However, a correlation  
367 between individual traits and the different adopted strategies may cause a consistent bias in  
368 the exact payoffs. Attractive males, for instance, may desert not only when their partner stays  
369 behind to care for the offspring but also when the partner already has deserted (as predicted in  
370 a Prisoner's Dilemma), whereas a less attractive male may be better off caring for the  
371 offspring in the latter case (as predicted in a Snowdrift Game). Such covariance of  
372 individual traits with parental care strategies is likely to influence the outcome of  
373 conflict over parental care. In our final model, we accounted for some potential  
374 correlations between individual traits and reproductive payoffs by including the effect  
375 of male attractiveness on the decision to care or desert. We showed that this  
376 substantially improved our model's predictions.

377         We assumed that the parents play a single-shot game because normally each pair  
378 only breeds together once in a breeding season, but in reality they are unlikely to play a  
379 strictly single-shot game. Parents may interact multiple times and repeatedly assess



380 each other's quality before they decide whether to care for the offspring or desert. Such  
381 interactive 'negotiation' behaviour likely influences decisions over parental care [55].  
382 However, although the male's own parental care decisions are known to be associated  
383 with his body condition or attractiveness, we have no evidence that these male traits  
384 influence the parental care decisions of females [38,43,56]. Additionally, it is worth  
385 noting that Eurasian penduline tit parents spend little time together at the nest during the  
386 period before desertion, making detailed monitoring of each other's behaviour, such as  
387 has been suggested for St Peter's fish [20], unlikely [43]. Nevertheless, the interaction  
388 between individual traits and environmental variables (e.g. mating opportunities) may  
389 be complex, and experimental manipulations would be useful for investigating  
390 systematically how these factors combine to influence patterns of parental care.

391 Balshine-Earn and Earn (1997) also showed in their model that natural variation  
392 between individuals and in the environment could promote the coexistence of different  
393 forms of parental care (see also [47]). A spatially heterogeneous distribution of strategies,  
394 such as desertion in high-quality habitats and care in poor habitats, or vice versa, could  
395 potentially confound the outcome of our analyses. Although it has been suggested that spatially  
396 diverse environments might favour multiple coexisting strategies [46], in earlier work we  
397 found no relationship between parental care category and habitat characteristics [39].  
398 Nonetheless, it would be worthwhile to investigate the possibility that mating opportunities  
399 might be spatially structured in some way, perhaps resulting in spatial variation in deserting  
400 strategies. Such extrinsic factors, the reputation of the players in the game and occasional  
401 mistakes made by those players may all influence conflict resolution and allow multiple  
402 strategies to persist [12,47,49,57].

403 In conclusion, we have shown that the resolution of conflict over care is highly  
404 variable and may be strongly influenced by individual differences in the expected  
405 reproductive payoffs for each male–female pair. Using a population payoff matrix to predict

406 the behaviour of individual pairs has severe limitations, because this is likely to be a poor  
407 representation of the particular conflict faced by each pair. We recommend the use of  
408 individual-specific information on the reproductive consequences of care decisions to obtain  
409 more accurate predictions of population-level patterns of parental care.

410

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418

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- 569

570 **TABLE CAPTIONS**

571 Table 1. (a) Summary of breeding parameters of Eurasian penduline tits in southern Hungary: number of eggs  
572 and nestlings produced in all first nests (including those of both ringed and unringed individuals) of the breeding  
573 season, with sample size (number of nests) between parentheses; the probability for ringed individuals to have at  
574 least one more successful breeding attempt after the first successful nest ('successful' meaning that pair formation  
575 and egg laying took place); the number of subsequent successful breeding attempts; the total number of eggs and  
576 nestlings produced in all subsequent nests; and the seasonal reproductive output (means  $\pm$  SD). SD of the total  
577 number of nestlings represents the pooled SDs of the first and subsequent nests. (b) Population strategy-  
578 dependent seasonal reproductive payoffs for males and females: mean number of nestlings  $\pm$  SD for males  
579 (below the diagonal) and females (above the diagonal) given the parental category of their first nest in the  
580 breeding season ( $n$  is the number of individuals). FC = female care, FD = female desertion, MC = male care,  
581 MD = male desertion. Arrows point from smaller to larger payoffs, representing the direction in which selection  
582 for a parental care strategy would act (dashed arrows indicating our assumption that unilateral desertion always  
583 yields a higher fitness payoff than caring (see §3b), continuous arrows are based on observed values). This  
584 matrix is consistent with that of the Snowdrift Game (see Table 2e).

585  
586 Table 2. Reproductive payoff matrices. For comparing alternative actions, arrows point from smaller to larger  
587 payoffs (indicating the expected direction of selection). (a) Generic version; our central assumption is that  
588 unilateral desertion yields a higher payoff for the deserting partner (both male and female) than biparental care (a  
589 behaviour we never observed in our population), i.e.  $b > a$  and  $B > A$ . (b)–(e) Four specific scenarios for the  
590 different relationships between the payoffs when caring alone ( $c$  for males,  $C$  for females) and when both parents  
591 desert ( $d$  for males,  $D$  for females).

592  
593 Table 3. (a) Payoff requirements, parental care ESSs and the probability (%) for each ESS. The question mark  
594 (?) indicates the percentage of pairs involved in a Snowdrift Game for which neither of the two ESSs (male-  
595 only care or female-only care) was payoff dominant. (b) The expected population strategy for three different  
596 assumptions for '?', i.e. the sum of the proportion predicted by payoff dominance and the proportion  
597 predicted by the Snowdrift Game.

598

599 Table 1.

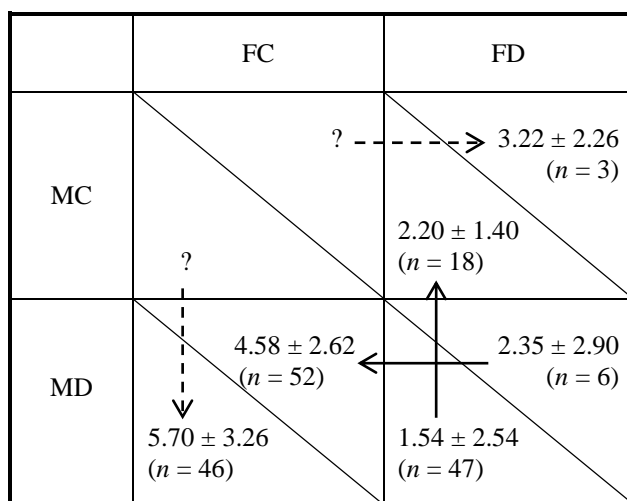
600 (a)

|            | female-only care |                  | male-only care   |             | biparental desertion |             |             |
|------------|------------------|------------------|------------------|-------------|----------------------|-------------|-------------|
|            | ♂                | ♀                | ♂                | ♀           | ♂                    | ♀           |             |
| first      | no. of eggs      | 6.37 ± 1.16 (41) | 3.17 ± 1.27 (12) |             | 2.84 ± 1.27 (51)     |             |             |
|            | no. of nestlings | 3.63 ± 2.00 (40) | 2.20 ± 1.40 (10) |             | 0.00 ± 0.00 (65)     |             |             |
| subsequent | probability      | 0.74             | 0.38             | 0.06        | 0.67                 | 0.34        | 0.83        |
|            | no. of nests     | 1.46 ± 1.39      | 0.58 ± 0.91      | 0.06 ± 0.24 | 0.67 ± 0.58          | 1.17 ± 1.20 | 1.33 ± 0.82 |
|            | no. of eggs      | 6.34 ± 6.05      | 2.61 ± 3.97      | 0.06 ± 0.24 | 2.91 ± 2.90          | 4.49 ± 4.66 | 7.12 ± 5.00 |
|            | no. of nestlings | 2.07 ± 2.58      | 0.95 ± 1.70      | 0.00 ± 0.00 | 1.02 ± 1.77          | 1.54 ± 2.54 | 2.35 ± 2.90 |
| total      | no. of nestlings | 5.70 ± 3.26      | 4.58 ± 2.62      | 2.20 ± 1.40 | 3.22 ± 2.26          | 1.54 ± 2.54 | 2.35 ± 2.90 |
|            | <i>n</i>         | 46               | 52               | 18          | 3                    | 47          | 6           |

601 *n* is the number of individually marked males or females, whereas sample sizes at the first nests of the season (in parentheses)  
 602 are the number of nests including those of both ringed and unringed individuals. Sample sizes for the former may be larger  
 603 than that for first nests only, because reproductive success for some nests was estimated using population means for a given  
 604 strategy (see §2b).

605

606 (b)



607

608

609

610 Table 2.

611 (a)

612  $b > a$  and  $B > A$

|    |                       |                      |
|----|-----------------------|----------------------|
|    | FC                    | FD                   |
| MC | $A$ $\rightarrow$ $B$ |                      |
| MD | $a$ $\downarrow$ $b$  | $c$ $\downarrow$ $d$ |

613

614 (b)

615  $c < d$  and  $C > D$

616 single ESS: female-only care

|    |               |               |
|----|---------------|---------------|
|    | FC            | FD            |
| MC | $\rightarrow$ | $\rightarrow$ |
| MD | $\downarrow$  | $\leftarrow$  |

617

(c)

615  $c > d$  and  $C < D$

single ESS: male-only care

|    |               |               |
|----|---------------|---------------|
|    | FC            | FD            |
| MC | $\rightarrow$ | $\rightarrow$ |
| MD | $\downarrow$  | $\uparrow$    |

618

619 (d)

620  $c < d$  and  $C < D$

621 single ESS: biparental desertion

622 Prisoner's Dilemma

|    |               |               |
|----|---------------|---------------|
|    | FC            | FD            |
| MC | $\rightarrow$ | $\rightarrow$ |
| MD | $\downarrow$  | $\rightarrow$ |

623

624

(e)

620  $c > d$  and  $C > D$

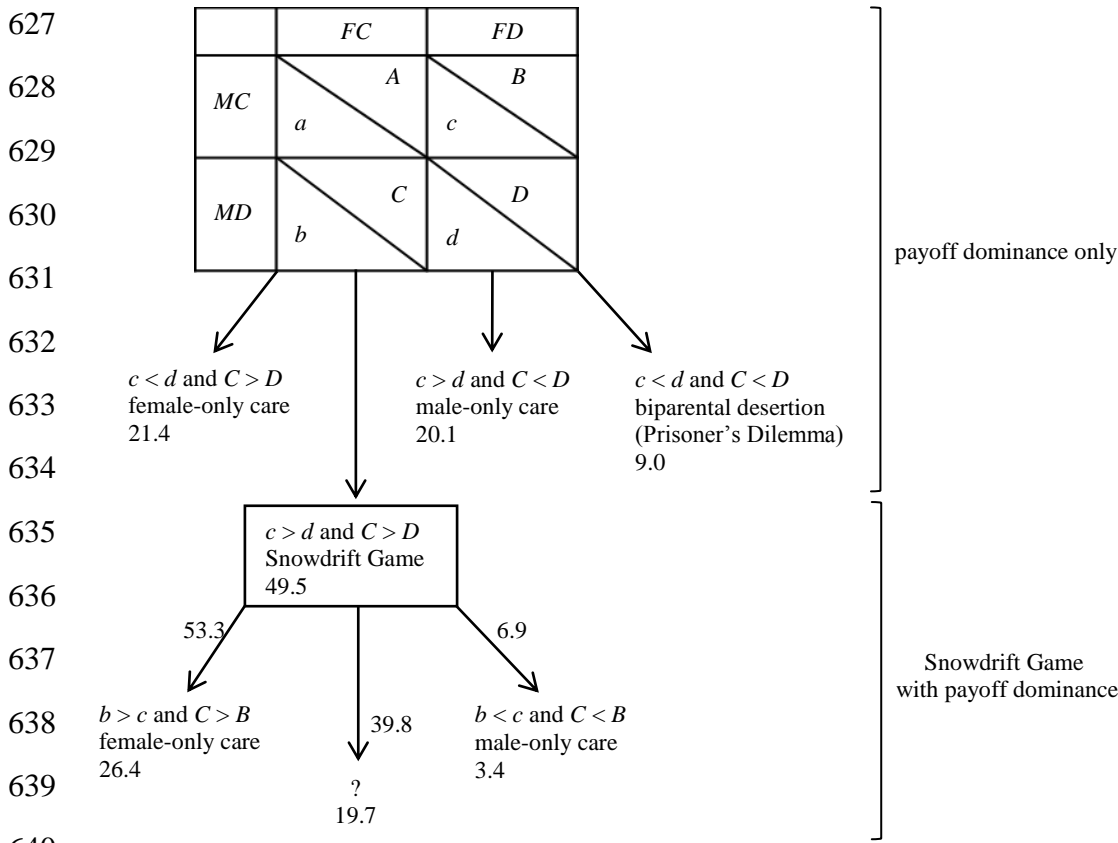
two ESSs: female-only care and male-only care

Snowdrift Game

|    |               |               |
|----|---------------|---------------|
|    | FC            | FD            |
| MC | $\rightarrow$ | $\rightarrow$ |
| MD | $\downarrow$  | $\uparrow$    |

625 Table 3.

626 (a)



641 (b)

|  | female-only care (%)             | male-only care (%)               | biparental desertion (%)         |
|--|----------------------------------|----------------------------------|----------------------------------|
| observed parental care $\pm$ CI                            | <b>47.4 <math>\pm</math> 8.6</b> | <b>13.5 <math>\pm</math> 6.0</b> | <b>39.1 <math>\pm</math> 8.4</b> |
| <i>(n = 534 pairs)</i>                                     |                                  |                                  |                                  |
| if ? = biparental desertion                                | <b>47.8</b> (21.4 + 26.4)        | <b>23.5</b> (20.1 + 3.4)         | <b>28.7</b> (9.0 + 19.7)         |
| if ? = female-only care                                    | <b>67.5</b> (21.4 + 26.4 + 19.7) | <b>23.5</b> (20.1 + 3.4)         | <b>9.0</b> (9.0)                 |
| if ? = 50% male-only care and 50%<br>female-only care      | <b>57.6</b> (21.4 + 26.4 + 9.9)  | <b>33.4</b> (20.1 + 3.4 + 9.9)   | <b>9.0</b> (9.0)                 |
| if ? = biparental desertion and<br>attractive males desert | <b>49.1</b> (24.4 + 24.7)        | <b>8.6</b> (7.5 + 1.1)           | <b>42.3</b> (22.6 + 19.7)        |

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