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Female-female competition is influenced by forehead patch expression in pied flycatcher females

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Abstract There is increasing evidence that sexual selection operates in females and not only in males. However, the function of female signals in intrasexual competition has been little studied in species with conventional sex roles. In the Iberian populations of the pied flycatcher (*Ficedula hypoleuca*), some females express a white forehead patch, a trait that in other European populations, only males exhibit and has become a classical example in studies of sexual selection. Here, we investigated whether the expression of this trait plays a role in female-female competition during early breeding stages. To test this hypothesis, we simulated territorial intrusions by challenging resident females with stuffed female decoys expressing or not a forehead patch. We found that resident females directed more attacks per trial and maintained closer distances to non-patched decoys than to patched ones. Also, patched females were more likely to attack the decoy than non-patched females. Interestingly, females were more aggressive against the decoys when their mate was absent. This may indicate that females relax territory vigilance in the presence of their mate or that males interfere in the interaction between competing females. The behavior of resident males was also observed, although it was not affected by decoy's patch expression. Our findings suggest that the forehead patch plays a role in female intrasexual competition. If the forehead patch signals fighting ability, as it does in males, we may interpret that non-patched females probably avoided repeating costly agonistic encounters with the most dominant rivals.

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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).

Here, we explored the role of a female plumage trait in female-female competition in a socially monogamous songbird, the pied flycatcher *Ficedula hypoleuca*. This is a suitable species to study female intrasexual competition because mated females are highly aggressive toward intruding females during initial breeding stages (i.e., nest-building and egg-laying periods; Breiehagen and Slagsvold 1988; Lifjeld and Slagsvold 1989). This behavior has been proposed as a mechanism to protect male parental investment, given that there is facultative polygyny in this species (Slagsvold et al. 1992; Slagsvold and Lifjeld 1994). Competition among females for breeding sites (nest boxes) can be rough and even lethal, especially during the nest-building period, and we have observed that females may be evicted from their nest box by other females even while incubating eggs and brooding hatchlings (Morales et al., personal observation). Aggressive encounters between females could favor the evolution of sexual signaling (or more generally, social signaling) in females just as in males (West-Eberhard 1983).

In Iberian populations of the pied flycatcher, almost half of the females express a white forehead patch (41 % in our study population between 1997 and 2006, *n*=596 females), a plumage trait that all males exhibit (see Fig. 1). In some cases, females' patches are as large as the largest patch in males (Potti 1993; Morales et al. 2007). This character has become a classical

example in studies of sexual selection on males in *Ficedula* flycatchers (see for instance, Gustafsson et al. 1995; Sanz 2001; Qvarnström et al. 2006). Forehead patch size in males signals fighting ability and predicts the outcome of male competition over territories (Pärt and Qvarnström 1997; Qvarnström 1997; Järvistö et al. 2013). In Iberian pied flycatchers, females prefer mates with larger forehead patch sizes (Potti and Montalvo 1991; but see Galván and Moreno 2009), and experimentally reduced male patch size results in lower female's reproductive investment (Osorno et al. 2006). In females, forehead patch expression is heritable (Potti 1993; Potti and Canal 2011) and positively related to age (Potti 1993; Potti et al. 2013), although many old females do not express the trait (29 % of females older than 4 years; Morales et al. 2007). Also, patch expression in females is correlated with lower risk of hemoparasite infections (Potti and Merino 1996) and with greater yearly production of fledglings (Morales et al. 2007; Potti et al. 2013). A long-term study shows that patched females invest more in reproduction at early ages than non-patched ones but, at advanced ages, they seem to pay a cost for expressing the ornament in terms of decreased fledging success, which could be indicative of advanced senescence (Potti et al. 2013). Interestingly, experimental (Moreno et al. 2013a) and correlative (Moreno et al. 2013b) evidence indicates that patched females suffer higher oxidative tissue damage. Thus, female's forehead patch could function as a badge of oxidative status. However, to date, the function of female's forehead patch as a badge of social status remains untested experimentally.

We hypothesized that the female's forehead patch plays a role as a badge of status in female-female competition. To test this hypothesis, we performed simulated territorial intrusion tests with stuffed female decoys either without patch or with a patch with the largest size recorded for females in the study population. We may predict very different outcomes. During social conflict, subordinate individuals can use information from signals of fighting ability and previous encounters to avoid repeatedly entering into unprofitable fights with higher-ranked individuals (reviewed by Cant and Young 2013). Thus, resident females (both patched and non-patched) should avoid encounters with patched decoys. Conversely, patched decoys may elicit more aggressiveness from the residents because they are perceived as larger threats (as found in male collared flycatchers *Ficedula albicollis* for the wing patch size; Garamszegi et al. 2006). Additionally, signal asymmetry between opponents could play a role in female-female competition (see Griggio et al. 2010, in the rock sparrow *Petronia petronia*), and we may thus expect an interaction between resident female's and decoy's patch expressions. On the one hand, resident patched females could be more aggressive against non-patched decoys than against patched ones (see Järvi and Bakken 1984, in the great tit *Parus major*). On the other hand, matched contestants may show the greatest tendency for escalation (Parker 1974; see Midamegbe et al. 2011, in the blue tit *Cyanistes caeruleus*). Finally, resident females could rely

Fig. 1 **a** Adult pied flycatcher female without forehead patch (credit J. Morales) and **b** adult pied flycatcher female with a forehead patch (*left*) and male showing the typical breeding plumage (*right*) (credit O. Gordo)
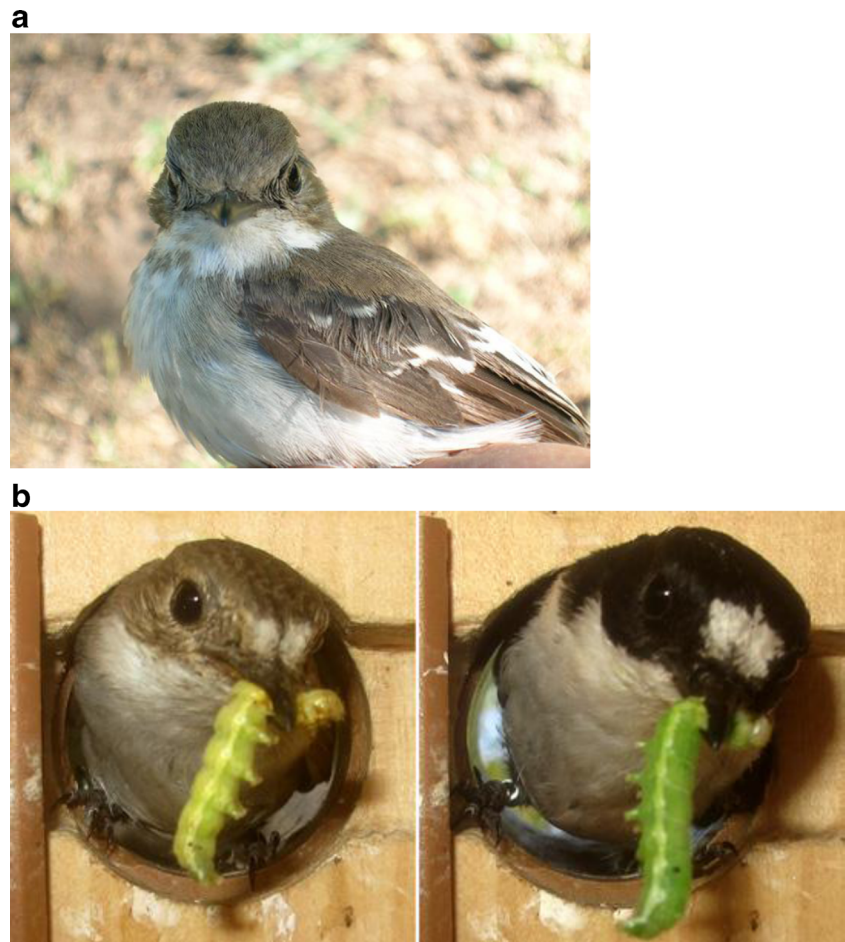
on their absolute badge size rather than relative to their opponents (see Pryke and Andersson 2003, in red-shouldered widowbirds *Euplectes axillari*).

Material and methods

Study population

The study was conducted in 2006 in a population of pied flycatchers breeding in 300 wooden nest boxes in a deciduous forest of Pyrenean oak (*Quercus pyrenaica*), at an elevation of 1,200 m in the locality of Valsaín, Segovia, central Spain (40° 53′ N, 4° 01′ W). The pied flycatcher shows a high degree of sexual dimorphism during the breeding season. Although variable among individuals, males in Iberian populations have a contrasting white and black plumage, while females are dull light brown. Thus, females either expressing or not a white forehead patch are visually distinct from males (see Fig. 1).

Simulated territorial intrusions

Nest boxes were checked every 3 days from 1st April to 10th May to detect the initiation and progress of nest construction, indicative of the establishment of a breeding pair. When nest construction was almost complete (i.e., just before the nest showed the rounded and closely knit nest cup), resident females were challenged with a pied flycatcher female decoy placed on top of the nest box to simulate a territorial intrusion. As decoys, we used two stuffed females that originally lacked a forehead patch. Both were found naturally dead in the population in previous years and were preserved frozen at −20 °C until stuffing. They were mounted in neutral lifelike perched postures. We made a removable patch by gluing pieces of white feathers cut from a stuffed female's wing patch on a cardboard of 9.9 × 5.7 mm (width × height; the maximum female forehead patch size recorded in the study population in the previous year). Decoy's phenotype (presence/absence of forehead patch) was randomly assigned in the first trial of each nest. When assigned, the fake patch was fixed on the

decoy's forehead with a thin metal wire concealed under head plumage. We used two different stuffed females to minimize pseudoreplication (Hurlbert 1984), as commonly used in bird studies to perform territorial intrusion tests (e.g., Vergara et al. 2007, 2013; Vergara and Fargallo 2007; Kingma et al. 2008; Pärn et al. 2008). Apparently, the resident pair recognized stuffed decoys as conspecifics, since not only some resident females attacked them but also around 20 % of resident males tried to copulate with the stuffed decoys (see "Results" section). On average, 2 days (mean ± SE 2.1±0.3, range 1–7 days) after the first test, females were challenged for a second time with the same decoy but with the alternative patch phenotype to that previously assigned. Thus, the two decoys presented to a given female only differed in forehead patch expression (presence/absence). All observations were performed before the first egg laying (on average, 7.5±0.5 days before). Thus, all females were likely observed during their fertile period (see Birkhead and Møller 1992; Lifjeld et al. 1997).

We were able to observe the behavior of 38 individual females twice (with patched and non-patched decoys) and of 6 once (3 with patched decoys and 3 with non-patched ones). Some females did not appear during the entire trial, and we supposed that they were away from the territory and did not perceive the stimuli of the intrusion. Therefore, we repeated the corresponding test on the following day, but in six cases, the focal female never appeared. Out of the 82 territorial trials, the resident male turned up in 67 (32 with patched decoys and 35 with non-patched ones) and was absent in 15. Later in the season, we captured 97 % of focal males in their nest box, and none of them was found to hold more than one territory.

After placing the decoy on top of the nest box, we retreated to a hidden observation position about 20 m away. Observations were performed with the aid of binoculars and recorded in real time in a digital voice recorder (Olympus VN-960PC). All tests were carried out from 7:00 a.m. to 12:30 p.m., because activity is usually reduced after this time. Although our aim was to record female behavioral responses, we also observed the behavior of males. We recorded the following behavioral variables for females and males: latency time to first appearance (min); presence/absence of attacks (pecking and flight attacks with or without direct contact); number of attacks per trial; and the degree of approach to the decoy, which was recorded according to three easily observed categories: 0 = the focal bird did not approach the decoy nor did it enter the nest box or fly around it; 1 = the focal bird did not approach the decoy but entered the nest box or flew around its entrance; 2 = the focal bird clearly approached the decoy either perching just beside it on the nest box or performing attacks against it with or without contact. During the tests, we also noted that 19 individual females expressed a distinctive forehead patch while 25 did not (this was later confirmed at capture). For males, we additionally recorded presence/absence of copulation attempts and presence/absence of enticement calls (hereafter song). We did not record the male's degree of approach to the decoy because of its ambiguous interpretation, for it may be either a sign of intimidation or enticement.

Following previous studies in pied (Breiehagen and Slagsvold 1988; Rätti 2000) and collared (Hegyi et al. 2008) flycatchers, we assumed that females' degree of approach to the decoy as well as direct attacks were accurate estimates of her aggressive motivation against the decoy. We may interpret that females with long latency to arrive were on average less engaged in territory vigilance. Pied flycatchers defend a rather small territory around the immediate vicinity of the nest (median radius 10 m; Lundberg and Alatalo 1992). Although feeding trips can sometimes be up to 100 m away, males and females seem to forage usually within a radius of 50 m around the nest (von Haartman 1956; maps 7 and 8). Females are able to detect intruder females at a distance of at least 40 m (Rätti 2000). Hence, it is likely that most females in our study were able to detect the decoy soon after placing it on top of the nest box, although we cannot exclude the possibility that some of them were far away from the territory. Observations lasted 15 min, although in 22 tests, they were finished before either because the female ($n=17$) or the male ($n=2$) knocked the decoy off the nest box after direct contact or because of heavy rain ($n=3$) (mean ± SE of total observation length 12.6±0.5, range 0.5–15.0 min). Among the 17 females that knocked the decoy off the nest box, 16 performed the highest number of attacks per trial registered. Thus, shorter duration length in most of these observations did not preclude the presence/absence of female's attack, number of attacks, and degree of approach to the decoy. Excluding the five shorter observations with no female attacks led to the same qualitative results (results not shown but available upon request).

Data analyses

We performed linear mixed effects models in SAS 9.2 (SAS Institute Inc. 2003) for all behavioral female traits with nest box identity as random factor. The presence/absence of patch in the decoy and the resident female was included as fixed factor to test for their effect and the interaction between both on female behavior. Additionally, the models included the presence/absence of the male and decoy's identity (stuffed female nos. 1 or 2) as fixed categorical factors. Observation length (total observation length minus female's latency time) was also included as an independent variable (except in the model of latency time), given that females varied in the time available to interact with the decoy. We used linear mixed models (MIXED procedure) for latency time, which was logarithmically transformed ($log_{10} + 1$) to normalize its distribution, and generalized linear mixed models (GLIMMIX procedure) for the presence/absence of attacks (binomial distribution), the number of attacks per trial

(Poisson distribution), and the degree of approach to the decoy (multinomial distribution). We did not calculate attack rate (number of attacks per trial divided by observation length), because the relationship between the number of attacks and observation length was not isometric (see García-Berthou 2001, for a review on the use of ratios).

To analyze male behavior, we performed similar linear mixed models with nest box identity as random factor and the following explanatory variables: female's and decoy's forehead patch expressions, the interaction between both, decoy's identity, and observation length (total observation length minus male's latency time). Additionally, we performed two mixed models with binomial distribution to analyze the presence/absence of copulation and song. Values for female and male behaviors are expressed as means ± SE.

Model selection was performed by an information theoretical approach. For each female and male behavioral trait, we run all possible models and ranked them according to their corrected Akaike's information criterion (AICc) values modified for finite sample size. In generalized linear mixed models (GLIMMIX procedure), we obtained AICc with Laplace estimation method (as recommended by Bolker et al. 2008). The Akaike weights (w_i) for each model were calculated (Anderson et al. 2000). Given that none of the models showed a $w_i > 0.90$ (see Tables A1 and A2), we performed model averaging as recommended by Anderson et al. (2000) and Burnham and Anderson (2002). Then, we calculated averaged estimates (b) and standard errors (SE) for all explanatory variables weighted by the w_i using only those most probable models (i.e., those models with $\Delta AICc < 2$; Burnham and Anderson 2002). The sum of w_i of the models where a certain explanatory variable was included quantified its relevance. We also calculated the amount of deviance explained

($D^2 = 100 \times$ (deviance of the null model − residual deviance)/ deviance of the null model; Zuur et al. 2009) by the most probable models weighed by the w_i.

## Results

Female behavior

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

Table 1 Averaged linear mixed models for female behavioral traits with their weighed D^2. Akaike weights (w_i) and weighted averaged estimates (b) and standard errors (SE) are shown for the explanatory variables included in the top ranked models (see model averaging in Table A1). For categorical explanatory variables, the weighted estimate and SE of the category specified between parentheses are shown. High w_i are shown in bold

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
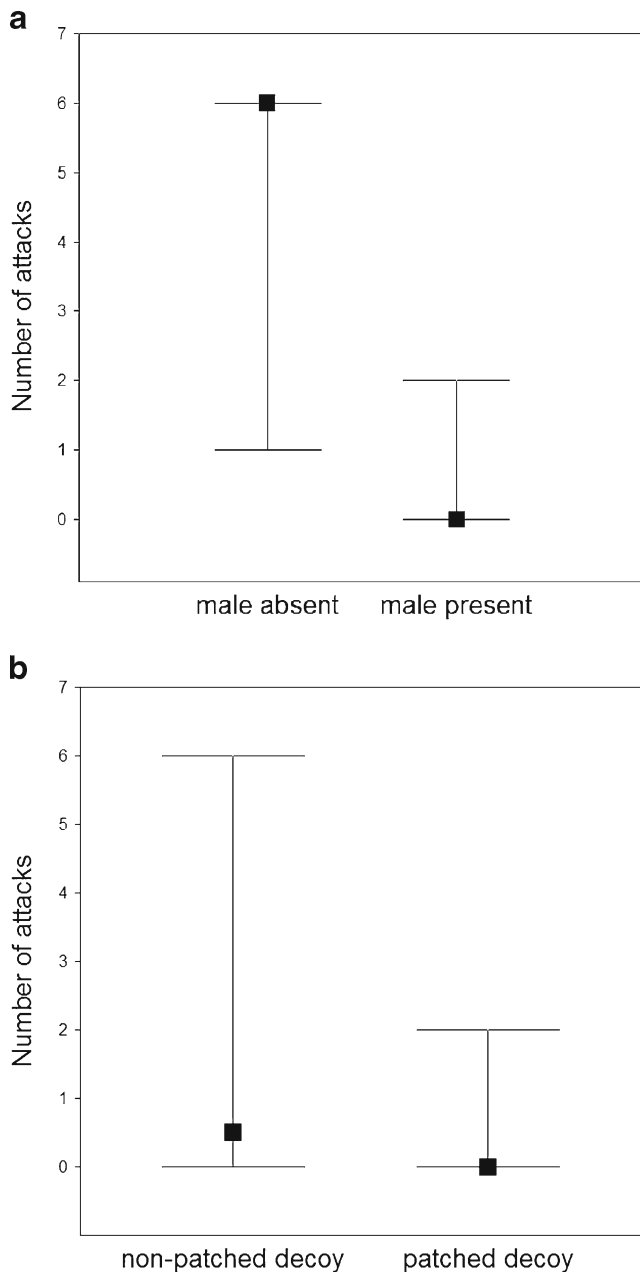
Fig. 2 Number of attacks per trial performed by resident pied flycatcher females against the female decoy in relation to **a** the presence/absence of the male and **b** the decoy's forehead patch expression. Values are medians with 25–75th percentile (*error bars*)

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 a higher degree when their mate was absent than when it was present (male absent: degree of approach 0 ($n=1$), 1 (2), 2 (12); male present: 0 (16), 1 (18), 2 (33)). Also, females approached non-

patched decoys to a higher degree than patched ones (non-patched decoy: degree of approach 0 ($n=6$), 1 (9), 2 (27); patched decoy: 0 (11), 1 (11), 2 (18)).

Male behavior

Female's patch expression had the strongest effect on male's latency time of first appearance (Table 2). Males mated with patched females showed up later during the trials than those mated with non-patched ones (respectively, mean ± SE of non-transformed data 4.85±0.66 and 2.62±0.56 min). Decoy's identity also had high influence on male's latency time (Table 2). Males appeared earlier in the trials of the stuffed female no. 1.

Males attacked the decoy in 15 out of 67 trials, sang in 19, and performed copulation attempts in 13. However, the averaged models explained very little amount of deviance, especially in the number of attacks and in the presence/absence of song and copulation. Only decoy's identity had influence on the probability and number of male's attacks (Table 2). The stuffed female no. 1 was more prone to be attacked and with more intensity by males. The presence/absence of copulation and song was not strongly affected by any explanatory variable (Table 2).

Interaction between mates

We also observed that the resident pair interacted in various ways. The male clearly attacked its mate in five trials. Conversely, females never attacked their mate, but in two trials, they attacked the decoy just when the male started copulation attempts with it. Finally, in nine trials, the male and the female chased each other or flew around the nest box together with no sign of 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

Table 2 Averaged linear mixed models for male behavioral traits. Akaike weights (w_i) and weighted averaged estimates (b) and standard errors (SE) are shown for the explanatory variables included in the top ranked models (see model averaging in Table A2). For categorical explanatory variables, the weighted estimate and SE of the category specified between parentheses are shown. High w_i are shown in bold

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

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 interaction effect. Manipulating female's patch expression as well as decoy's would shed light on this issue (see Searcy and Beecher 2009, for a review of aggressive signals).

The presence/absence of the mate was the most important factor affecting females' behavior against the decoy. Male absence increased female aggressiveness in almost all the behavioral variables studied, suggesting that females take on extra costs of territoriality when their mates are not present. If female-female competition was directed at guarding the male's parental investment (Slagsvold and Lifjeld 1994) or at avoiding male's extra pair copulations, we may have expected higher aggressiveness in the presence of the male. One possible explanation for the opposite trend is that males, when present, have a more prominent role in territory defense than females, probably because of their bigger size that confers a

physical advantage. Another possibility is that females were more interested in the male (when present) than in fighting the decoy or that the male actively interfered to circumvent female-female aggression (see Slagsvold and Lifjeld 1994). We registered 14 interactions within the resident pair in which the male and the female flew around together or the male was observed attacking its mate. Only in 3 out of these 14 trials, the females were aggressive against the decoy, which could support that intrapair interactions prevented female-female aggression. Another possibility is that the most aggressive females were paired with males that spent less time guarding their mate and territory. In any case, our findings highlight the importance of controlling for the mate's presence when observing female behavior.

Males showed up later during the trials when mated with patched females. This may indicate that males were less engaged in territory vigilance when paired with a dominant female that was able to evict intruders. It may also suggest that males invested less time in guarding patched females in their fertile period than non-patched ones. However, data collected in the study population indicate that extra pair copulations are not related to females' forehead patch expression (J. Moreno, unpublished data). Additionally, we found no evidence of a male preference for decoy's forehead patch, since neither song nor copulation attempts were related to decoy's patch phenotype. Yet, we cannot exclude the possibility that males do show a preference for patched females during the mating period, as correlative evidence suggests (i.e., assortative mating; Potti and Merino 1996). Nevertheless, although the preference for patched females may confer certain benefits to males in terms of health and reproductive success (Potti and Merino 1996; Morales et al. 2007), too highly dominant females may not necessarily be more fecund, given that patch

expression implies costs in terms of oxidative stress (Moreno et al. 2013a, b). In that case, the optimal strategy for males would be to develop stabilizing mating preferences for female's forehead patch to avoid females that risk their fecundity for signaling (Chenoweth et al. 2006; see also Morales et al. 2012 in seabirds). Finally, various male behavioral traits were affected by decoy's identity. Although the decoys used were apparently similar to a human observer and were mounted in the same position, they might have differed in features that we did not acknowledge (e.g., wing patch size, UV-coloration).

Female intrasexual competition should occur when variation in male quality is high or access to reproductive resources is limited (Amundsen 2000). Our results support that reproductive resources (nest site or mate) are valuable for females close to egg laying, since many of them behaved aggressively against the decoys. Nest sites are crucial for non-excavating hole nesters (Newton 1994), and their loss may imply a total seasonal reproductive failure in a short-lived migratory bird with short-breeding seasons like the pied flycatcher. Competition for nest sites in females may be similar to selection in males for breeding resources (territories and females) or be related to social selection for nonreproductive resources like food or shelter (West-Eberhard 1983). Nest sites are as important as mates for reproduction when they are limited, and thus, there should be stiff competition for them leading to signals of status also in females (Rosvall 2011; Tobias et al. 2012). Alternatively, females expressing a forehead patch could mimic young males (which are mostly brown in their first year) and thus avoid competitive fights with other females and males. However, this is unlikely since no female-like light brown males exist in Iberian populations, contrary to pied flycatchers in other European populations (see Potti and Merino 1996; see also Fig. 1). Moreover, females are recognized as females by their conspecifics independently of their forehead patch expression (Sætre and Slagsvold 1992).

A recent study has shown that the experimental addition of a fake forehead patch to females without one in the study population increases the bearer's oxidative tissue damage (Moreno et al. 2013a). Although the physiological mechanism remains to be elucidated, the link between oxidative damage and patch expression is probably mediated by social control (see Safran et al. 2008). Females without patches may avoid high oxidative damage implied by social interactions but might lose breeding opportunities when competition for breeding resources is strong (Moreno et al. 2013a, b). Interestingly, the forehead patch is expressed in pied flycatcher females only in southern European populations. One possibility is that selection on the forehead patch is higher in southern populations than farther north because of a stronger negative effect of oxidative stress and parasites in southern latitudes (Moreno 2004). Additionally, the low availability of suitable breeding habitat and its high degree of fragmentation in the Iberian Peninsula could facilitate higher territoriality and stronger sexual selection in southern populations.

In conclusion, our results suggest that a trait that has become a classical example in studies of male intrasexual selection plays also a role in female-female contests, as found in other socially monogamous bird species (e.g., the rock sparrow: Griggio et al. 2007, 2009; the diamond firetail, *Stagonopleura guttata*: Crowhurst et al. 2012). Our results oppose to the classical view portraying females as merely passive and choosy, which is being reevaluated in the light of recent research (Clutton-Brock and Huchard 2013).

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