1 # Female-female competition is influenced by forehead patch

2 # expression in pied flycatcher females

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23 concise title: forehead patch and female intrasexual competition

24 **Abstract**

25 There is increasing evidence that sexual selection operates in females and not only in males.

26 However, the function of female signals in intrasexual competition has been little studied in

27 species with conventional sex roles. In the Iberian populations of the pied flycatcher (*Ficedula*

28 *hypoleuca*), some females express a white forehead patch, a trait that in other European

29 populations only males exhibit and has become a classical example in studies of sexual

30 selection. Here, we investigated whether the expression of this trait plays a role in female-

31 female competition during early breeding stages. To test this hypothesis, we simulated

32 territorial intrusions by challenging resident females with stuffed female decoys expressing or

33 not a forehead patch. We found that resident females directed more attacks per trial and

34 maintained closer distances to non-patched decoys than to patched ones. Also, patched

35 females were more likely to attack the decoy than non-patched females. Interestingly, females

36 were more aggressive against the decoys when their mate was absent. This may indicate that

37 females relax territory vigilance in the presence of their mate or that males interfere in the

38 interaction between competing females. The behavior of resident males was also observed,

39 although it was not affected by decoy's patch expression. Our findings suggest that the

40 forehead patch plays a role in female intrasexual competition. If the forehead patch signals

41 fighting ability, as it does in males, we may interpret that non-patched females probably

42 avoided repeating costly agonistic encounters with the most dominant rivals.

43

44 **Keywords** Aggression, Communication, Female competition, Female ornamentation,

45 Intrasexual selection, *Ficedula hypoleuca*, Sexual selection, Signaling

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2

Introduction

Sexual selection in species with conventional sex roles has been traditionally thought to act mainly in males because of sex differences in gamete size, mating success and parental investment (Bateman 1948; Trivers 1972). However, there is an increasing interest in the view that sexual selection also operates on females (reviewed by Amundsen 2000; LeBas 2006; Kraaijeveld et al. 2007; Clutton-Brock 2007, 2009; Clutton-Brock and Huchard 2013). Yet, the extent of this selection and the mechanisms involved are less well understood. For instance, where females have developed secondary sexual characters, it is often uncertain whether they are used to attract males, induce male parental investment or to compete with other females for breeding resources (Clutton-Brock 2007).

The importance of female-female competition has received little attention, probably because it is usually less conspicuous than competition among males (Stockley and Campbell 2013). However, because of their greater energetic investment in gametes and parental care, females are expected to compete over mate quality (Petrie 1983) or over resources that directly influence the probability of mating or maintaining a monogamous pair-bond (Slagsvold and Lifjeld 1994). This is crucial in socially monogamous species, where pair bonds persist throughout a breeding season and sometimes for life. Therefore, sexual selection (or more generally, natural selection; Clutton-Brock and Huchard 2013) may favor the evolution of female traits that signal their capacity to outcompete other females for indirect genetic benefits or for direct benefits held by preferred males (e.g., territories, nesting sites or paternal care; Servedio et al. 2013). Indeed, there is evidence that female visual, odor or vocal signals are involved in female intrasexual competition in various taxa (see reviews by Tobias et al. 2012; Clutton-Brock and Huchard 2013; Stockley and Campbell 2013; Stockley et al. 2013). However, despite recent interest in the evolution of female ornamentation and weaponry, there are very few demonstrations compared with male signals (Rosvall 2011).

3

72   Here, we explored the role of a female plumage trait in female-female competition in a

73   socially monogamous songbird, the pied flycatcher *Ficedula hypoleuca*. This is a suitable

74   species to study female intrasexual competition because mated females are highly aggressive

75   towards intruding females during initial breeding stages (i.e., nest-building and egg laying

76   periods; Breiehagen and Slagsvold 1988; Lifjeld and Slagsvold 1989). This behavior has been

77   proposed as a mechanism to protect male parental investment, given that there is facultative

78   polygyny in this species (Slagsvold et al. 1992; Slagsvold and Lifjeld 1994). Competition among

79   females for breeding sites (nest-boxes) can be rough and even lethal, especially during the

80   nest-building period, and we have observed that females may be evicted from their nest-box

81   by other females even while incubating eggs and brooding hatchlings (J. Morales et al.,

82   personal observation). Aggressive encounters between females could favor the evolution of

83   sexual signaling (or more generally, social signaling) in females just as in males (West-Eberhard

84   1983).

85   In Iberian populations of the pied flycatcher almost half of the females express a white

86   forehead patch (41% in our study population between 1997 and 2006, n=596 females), a

87   plumage trait that all males exhibit (see Fig. 1). In some cases, females' patches are as large as

88   the largest patch in males (Potti 1993; Morales et al. 2007). This character has become a

89   classical example in studies of sexual selection on males in *Ficedula* flycatchers (see for

90   instance Gustafsson et al. 1995; Sanz 2001; Qvarnström et al. 2006). Forehead patch size in

91   males signals fighting ability and predicts the outcome of male competition over territories

92   (Pärt and Qvarnström 1997; Qvarnström 1997; Järvistö et al. 2013). In Iberian pied flycatchers,

93   females prefer mates with larger forehead patch sizes (Potti and Montalvo 1991; but see

94   Galván and Moreno 2009) and experimentally reduced male patch size results in lower

95   female's reproductive investment (Osorno et al. 2006). In females, forehead patch expression

96   is heritable (Potti 1993; Potti and Canal 2011) and positively related to age (Potti 1993; Potti et

97 al. 2013), although many old females do not express the trait (29% of females older than 4

98 years; Morales et al. 2007). Also, patch expression in females is correlated with lower risk of

99 haemoparasite infections (Potti and Merino 1996) and with greater yearly production of

100 fledglings (Morales et al. 2007; Potti et al. 2013). A long-term study shows that patched

101 females invest more in reproduction at early ages than non-patched ones, but at advanced

102 ages they seem to pay a cost for expressing the ornament in terms of decreased fledging

103 success, which could be indicative of advanced senescence (Potti et al. 2013). Interestingly,

104 experimental (Moreno et al. 2013a) and correlative (Moreno et al. 2013b) evidence indicates

105 that patched females suffer higher oxidative tissue damage. Thus, female's forehead patch

106 could function as a badge of oxidative status. However, to date, the function of female's

107 forehead patch as a badge of social status remains untested experimentally.

108   We hypothesized that the female's forehead patch plays a role as a badge of status in

109 female-female competition. To test this hypothesis we performed simulated territorial

110 intrusion tests with stuffed female decoys either without patch or with a patch with the largest

111 size recorded for females in the study population. We may predict very different outcomes.

112 During social conflict, subordinate individuals can use information from signals of fighting

113 ability and previous encounters to avoid repeatedly entering into unprofitable fights with

114 higher ranked individuals (reviewed by Cant and Young 2013). Thus, resident females (both

115 patched and non-patched) should avoid encounters with patched decoys. Conversely, patched

116 decoys may elicit more aggressiveness from the residents because they are perceived as larger

117 threats (as found in male collared flycatchers *Ficedula albicollis* for the wing patch size;

118 Garamszegi et al. 2006). Additionally, signal asymmetry between opponents could play a role

119 in female-female competition (see Griggio et al. 2010, in the rock sparrow *Petronia petronia*),

120 and we may thus expect an interaction between resident female's and decoy's patch

121 expression. On the one hand, resident patched females could be more aggressive against non-

122 patched decoys than against patched ones (see Järvi and Bakken 1984, in the great tit *Parus*

123 *major*). On the other hand, matched contestants may show the greatest tendency for

124 escalation (Parker 1974; see Midamegbe et al. 2011, in the blue tit *Cyanistes caeruleus*).

125 Finally, resident females could rely on their absolute badge size rather than relative to their

126 opponents (see Pryke and Andersson 2003, in red-shouldered widowbirds *Euplectes axillari*).

127

128 **Material and methods**

129 *Study population*

130 The study was conducted in 2006 in a population of pied flycatchers breeding in 300 wooden

131 nest-boxes in a deciduous forest of Pyrennean oak (*Quercus pyrenaica*), at an elevation of

132 1200 m in the locality of Valsaín, Segovia, central Spain (40°53'N, 4°01'W). The pied flycatcher

133 shows a high degree of sexual dimorphism during the breeding season. Although variable

134 among individuals, males in Iberian populations have a contrasting white and black plumage,

135 while females are dull light brown. Thus, females either expressing or not a white forehead

136 patch are visually distinct from males (see Fig. 1).

137

138 *Simulated territorial intrusions*

139 Nest-boxes were checked every three days from 1st April to 10th May to detect the initiation

140 and progress of nest construction, indicative of the establishment of a breeding pair. When

141 nest construction was almost complete (i.e., just before the nest showed the rounded and

142 closely knit nest cup), resident females were challenged with a pied flycatcher female decoy

143 placed on top of the nest-box to simulate a territorial intrusion. As decoys, we used two

144 stuffed females that originally lacked a forehead patch. Both were found naturally dead in the

145 population in previous years and were preserved frozen at - 20°C until stuffing. They were

146 mounted in neutral lifelike perched postures. We made a removable patch by gluing pieces of

6

147 white feathers cut from a stuffed female's wing patch on a cardboard of 9.9 x 5.7 mm (width x

148 height; the maximum female forehead patch size recorded in the study population in the

149 previous year). Decoy's phenotype (presence/absence of forehead patch) was randomly

150 assigned in the first trial of each nest. When assigned, the fake patch was fixed on the decoy's

151 forehead with a thin metal wire concealed under head plumage. We used two different stuffed

152 females to minimize pseudo-replication (Hurlbert 1984), as commonly used in bird studies to

153 perform territorial intrusion tests (e.g., Vergara et al. 2007, 2013; Vergara and Fargallo 2007;

154 Kingma et al. 2008; Pärn et al. 2008). Apparently, the resident pair recognized stuffed decoys

155 as conspecifics, since not only some resident females attacked them but also around 20% of

156 resident males tried to copulate with the stuffed decoys (see results). On average, two days

157 (mean ± SE: 2.1 ± 0.3; range 1-7 days) after the first test, females were challenged for a second

158 time with the same decoy but with the alternative patch phenotype to that previously

159 assigned. Thus, the two decoys presented to a given female only differed in forehead patch

160 expression (presence/absence). All observations were performed before first egg laying (on

161 average, 7.5±0.5 days before). Thus, all females were likely observed during their fertile period

162 (see Birkhead and Møller 1992; Lifjeld et al. 1997).

163   We were able to observe the behavior of 38 individual females twice (with patched

164 and non-patched decoys) and of 6 once (3 with patched decoys and 3 with non-patched ones).

165 Some females did not appear during the entire trial and we supposed they were away from the

166 territory and did not perceive the stimuli of the intrusion. Therefore, we repeated the

167 corresponding test on the following day, but in 6 cases the focal female never appeared. Out

168 of the 82 territorial trials, the resident male turned up in 67 (32 with patched decoys and 35

169 with non-patched ones) and was absent in 15. Later in the season we captured 97% of focal

170 males in their nest-box and none of them was found to hold more than one territory.

7

171   After placing the decoy on top of the nest-box, we retreated to a hidden observation

172   position about 20 m away. Observations were performed with the aid of binoculars and

173   recorded in real time in a digital voice recorder (Olympus VN-960PC). All tests were carried out

174   from 7:00 am to 12:30 pm, because activity is usually reduced after this time. Although our aim

175   was to record female behavioral responses, we also observed the behavior of males. We

176   recorded the following behavioral variables for females and males: latency time to first

177   appearance (min), presence/absence of attacks (pecking and flight attacks with or without

178   direct contact), number of attacks per trial, and the degree of approach to the decoy, which

179   was recorded according to three easily observed categories: 0=the focal bird did not approach

180   the decoy, nor did it enter the nest-box or fly around it; 1=the focal bird did not approach the

181   decoy but entered the nest-box or flew around its entrance; 2=the focal bird clearly

182   approached the decoy either perching just beside it on the nest-box or performing attacks

183   against it with or without contact. During the tests we also noted that 19 individual females

184   expressed a distinctive forehead patch while 25 did not (this was later confirmed at capture).

185   For males, we additionally recorded presence/absence of copulation attempts and

186   presence/absence of enticement calls (hereafter song). We did not record the male's degree of

187   approach to the decoy because of its ambiguous interpretation, for it may be either a sign of

188   intimidation or enticement.

189   Following previous studies in pied (Breiehagen and Slagsvold 1988; Rätti 2000) and

190   collared (Hegyi et al. 2008) flycatchers, we assumed that females' degree of approach to the

191   decoy as well as direct attacks were accurate estimates of her aggressive motivation against

192   the decoy. We may interpret that females with long latency to arrive were on average less

193   engaged in territory vigilance. Pied flycatchers defend a rather small territory around the

194   immediate vicinity of the nest (median radius 10 m; Lundberg and Alatalo 1992). Although

195   feeding trips can sometimes be up to 100 m away, males and females seem to forage usually

196   within a radius of 50 m around the nest (von Haartman 1956; Maps 7 and 8). Females are able

197   to detect intruder females at a distance of at least 40 m (Rätti 2000). Hence, it is likely that

198   most females in our study were able to detect the decoy soon after placing it on top of the

199   nest-box, although we cannot exclude the possibility that some of them were far away from

200   the territory. Observations lasted 15 minutes, although in 22 tests they were finished before

201   either because the female (n=17) or the male (n=2) knocked the decoy off the nest-box after

202   direct contact or because of heavy rain (n=3) (mean ± SE of total observation length: 12.6 ±

203   0.5; range: 0.5 - 15.0 min). Among the 17 females that knocked the decoy off the nest-box, 16

204   performed the highest number of attacks per trial registered. Thus, shorter duration length in

205   most of these observations did not preclude the presence/absence of female's attack, number

206   of attacks and degree of approach to the decoy. Excluding the five shorter observations with

207   no female attacks led to the same qualitative results (results not shown but available upon

208   request).

209

210   *Data analyses*

211   We performed linear mixed effects models in SAS 9.2 (SAS Institute Inc. 2003) for all behavioral

212   female traits with nest-box identity as random factor. The presence/absence of patch in the

213   decoy and the resident female were included as fixed factors to test for their effect and the

214   interaction between both on female behavior. Additionally, the models included the

215   presence/absence of the male and decoy's identity (stuffed female no. 1 or 2) as fixed

216   categorical factors. Observation length (total observation length minus female's latency time)

217   was also included as an independent variable (except in the model of latency time), given that

218   females varied in the time available to interact with the decoy. We used linear mixed models

219   (MIXED procedure) for latency time, which was logarithmically transformed ($\log_{10} + 1$) to

220   normalize its distribution, and generalized linear mixed models (GLIMMIX procedure) for the

221   presence/absence of attacks (binomial distribution), the number of attacks per trial (Poisson

222   distribution) and the degree of approach to the decoy (multinomial distribution). We did not

223   calculate attack rate (number of attacks per trial divided by observation length), because the

224   relationship between the number of attacks and observation length was not isometric (see

225   García-Berthou 2001, for a review on the use of ratios).

226   To analyze male behavior, we performed similar linear mixed models with nest-box

227   identity as random factor and the following explanatory variables: female's and decoy's

228   forehead patch expression, the interaction between both, decoy's identity and observation

229   length (total observation length minus male's latency time). Additionally, we performed two

230   mixed models with binomial distribution to analyze the presence/absence of copulation and

231   song. Values for female and male behavior are expressed as means ± SE.

232   Model selection was performed by an information theoretical approach. For each

233   female and male behavioral trait we run all possible models and ranked them according to

234   their Akaike's Information Criterion values modified for finite sample size (AICc). In generalized

235   linear mixed models (GLIMMIX procedure), we obtained AICc with Laplace estimation method

236   (as recommended by Bolker et al. 2008). The Akaike weights (w_i) for each model were

237   calculated (Anderson et al. 2000). Given that none of the models showed a $w_i > 0.90$ (see

238   Tables A1 and A2), we performed model averaging as recommended by Anderson et al. (2000)

239   and Burnham and Anderson (2002). Then, we calculated averaged estimates (b) and standard

240   errors (SE) for all explanatory variables weighted by the w_i using only those most probable

241   models (i.e., those models with ΔAICc < 2; Burnham and Anderson 2002). The sum of w_is of the

242   models where a certain explanatory variable was included quantified its relevance. We also

243   calculated the amount of deviance explained ($D^2 = 100*$(deviance of the null model - residual

244   deviance)/ deviance of the null model; Zuur et al. 2009) by the most probable models weighed

245   by the w_i.

246

Results

Female behavior

Females were first observed in the territory on average after 3.90±0.50 minutes of the

beginning of the observation, but female's latency time of first appearance was not strongly

explained by any variable (Table 1). Although female's patch expression showed relatively high

w_i, the averaged model explained very little amount of deviance (D^2) in female's latency time

(Table A1).

Females attacked the decoy in 36 out of 82 trials. Some females attacked as soon as

they appeared in the territory, while others did it in the very last minute of the observation

(timing of first attack: 6.12 ± 0.85 min). Male presence/absence and female's patch expression

had the strongest influence on the probability of attacks (Table 1). Male absence increased

twofold the probability of female attack (12 out 15 trials when the male was absent vs. 24 out

of 67 when the male was present). Patched females were more likely to attack than non-

patched ones (they attacked in 20 trials out of 35, while non-patched females attacked in 16

trials out of 47).

The number of attacks per trial was best explained by male presence/absence and

decoy's patch expression (Table 1). Females performed on average more attacks in trials in

which their mate was absent than when it was present (Fig. 2a). Also, non-patched decoys

received on average more attacks per trial than patched ones (Fig. 2b). Observation length had

relatively high w_i suggesting a negative effect on the number of attacks (Table 1), which is not

surprising given that some observations were interrupted when females knocked the decoy off

the nest-box.

The female's degree of approach to the decoy was best explained by male

presence/absence and decoy's patch expression (Table 1). Females approached the decoys to

271   a higher degree when their mate was absent than when it was present (male absent: degree of

272   approach 0 (n=1), 1 (2), 2 (12); male present: 0 (16), 1 (18), 2 (33)). Also, females approached

273   non-patched decoys to a higher degree than patched ones (non-patched decoy: degree of

274   approach 0 (n=6), 1 (9), 2 (27); patched decoy: 0 (11), 1 (11), 2 (18)).

275

276   *Male behavior*

277   Female's patch expression had the strongest effect on male's latency time of first appearance

278   (Table 2). Males mated with patched females showed up later during the trials than those

279   mated with non-patched ones (respectively, mean ± SE of non-transformed data: 4.85 ± 0.66

280   and 2.62 ± 0.56 min). Decoy's identity also had high influence on male's latency time (Table 2).

281   Males appeared earlier in the trials of the stuffed female no. 1.

282   Males attacked the decoy in 15 out of 67 trials, sang in 19 and performed copulation

283   attempts in 13. However, the averaged models explained very little amount of deviance,

284   especially in the number of attacks and in the presence/absence of song and copulation. Only

285   decoy's identity had influence on the probability and number of male's attacks (Table 2). The

286   stuffed female no. 1 was more prone to be attacked and with more intensity by males. The

287   presence/absence of copulation and song were not strongly affected by any explanatory

288   variable (Table 2).

289

290   *Interaction between mates*

291   We also observed that the resident pair interacted in various ways. The male clearly attacked

292   its mate in 5 trials. Conversely, females never attacked their mate, but in 2 trials they attacked

293   the decoy just when the male started copulation attempts with it. Finally, in 9 trials the male

294   and the female chased each other or flew around the nest-box together with no sign of

295   aggression.

Discussion

We found that resident females expressing a forehead patch were more likely to attack the

decoys than non-patched females. However, irrespective of their own patch expression,

resident females directed more attacks per trial against non-patched decoys than against

patched ones. Also, they approached non-patched decoys to a higher degree than patched

ones. Overall, these results support a signaling role for the forehead-patch in female-female

interactions. If the forehead patch signals dominance and fighting ability, as it does in males

(e.g., Järvistö et al. 2013), patched decoys were probably perceived by resident females as the

highest ranked individuals, given that we provided them with an artificial patch with the

largest size recorded for females in the study population. We may thus interpret that high-

ranked (patched) females were more willing to perform a first attack against intruders of any

phenotype, but both patched and non-patched females avoided repeated attacks against the

highest ranked rivals. We may have expected that patched decoys were considered as larger

threats and elicited more aggressiveness from the residents (see Garamszegi et al. 2006), at

least from patched resident females of presumably high rank. However, given that fighting is

costly for both opponents (Maynard-Smith and Price 1973; Senar 2006), it is likely that resident

females just tried to avoid unprofitable fights with the most dominant individuals (see Cant

and Young 2013). An interaction between female's own patch and decoy's patch expression

would have suggested that females were able to perceive their own patch phenotype and to

match their fighting ability with that of their contestants (see for instance, Griggio et al. 2010).

One possibility for the lack of an interaction effect is that females relied on their absolute

patch size rather than relative to their opponents (see Pryke and Andersson 2003).

Alternatively, the fact that patched decoys had the largest badge may have obscured the

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320 interaction effect. Manipulating female's patch expression as well as decoy's would shed light

321 on this issue (see Searcy and Beecher 2009, for a review of aggressive signals).

322   The presence/absence of the mate was the most important factor affecting females'

323 behavior against the decoy. Male absence increased female aggressiveness in almost all the

324 behavioral variables studied, suggesting that females take on extra costs of territoriality when

325 their mates are not present. If female-female competition was directed at guarding the male's

326 parental investment (Slagsvold and Lifjeld 1994) or at avoiding male's extra-pair copulations

327 we may have expected higher aggressiveness in the presence of the male. One possible

328 explanation for the opposite trend is that males, when present, have a more prominent role in

329 territory defence than females, probably because of their bigger size that confer a physical

330 advantage. Another possibility is that females were more interested in the male (when

331 present) than in fighting the decoy, or that the male actively interfered to circumvent female-

332 female aggression (see Slagsvold and Lifjeld 1994). We registered fourteen interactions within

333 the resident pair in which the male and the female flew around together or the male was

334 observed attacking its mate. Only in three out of these fourteen trials the females were

335 aggressive against the decoy, which could support that intra-pair interactions prevented

336 female-female aggression. Another possibility is that the most aggressive females were paired

337 with males that spent less time guarding their mate and territory. Manipulation of male

338 presence would be needed to understand these results. In any case, our findings highlight the

339 importance of controlling for the mate's presence when observing female behavior.

340   Males showed up later during the trials when mated with patched females. This may

341 indicate that males were less engaged in territory vigilance when paired with a dominant

342 female that was able to evict intruders. It may also suggest that males invested less time in

343 guarding patched females in their fertile period than non-patched ones. However, data

344 collected in the study population indicate that extra-pair copulations are not related to

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345   females' forehead patch expression (J. Moreno, unpublished data). Additionally, we found no

346   evidence of a male preference for decoy's forehead patch, since neither song nor copulation

347   attempts were related to decoy's patch phenotype. Yet, we cannot exclude the possibility that

348   males do show a preference for patched females during the mating period, as correlative

349   evidence suggests (i.e., assortative mating; Potti and Merino 1996). Nevertheless, although the

350   preference for patched females may confer certain benefits to males in terms of health and

351   reproductive success (Potti and Merino 1996; Morales et al. 2007), too highly dominant

352   females may not necessarily be more fecund, given that patch expression implies costs in

353   terms of oxidative stress (Moreno et al. 2013a, b). In that case, the optimal strategy for males

354   would be to develop stabilizing mating preferences for female's forehead patch to avoid

355   females that risk their fecundity for signaling (Chenoweth et al. 2006; see also Morales et al.

356   2012 in seabirds). Finally, various male behavioral traits were affected by decoy's identity.

357   Although the decoys used were apparently similar to a human observer and were mounted in

358   the same position, they might have differed in features that we did not acknowledge.

359   Female intrasexual competition should occur when variation in male quality is high or

360   access to reproductive resources is limited (Amundsen 2000). Our results support that

361   reproductive resources (nest-site or mate) are valuable for females close to egg laying, since

362   many of them behaved aggressively against the decoys. Nest-sites are crucial for non-

363   excavating hole-nesters (Newton 1994) and their loss may imply a total seasonal reproductive

364   failure in a short-lived migratory bird with short breeding seasons like the pied flycatcher.

365   Competition for nest-sites in females may be similar to selection in males for breeding

366   resources (territories and females), or be related to social selection for non-reproductive

367   resources like food or shelter (West-Eberhard 1983). Nest-sites are as important as mates for

368   reproduction when they are limited, and thus there should be stiff competition for them

369   leading to signals of status also in females (Rosvall 2011; Tobias et al. 2012). Alternatively,

370   females expressing a forehead patch could mimic young males (which are mostly brown in

371   their first year) and thus avoid competitive fights with other females and males. However, this

372   is unlikely since no female-like light brown males exist in Iberian populations, contrary to pied

373   flycatchers in other European populations (see Potti and Merino 1996; see also Fig. 1).

374   Moreover, females are recognized as females by their conspecifics independently of their

375   forehead patch expression (Sætre and Slagsvold 1992).

376   A recent study has shown that the experimental addition of a fake forehead patch to

377   females without one in the study population increases the bearer's oxidative tissue damage

378   (Moreno et al. 2013a). Although the physiological mechanism remains to be elucidated, the

379   link between oxidative damage and patch expression is probably mediated by social control

380   (see Safran et al. 2008). Females without patches may avoid high oxidative damage implied by

381   social interactions, but might lose breeding opportunities when competition for breeding

382   resources is strong (Moreno et al. 2013a, b). Interestingly, the forehead patch is expressed in

383   pied flycatcher females only in southern European populations. One possibility is that selection

384   on the forehead patch is higher in southern populations than farther north because of a

385   stronger negative effect of oxidative stress and parasites in southern latitudes (Moreno 2004).

386   Additionally, the low availability of suitable breeding habitat and its high degree of

387   fragmentation in the Iberian Peninsula could facilitate higher territoriality and stronger sexual

388   selection in southern populations.

389   In conclusion, our results suggest that a trait that has become a classical example in

390   studies of male intrasexual selection plays also a role in female-female contests, as found in

391   other socially monogamous bird species (e.g., the rock sparrow: Griggio et al. 2007, 2009; the

392   diamond firetail, *Stagonopleura guttata*: Crowhurst et al. 2012). Our results oppose to the

393   classical view portraying females as merely passive and choosy, which is being re-evaluated in

394   the light of recent research (Clutton-Brock and Huchard 2013).

395

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Ethical standards

The present study was performed under the license of Dirección General del Medio Natural

(Junta de Castilla y León, Spain) and complies with the Spanish current laws and with

ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research (2012).

The authors declare that they have no conflict of interest.

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562 **Table 1** Averaged linear mixed models for female behavioral traits with their weighed D^2.

563 Akaike weights (w_i) and weighted averaged estimates (b) and standard errors (SE) are shown

564 for the explanatory variables included in the top ranked models (see model averaging in Table

565 A1). For categorical explanatory variables, the weighted estimate and SE of the category

566 specified between parentheses are shown. High w_i are shown in bold

567

female behavioral trait	D^2	explanatory variable	w_i	b	SE
latency time (log-min)	3.11	female's patch (absent)	0.74	-0.13	0.067
		male (absent)	0.26	-0.032	0.030
attacks (presence/absence)	13.88	male (absent)	**1.00**	1.84	0.73
		female's patch (absent)	**1.00**	-1.20	0.64
		decoy's patch (absent)	0.47	0.26	0.29
		female's x decoy's patch	0.16	0.17	0.17
		observation length	0.16	-0.006	0.008
no. of attacks	10.90	male (absent)	**1.00**	1.55	0.36
		decoy's patch (absent)	**1.00**	0.41	0.19
		observation length	0.79	-0.036	0.017
		decoy's identity (no. 1)	0.68	0.50	0.27
		female's patch (absent)	0.44	-0.25	0.19
degree of approach	9.04	male (absent)	**1.00**	-3.12	1.28
		decoy's patch (absent)	**1.00**	-0.73	0.66
		female's patch (absent)	0.27	0.15	0.24

568

569

570 **Table 2** Averaged linear mixed models for male behavioral traits. Akaike weights (w_i) and

571 weighted averaged estimates (b) and standard errors (SE) are shown for the explanatory

572 variables included in the top ranked models (see model averaging in Table A2). For categorical

573 explanatory variables, the weighted estimate and SE of the category specified between

574 parentheses are shown. High w_i are shown in bold

575

male behavioral trait	D^2	explanatory variable	w_i	b	SE
latency time (log-min)	17.22	female's patch (absent)	**1.00**	-0.21	0.088
		decoy's identity (no. 1)	0.84	-0.16	0.072
		decoy's patch (absent)	0.23	0.014	0.020
attacks (presence/absence)	8.35	decoy's identity (no. 1)	**1.00**	1.03	0.45
		observation length	0.31	0.016	0.022
no. of attacks	2.52	decoy's identity (no. 1)	0.77	0.93	0.52
		observation length	0.27	0.011	0.011
copulation (presence/absence)	0.52	female's patch (absent)	0.20	-0.12	0.12
		decoy's identity (no. 1)	0.15	-0.060	0.095
		observation length	0.15	0.007	0.011
		decoy's patch (absent)	0.14	-0.042	0.086
song (presence/absence)	1.43	decoy's identity (no. 1)	0.41	-0.53	0.43
		female's patch (absent)	0.29	0.24	0.28
		decoy's patch (absent)	0.13	-0.066	0.10

576

577

578   Figure caption

579   **Fig. 1a)** Adult pied flycatcher female without forehead patch (credit J. Morales); **1b)** adult pied

580   flycatcher female with a forehead patch (left) and male showing the typical breeding plumage

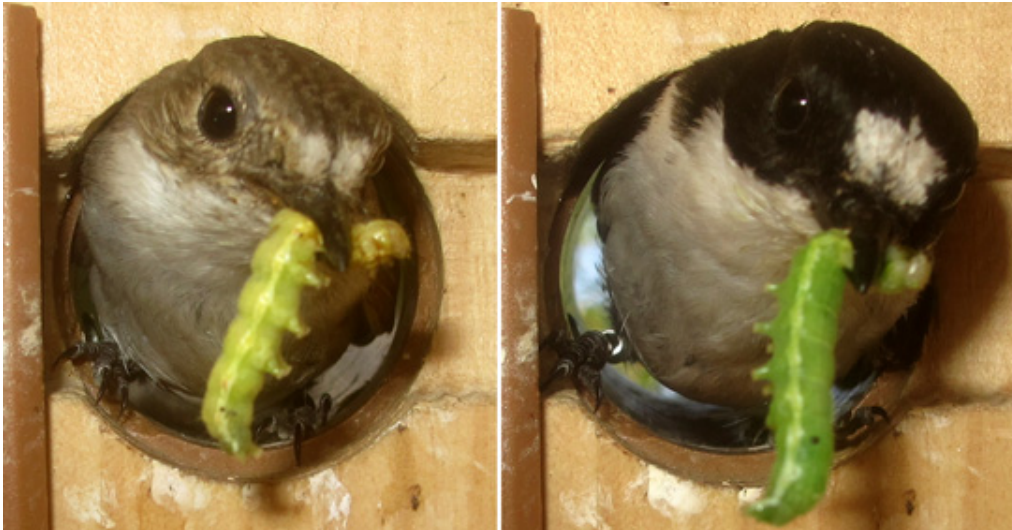581   (right) (credit OG)

582

583   **Fig. 2** Number of attacks per trial performed by resident pied flycatcher females against the

584   female decoy in relation to: **a)** the presence/absence of the male; **b)** the decoy's forehead

585   patch expression. Values are medians with 25-75th percentile (error bars)
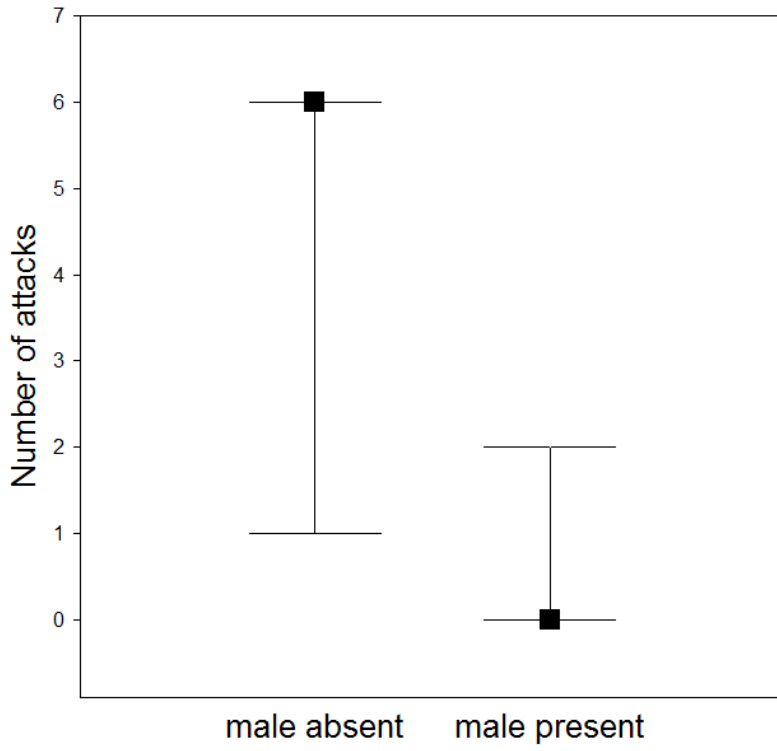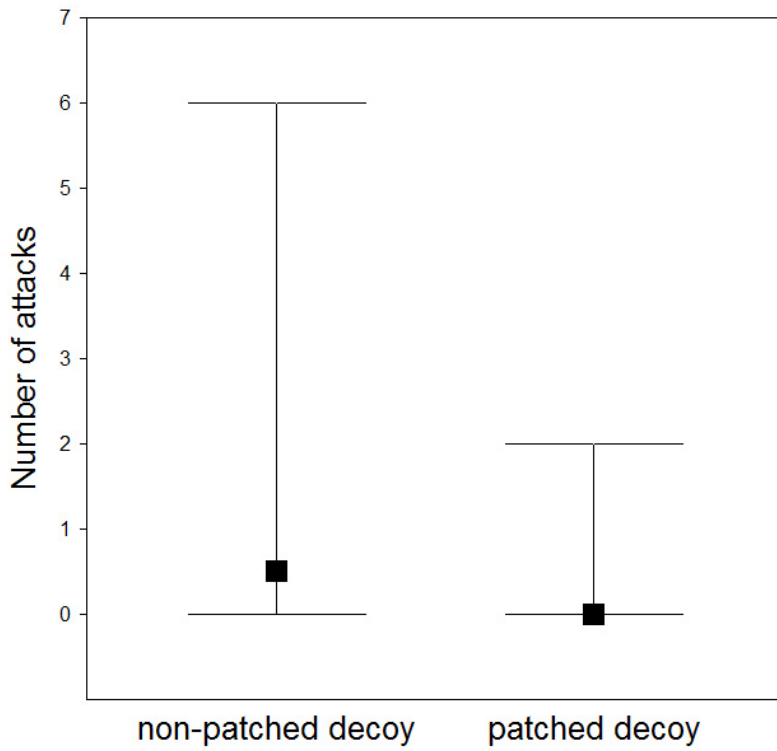
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587

588   Fig. 1a

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590   Fig. 1b

591

592

593   Fig. 2a

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595   Fig. 2b