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Female incubation attendance and nest vigilance reflect social signaling capacity: a field experiment

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Abstract

Due to the reduced conspicuousness of female signals, their evolution has traditionally been interpreted as a by-product of sexual or natural selection in males. Recent studies have argued that they may be the result of sexual or social selection acting on females. Here, we explored the role of the white wing patch during the incubation period in female-female competition contests in a migratory cavity-nesting songbird, the pied flycatcher *Ficedula hypoleuca*. At this stage, female investment is crucial for offspring survival, while competition among females for nest cavities is still operating. We experimentally performed an extreme reduction of signaling capacity by covering the wing patch with dark paint in a group of females and compared their incubation attendance and social interaction patterns (vigilance and aggression at the nest as defense variables) during simulated territorial intrusion tests with female decoys, with those of an unmanipulated group of females. Tests were performed both before and after the manipulation. We hypothesized that these patches constitute signals of social dominance in female-female interactions that allow them to maintain high levels of incubation attendance by reducing the need for vigilance. We found a marked decrease in incubation attendance in experimental females after manipulation, a change not detected in manipulated females. No effects on aggressive nest defense were found. Female wing ornamental traits would act as a badge of status in social interactions allowing more intense incubation and reduced vigilance. Implications of social interactions on incubation patterns should be incorporated in future studies.

Significance statement

Animals can transmit information to the others through different traits. Ornamental signals have been proposed as status indicators in social interactions in birds in many studies. Although some of them concern their function and evolution in females, only a few have been focused on their role during incubation. Our experimental study suggests that the female's white wing patch in pied flycatchers acts as a badge of dominance status in social encounters. Thus, dominant females may enforce respect from competitors through signaling, thereby being able to reduce vigilance at the nest with positive effects on incubation efficiency. Implications of social status for incubation patterns should be considered in future studies as an additional factor modulating this crucial parental activity.

Keywords Experimental patch manipulation \cdot Female ornamental traits \cdot Incubation behavior \cdot Nest vigilance \cdot Signaling status \cdot Social interaction

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Introduction

Animals can transfer information to conspecifics through morphological or behavioral traits, such as colored ornamental plumages or courtship displays (Maynard Smith and Harper 2003). These signals may function to communicate phenotypic traits of the signaler like those involved in competitive capacity or reproductive efficiency. This type of communication

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has usually been studied from the male perspective, presumably due to the higher conspicuousness of male signaling traits, compared with those of females. Since Darwin (1871), the evolution of female ornamental features has been thought of as a by-product of sexual or natural selection in males through their genetic correlation (Lande 1980). This conclusion has been supported by several studies (Muma and Weatherhead 1989; Cuervo et al. 1996; Rohde et al. 1999; Hill 2006; Dale et al. 2015). However, some authors have argued that female signals may have an adaptive meaning (Jones and Hunter 1993; Amundsen 2000; Torres and Velando 2005; López-Idiáquez et al. 2016). Two scenarios could lead to female functional signals. On the one hand, males may choose some traits in their mates, and females may compete for the attention of males (intersexual selection), so sexual selection could act on females in exactly the same way as it operates on males of many species (Clutton-Brock 2009). On the other hand, because of their high energetic investment in gametes and parental care, females are expected to compete for limited resources during the breeding period (intrasexual competition), a form of social selection that is not sexual (Bleiweiss 1997; Cain and Langmore 2016), and conspicuous signals could be positively selected during these interactions by social selection (West-Eberhard 1983; Hegyi et al. 2008; Rosvall 2011; Soler and Moreno 2012; Morales et al. 2014). Both possibilities are not exclusive, and vestigial trait expression in females resulting from genetic correlation with male traits can be the starting point for further trait elaboration through sexual and social selection (Lyon and Montgomerie 2012; Tobias et al. 2012; Dale et al. 2015). Thus, female sexual selection has recently been included under the wider concept of social selection (West-Eberhard 1983; Lyon and Montgomerie 2012; Tobias et al. 2012). In this context, it has been shown for instance that female song is widespread and ancestral in songbirds to communicate territorial defense or coordination of breeding activities (Langmore 1998; Riebel et al. 2005; Odom et al. 2014; Webb et al. 2016). Again, there is recent evidence that in some species like the rock sparrow Petronia petronia, females collect specific materials to decorate their nests, to indicate their status to the rivals or predators (García-Navas et al. 2015).

Several scenarios have been proposed to explain the functionality of plumage badges of status (Rohwer and Ewald 1981; Maynard Smith and Harper 2003; Senar 2006) as the expression of the concomitant costs of developing or bearing the signal (Senar 2006). Theoretical studies suggested that only highquality individuals are able to sustain the cost of expressing an enhanced signal of status due to the behavioral cost of dominance interactions in a context of a high intrasexual encountering rate (social control hypothesis) (Ketterson 1979; Slotow et al. 1993) or of avoiding increased predation due to elevated conspicuousness (differential predation hypothesis) (Fugle and Rothstein 1987; Moreno Rueda 2003). A physiological cost of badge production has also been proposed in relation with the cost of modified hormone levels or trade-offs with the immune response that could be related to individual quality (Owens and Hartley 1991; Poiani et al. 2000). In addition, information about social dominance obtained from the signals must be backed by corresponding dominant behavior because potential opponents may be focused on both aspects simultaneously (skeptical receptor hypothesis) (Rohwer 1977; Caryl 1982; Maynard Smith et al. 1988). From another point of view, some studies have proposed that social hierarchies may be the product of mixed evolutionary stable strategies, whereby individuals of different social dominance are able to coexist evolutionarily by allocating their resources differently, leading to general benefits from signaling social status (Maynard Smith 1988).

In many species of birds, the two sexes exhibit common plumage signals, although with more intense expression in males (del Hoyo et al. 1992), which makes it easier to investigate in this sex. Some plumage characteristics of females have been shown to be positively associated with individual rank and aggressive behavior, for example, the wing patch size of the collared flycatcher Ficedula albicollis (Hegyi et al. 2008), the ornamental facial patterns of the northern cardinal Cardinalis cardinalis (Jawor et al. 2004), the bib size in the social weaver Philetairus socius (Rat et al. 2015), and the color and size of the crown patch in the golden-crowned sparrow Zonotrichia atricapilla (Chaine et al. 2011). Nevertheless, in some comparative studies, the functionality of ornaments is very clear in one sex, but not in the other, as is the case of the throat patch in the Eurasian tree sparrow Passer montanus (Mónus et al. 2017) which is suggested to be a status signal in males but not in females, or the white flank spots in the diamond firetail Stagonopleura guttata (Crowhurst et al. 2012) and the breast patch of the rock sparrow P. petronia (Cantarero et al. 2017) that, on the contrary, seem to be reliable signals in females but not in males. Thus, the same ornaments can have different functions in the two sexes.

Competition among female birds could operate in order to achieve access to preferred males (Petrie 1983), to protect male parental investment (Slagsvold et al. 1992; Slagsvold and Lifjeld 1994), or over resources necessary for breeding like territories or nest sites (Servedio et al. 2013; Stockley and Campbell 2013), that directly influence the probability of reproducing successfully. It operates not only during territory acquisition, but also during the incubation period. This competition could be crucial in species with limited access to strictly necessary breeding resources like nest sites for cavity-nesting birds (Sandell and Smith 1997). In this case, documented female defense behaviors against female intruders (Jawor and Ketterson 2006; Jawor et al. 2006; Goymann et al. 2008) may have been favored especially when nests can be taken over during the initial stages of reproduction (Rosvall 2011). In this context, the female signaling function could be interacting with male behavior giving a final result in terms of reproductive performance, so the influence of mutual ornamentation and male behavior must be taken into account to correctly interpret the results of experimental manipulations of female signaling capacity (Kraaijeveld et al. 2007; Kötél et al. 2016).

Incubation is a crucial phase of avian reproduction, given the intense need for care of developing embryos and the impact of embryonic condition for subsequent nestling growth (Deeming and Ferguson 1991). Thus, parental investment during this phase has important consequences for fitness (Reid et al. 2000). In many species like the pied flycatcher Ficedula hypoleuca, females incubate alone (Deeming 2002), although males often feed them at this stage (Cantarero et al. 2014, 2016b; Kötél et al. 2016). This is why female behavior during this period may become essential, as females must find an equilibrium between the time spent on feeding herself and attending the clutch in species with uniparental incubation, as predicted by the female nutrition hypothesis (von Haartman 1958; Royama 1966; Cantarero et al. 2016b). A factor not often considered when discussing the compromise between embryo thermal needs and the incubating parent's energy requirements is the added demand to defend the territory, nest site, or nest cavity against potential competitors. In some studies, aggressive competition between females has been detected (Rosvall 2008, 2011; Moreno 2015). Sometimes, these competitive interactions involve clutch destruction and replacement through egg burial and ejection during egg laving or incubation, and/or results in the loss of the reproductive season (Moreno 2015). The intensity of competition between females during early-breeding phases may depend on the degree of limitation in the availability of resources crucial for breeding successfully, such as nest cavities or high-quality mates or territories. Accordingly, there could be strong selection to advertise social dominance in the pied flycatcher during forays out of the nest while incubating (Moreno et al. 2013; Morales et al. 2014). Thus, social signaling at this stage could ensure adequate incubation attendance.

Here, we explored the role of a female plumage trait, the white wing patch, in female-female competition in a migratory cavity-nesting songbird, the pied flycatcher, during the incubation period. Both males and females exhibit a conspicuous white patch on the wing based on the white edges of tertials and secondary coverts and on white bands on some secondaries and primaries, male patches being larger and more conspicuous (Lundberg and Alatalo 1992). These patches are exhibited by birds of both sexes in social interactions by repeatedly flicking the folded or partly folded wings (Curio 1978). Sexual selection has been shown to act in favor of larger wing patch size in males (Sirkiä and Laaksonen 2009; Sirkiä et al. 2010). Furthermore, females with larger wing patches breed earlier and have a higher hatching success (Morales et al. 2007). The extent of the wing patch in females is also positively linked to testosterone levels during incubation (Moreno et al. 2014; Cantarero et al. 2015, 2016a). Moreover, there is strong female intrasexual competition for nest cavities during the incubation stage (Moreno 2015) as indicated by the intense aggression of territorial females towards female intruders during initial breeding stages (Breiehagen and Slagsvold 1988; Lifjeld and Slagsvold 1989; Morales et al. 2014; Cantarero et al. 2015; Moreno et al. 2016).

There is a large degree of variation in the extent of the white wing patch of females, ranging from highly conspicuous badges to barely noticeable feather edges (Moreno et al. 2014; Cantarero et al. 2016a). Given the positive links between the extent of female wing patches and testosterone, early breeding and hatching success, we hypothesized that these patches constitute signals of social dominance in female-female interactions that allow them to maintain high levels of incubation attendance by reducing the need for vigilance at this stage. To evaluate this hypothesis, we experimentally performed an extreme reduction of female signaling capacity by covering the wing patch in an experimental group of females and compared their incubation attendance and social interaction patterns during simulated territorial intrusion tests with female decoys with those exhibited by unmanipulated females. We predicted that the absence of the wing patch should be associated with an increase in territorial defense and a decrease in incubation attendance.

Material and methods

General field methods

The study was carried out during the spring of 2015 in a montane forest of Pyrenean oak Quercus pyrenaica, located at 1200 m above sea level near the village of Valsaín, Central Spain (40° 54' N, 4° 01' W), where long-term studies on breeding pied flycatchers have been ongoing since 1991. In the area, 300 nest boxes (see Lambrechts et al. 2010 for dimensions, structure, and placement) are routinely checked during the pied flycatcher breeding season, lasting from the middle of April when the first males arrive to the first days of July when the latest broods fledge. Nest boxes were checked every 4 days from April 15 to the finalization of nest construction, to detect the initiation and progress of nest building for every breeding pair. Afterwards, all the nest boxes occupied by flycatchers were checked every 3 days to record laying date. As most females begin incubation on the laying of the penultimate egg (Ruiz-de-Castañeda et al. 2012) and the modal clutch size in the population is six, we considered incubation to begin on the laying of the fifth egg (mean incubation period is 14 days). Hatching success was estimated as the percentage of hatched eggs in relation to clutch size. It was not possible to record data blind because our study involved focal animals in the field.

Female patch manipulation

Nests were assigned randomly to either control or experimental treatments on the sixth day of incubation. On that day, all females were captured in the nest box during daytime incubation without the need of using a trap, as at this stage, they are not easily frightened away from the nest. They were identified by their rings or ringed if necessary, and a digital photograph of the natural white wing patch was taken from above at a height of 10 cm from the animal by placing the wing in its natural folded position on a flat surface with a ruler besides for reference, and forming a 135° angle with the wing. All photographs were taken with the same camera, and during the morning hours so that lighting conditions were always similar. The same photographic technique has been used in previous studies (Moreno et al. 2014; Cantarero et al. 2016a). After that, the experimental treatment was applied: experimental females were painted on the wing patch with permanent nontoxic water-based brown paint markers (GALIAN COGASA, Murcia, Spain), obtained by mixing 60 ml of green, 20 ml of red, and 4 ml of yellow to achieve a color similar to that exhibited by brown dorsal body feathers, and within the natural range of plumage color (Fig. 1). This color was not estimated by using a spectrophotometer because this would have prolonged the manipulation in the field and augmented stress. This kind of paint is commonly used by pigeon keepers and is suitable for birds because it quickly dyes the feathers but keeps barbule integrity intact (and thus flight and insulation capacity), in contrast to non-water-based paints. A reduction (albeit extreme) of the natural patch was simulated in this way in experimental females, while control ones were swabbed with water on the same area of the wing, as it was impossible to find in the market a nontoxic water-based white paint that did not affect feather integrity. The paint used in the experimental group had exactly the same texture and consistency as water, thus expanding on feathers and covering the whole white patch as soon as it was applied. This prevented the establishment of other experimental groups



Fig. 1 Adult pied flycatcher female with (right) and without (left) applied treatment

through covering only part of the white wing patch as would have been ideal, or through increasing patch size. In the field, we have observed a wide patch size range, from females showing large badges to others with practically imperceptible ones (Fig. 2). We assume that females in the experimental group approached the signaling capacity of some females with minimal wing patches, as observed in our population. In total, we included 31 experimental females and 31 control females. Manipulation intensity was identical for both groups, and it took the same time (around 5 min for the whole procedure per individual), so the potential stress suffered by all animals was approximately the same. All females resumed incubation after being put back on the nest and no nest was deserted after manipulation.

Male ornamental plumage measurements

All males were captured in their nest boxes with traps while feeding nestlings of 7–8 days old (nestlings fledge 16–17 days after hatching). They were identified by their rings or ringed if necessary, and digital photographs of the white forehead and wing patches were taken using exactly the same methodology described for females. Moreover, the percentage of black feathers on back and head was recorded on a 0–100 scale with 10% interval scores, as they exhibit a melanin-based dorsal coloration. This scale is strongly correlated with the Drost scale used by other authors (Galván and Moreno 2009).

Photo analysis

Digital photographs were analyzed with Adobe Photoshop CS5 v.11.0. To estimate surfaces, the distance of 1 mm on the ruler was related to number of pixels. A zoom of 400% and a paintbrush of 17 pixels, with 100% hardness and 25% spacing, were used to score white wing patch areas estimated in square centimeter (Sirkiä et al. 2015).

Simulated territorial intrusion tests and video recordings

Simulated territorial intrusions were staged by presenting a pied flycatcher female decoy on a flat surface hanging on a branch, at approximately 0.5 m away from the nest box, during the whole duration of the test. This distance was chosen because female aggressiveness towards intruders decreases with increasing distance to the nest, as the maximum level of aggressive behavior occurs at a distance of less than 1 m (Rätti 2000). Thus, we tried to maximize the potential effect of our treatment. As decoys, we used four stuffed females that had been found naturally dead in the same population in previous years and that had been preserved at -20 °C until preparation (Morales et al. 2014). Tests were conducted in an identical manner twice, firstly 3 days before the experimental manipulation (third day of incubation) and again 3 days after the experimental manipulation (ninth day of incubation). We





randomly selected one decoy for each nest in both tests, taking into account not to repeat any decoy in the same nest for the second test, following the methodology of other studies (e.g., Vergara et al. 2007; Morales et al. 2014; Moreno et al. 2014). Every nest box and its surrounding area including the decoy were filmed during 40 min (first tests: mean \pm SE = 42.6 \pm 5.5 min, *n* = 62; second tests: mean \pm SE = 41.3 \pm 5.5 min, *n* = 62) with digital video cameras placed 50 m away from the nest box tree, and covering a space of approximately 2 m around the nest box.

All films were recorded from 8:00 to 12:00 h, and we did not find significant relationships between behavioral variables and time of day (P > 0.10 in all tests). We ignored if females were inside the nest box when we started video recordings. and we decided not to force them to escape from the nest box, as we did not want to introduce an unwanted factor in the analyses (scared females compared with non-scared ones). Due to time constraints, we could not wait until females left the box unprompted before filming. Thus, some females detected the decoy after naturally flying out of the nest box, while others did when returning after having left the box without being prompted. We assume that the response to the decoy would be similar in both situations. However, this precluded us from using latency time as a response variable. No evidence of stress or unnatural behavior like extremely long absence periods from the nest were observed after the visit.

Behavioral data analysis

Films were viewed with VLC Media Player software always by the same observer, and from them, we extracted the following information about female defensive behavior: appearance on film estimated as the percentage of time that the female is in the field of view with respect to the observation time (vigilance), percentage of time considered spent at less than 30 cm from the decoy with respect to the time that the female appears in the film (proximity), number of flights towards the decoy per time unit (min), and number of attacks or physical contacts with the decoy per min (attack rate). Following Rätti (2000), proximity is significantly associated with female attack rate, so it is considered an index of aggressive disposition. Because of technical problems, we failed to record the behavior at some nests, in which cases behavioral response variables could not be estimated (one nest each for the first and second tests).

We also estimated three incubation variables: number of incubation sessions per hour (recalculated as the number of incubation sessions per 60 min with respect to actual observation time), mean duration of incubation sessions (incubation rhythm), and percentage of time spent by the female inside the nest box (intensity of incubation or "nest attendance") which includes the time allocated to incubating and turning the eggs (Cantarero et al. 2015).

When an intrusion trial was started, three different situations could be present, and the observation time used to obtain the variables for each of these situations was calculated as follows: (a) the focal bird was present outside the nest box in the image within the field of view, so all variables were calculated using the total film time; (b) the focal bird was not present within the field of view at the start and it arrived in the course of the film, so variables were calculated using the total film time excluding the latency time (the time that it took for the bird to appear); (c) the focal bird was inside the nest box, so variables were calculated in reference to the film time after she left the nest box. No female took more than 10 min to notice the presence of the decoy, so the minimum time used to calculate variables was 30 min.

Male behavior during incubation was also analyzed and two variables were extracted: male incubation feeding behavior (number of feedings to the female per hour) and male presence (defined as the percentage of film time that the male was present within the field of view).

Statistical analyses

All the analyses were performed using STATISTICA package, version 10.0 (StatSoft, Inc., Tulsa, OK, USA). Due to the strong association among defensive variables on one side, and among incubation variables on the other, but the weak links between the two groups of variables, we performed two different principal component analyses (PCA) for defensive and incubation groups of variables, respectively. Both sets of data (first and second tests) were included in these analyses.

For female defense variables, two factors were extracted by a principal component analysis (PCA1) that together explained 81.1% of behavioral variation. The criterion for factor extraction was an eigenvalue > 1 and we used Varimax rotation to maximize the normalization of the variables. Factor1 explained 52.8% of variance and was strongly positively loaded for vigilance and proximity (correlations were 0.97 and 0.96, respectively). Factor2 explained 28.3% and was positively loaded for attack rate and flights towards the decoy per hour (0.78 and 0.82, respectively). Thus, Factor1 represents an index of female vigilance and Factor2 provides an index of aggression.

For female incubation-related variables, the PCA (PCA2) extracted only one factor that explained 59.8% of behavioral variation, where mean incubation sessions and incubation intensity were negatively loaded (correlations were -0.91 and -0.71, respectively). Therefore, this factor represents an inverse index of incubation attendance. This inverse index was multiplied by -1 before analyses.

Given that defense and incubation PCA factors were normally distributed, we used two-way ANCOVAs with repeated measures in one factor to analyze potential differences between groups in relation to the test comparison for the vigilance and defense factors. Two covariates were included in analyses: the laying date, since previous work has shown that females breeding later in the season tend to have higher levels of testosterone, which is positively associated with nest defense behavior (Cantarero et al. 2015), and the wing patch size before manipulation as it has been related to individual signaling capacity in previous studies (Cantarero et al. 2016a) and thereby could interact with the effect of the manipulation (Osorno et al. 2006). Tests of collinearity to explore the influence of covariates on the vigilance, aggression, and incubation factors were not significant, so the effects of the independent variables can be generalized. Our main prediction is that for the treatment to be effective, there should be a significant interaction between treatment and the temporal (test) factor. Differences between first and second tests within each experimental treatment were checked a posteriori with paired t tests.

As the requirements for parametric statistics were not obtained for hatching success, a Mann–Whitney U test was used for comparing this variable between groups.

Male ornamental features were also analyzed in order to avoid unintended differences in male behavior between experimental and control groups. We used Student's t tests to analyze the extent of the white wing and forehead patches given the normal distribution of these ornamental variables, and a Mann–Whitney U test for the percentage of dorsal black, as the normal distribution was not obtained for this variable.

To analyze the interaction between male and female behaviors during incubation, we performed two-way ANOVAs with repeated measures in one factor to compare male incubation feeding and vigilance behavior during incubation in order to investigate potential differences between experimental groups in male behavior caused by the treatment applied to the females. We also analyzed the correlation between male behavioral variables and the female incubation factor in the second test to ascertain if male behavior directly affects female incubation attendance.

Data availability The datasets during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Results

Our patch manipulation treatment had an effect on female vigilance, as shown by a significant interaction between treatment and test (Table 1, Fig. 3). This effect is due to an absence of significant differences in vigilance between first and second tests for the experimental treatment (paired *t* test: t = -9.97, P = 0.339), in relation with a decline in the control group (paired *t* test: t = 2.051, P = 0.048) (Table 1, Fig. 3). A significant interaction was found also between laying date and test, due to an increase in vigilance scores with laying date only for the second test. No effect of treatment on female aggression was found (Table 1).

We also found a strong effect on female incubation attendance scores as shown by a significant interaction between treatment and the test factor (Table 1, Fig. 4). There was a marked decrease in incubation attendance for the experimental group between first and second tests (paired *t* test: t = 2.749, P = 0.009), while there were no significant differences between tests for the control group (paired *t* test: t = -1.166, P = 0.252) (Table 1, Fig. 4). A significant interaction was found between laying date and test, due to a decrease in incubation scores with date only for the second test.

There were no significant differences between control and experimental nests in hatching success (U = 483.5, P = 0.5).

Table 1Two-way ANCOVAs with repeated measures in one factor forvigilance behavior scores (Factor1, PCA1), aggression behavior scores(Factor2, PCA1), and incubation attendance scores (Factor1, PCA2) inrelation to experimental treatment ("Experimental" and "Control"groups), the test factor (before manipulation, first test, and aftermanipulation, second test), and their interaction

Response	Predictor	Degrees of freedom	F	Р
Vigilance Factor1(PCA1)	Treatment	1	3.904	0.052
	Test	1	7.735	0.007
	Test×Treatment	1	4.176	0.045
Aggression Factor2(PCA1)	Treatment	1	0.695	0.407
	Test	1	1.883	0.175
	Test×Treatment	1	1.120	0.294
Incubation Factor1(PCA2)	Treatment	1	0.447	0.505
	Test	1	4.031	0.049
	Test×Treatment	1	8.699	0.004

p values < 0.05 shown in italics, were considered statistically significant

Fig. 3 Mean (\pm 0.95 SE) vigilance behavior scores (Factor1, PCA1) in "Experimental" and "Control" groups, first and second tests. Empty dots and continuous line represent the "Control group" while filled circles and dashed line represent the "Experimental group"



We found a significant interaction between female treatment and male presence ($F_{1,31} = 4.05$, P = 0.048), caused by a longer male presence in the experimental group in the second test. There was a negative, albeit no quite significant association, between female incubation and male presence (r = -0.245, P = 0.054), but we found no association between female vigilance and male presence (r = -0.04, P = 0.75). No effect of female treatment was found for male incubation feeding behavior ($F_{1,31} = 0.05$, P = 0.816). Furthermore, there was no correlation between male incubation feeding behavior and the female incubation factor in the second test (r = 0.021, P = 0.87). There were no significant differences between experimental groups in the extent of the male white forehead patch (t = -0.01, P = 0.990), the male white wing patch (t = -0.65, P =0.512), or male dorsal blackness (U = 449.5, P = 1.0).

Discussion

Experimentally covered wing patches resulted in a marked decrease in incubation attendance and the absence of a decrease in female vigilance when an intrusion was simulated

Fig. 4 Mean (\pm 0.95 SE) incubation attendance scores (Factor1, PCA2) in "Experimental" and "Control" groups, first and second test. Empty dots and continuous line represent the "Control group" while filled dots and dashed line represent the "Experimental group"



when compared with unmanipulated control females. No significant effects on aggressive nest defense or hatching success were detected. Male vigilance increased after the manipulation although it had no bearing on female incubation. In addition, females breeding later in the season showed significantly lower incubation attendance and higher vigilance scores after the experimental manipulation compared to females breeding earlier. No effect of the original white wing patch on treatment was detected.

The extent of white on female pied flycatcher wings has been proposed as a signal of dominance through its association with testosterone levels during incubation (Moreno et al. 2014; Cantarero et al. 2015). Moreover, female vigilance towards an intruder is negatively associated with circulating levels of this hormone (Cantarero et al. 2015). Vigilance and aggression have been also related in other species to levels of progesterone (Weiss and Moore 2004; Goymann et al. 2008) and corticosterone (van Duyse et al. 2004) or dehydroepiandrosterone and its conversion to other steroid hormones (Jawor et al. 2006), whose levels fluctuate throughout the reproductive period and interact with testosterone, leading to a joint behavioral expression. Thus, dominant females may enforce respect from competitors through signaling, thereby being able to reduce vigilance at the nest during incubation. The link between wing patch size and dominance in females is supported by the association of large patches with early breeding and improved hatching success in this species (Morales et al. 2007). Females with larger wing patches either arrive earlier at the breeding grounds or are more effective at securing a nest cavity, and they seem to be more efficient incubators as well (Morales et al. 2007). Here, we show that late-breeding females without signaling capacity had to increase their vigilance more and incubate less intensively than early-breeding females, while no association between breeding date and female behavior was observed prior to the manipulation. No replacement clutches have been detected in our population so they cannot be considered as a factor exerting differences in female's behavior. These results support the increasing importance of the signal with decreasing female status as expressed by laying date.

The link between competitiveness and incubation efficiency could be mediated through plumage signals, if the latter are perceived by rival females as signals of resource holding capacity. We have proposed that females could ensure proper incubation attentiveness through signaling during their foraging forays out of the nest. Here, we show that females being incapable of signaling with their wing patches incubate less intensively which could have detrimental effects on embryonic growth and development. Although we did not find an effect on hatching success, it has to be borne in mind that our disturbance by intruder simulation was brief and unique, and we do not know the real intruder pressure throughout incubation at the different nests. Presumably, only when exposed to intense intruder pressure, as in high-density populations, would reduced incubation intensity translate into heightened embryo mortality. However, more subtle effects on embryonic fitness due to reduced attendance cannot be ruled out (Hepp et al. 2015).

Incubation intensity would be affected by the need to frequently leave the nest to check on intruders and to try to evict them. This need would presumably decrease in the course of the incubation stage for two reasons: first, intruder pressure may decline with date given the seasonal decrease in reproductive prospects (Perrins 1970), and second, there may exist a territorial "residency effect" (Davies 1978; Kemp and Wiklund 2004) whereby increased time since settlement leads to higher competitive capacity. These trends would explain why vigilance decreased from the first to the second test for control females. Females with experimentally concealed wing patches did not show this decline in vigilance from the first to the second test, possibly because they became more restless and insecure than control females. By leaving the nest more frequently and spending more time outside, they also reduced incubation attendance. Probably for the same reason, they did not attack intruders more than control females, as they would not be able to properly signal their status. An altered signaling capacity caused by experimental size modification of the female white forehead patch has been shown before in this species to cause a decrease in incubation attendance (Moreno et al. 2013).

Male ornamentation did not differ significantly between experimental treatments, so the quality or social status of mates can have hardly interfered with the experiment on females. Our results regarding male behavior show no effect of the experiment on male incubation feeding frequency, but we found longer male presence caused by the absence of female signaling capacity. However, these changes do not clearly influence female incubation patterns, and what is more, it seems that those females whose males are more present at the nest box may even incubate less. So that our results could be considered as conservative, pointing out that although the change in the female signals could potentially be perceived by males as a change in the quality of their mate (Kötél et al. 2016), female incubation can hardly have suffered because of loss of interest by mates as these increased instead of reducing their presence near the nest box. Moreover, it seems that male presence can hardly explain the results of the experiment as it showed no significant association with female incubation attendance (the tendency if anything was negative) or female vigilance. Thus, we conclude that neither male quality nor male behavior explains the results reported here regarding female incubation behavior.

In the framework of our results, social selection might enforce a high pressure on female ornamental traits, and females, as well as males, would experience intense competition over ecological resources, which may select for traits that signal their competitive hability. This results, are consistent with those obtained in the collared flycatcher (Hegyi et al. 2008) during nest settlement, where the aggressiveness of females against simulated intruder female decoys was related to wing patch size. Similar results were found in studies of the function of status signals by recording female reactions towards taxidermy models or conspecifics in other species (Murphy et al. 2009a, b; Griggio et al. 2010; Midamegbe et al. 2011). The capacity to signal social dominance by females during nest box settlement and incubation through wing patches may have associated physiological costs in terms of reduced antioxidant defenses possibly mediated by social control. It has been observed in pied flycatchers that female oxidative status is associated with plumage badges, and that a reduced nest attendance may be the outcome of increased social interactions (Moreno et al. 2013; López-Arrabé et al. 2014). Thus, badges of status in female pied flycatchers may operate as badges of oxidative status as a consequence of female capacity to obtain resources necessary for breeding (Rosvall 2011) in competitive circumstances.

This signaling capacity may also contribute to efficient incubation in the presence of significant intruder pressure in some populations. Clutch destruction and replacement is often observed in some populations, being accompanied in some cases by evidence of violent fights between females and destruction of eggs or hatchlings (Moreno 2015). The importance of intrasexual dominance status on reproductive success due to aggression between females has been documented in various studies in different species (Jawor and Ketterson 2006; Jawor et al. 2006; Goymann et al. 2008). Our findings suggest that female social requirements can influence incubation patterns, in association with other more commonly studied factors such as female food requirements and embryo thermal needs (Deeming 2002; Deeming and Reynolds 2015). The importance of female social interactions for incubation intensity has not been sufficiently stressed in recent reviews on incubation behavior (Marasco and Spencer 2015) and should be considered as an additional factor, modulating the evolution of incubation patterns.

Some studies have related incubation attendance to social or sexual signals but without experimentally manipulating the social context. In the closely related collared flycatcher, it was found that, although the extent of the female white wing patch was negatively correlated with incubation intensity, the incubation behavior of both partners was related to their own or to their partner's ornamentation (Kötél et al. 2016), so that plumage badges may act as potential signals of reproductive performance in both sexes. Similar results were found in plumage ornamental characteristics of other species like the European starling Sturnus vulgaris (Komdeur et al. 2005), the barthroated apalis Apalis thoracica (van Dijk et al. 2015), or in some cardueline finches (Bókony and Liker 2005), where negative associations between ornament expression and incubation duration were found. In contrast, plumage coloration in the great tit Parus major does not predict nest attentiveness of either parent, which is related mainly to environmental conditions (Matysioková and Remeš 2010, 2011). However, all results of these studies were not experimentally related to female social competition.

In summary, information transmission patterns are complex, modulated by a combination of information sources and parental decisions, and highlight the role of signals under a complex picture that depends on a tangle of relationships, including hormonal interactions, life history traits, and sex role components (Harris and Uller 2009). Within this complex network, ornamental traits may be acting as quality signals. Female wing ornamental traits in our population should be therefore functional, and may act as a signal of dominance status in social interactions. This signal should not only be of importance during territory acquisition and mating but during incubation as well. Social selection in females should thus operate during a good part of the breeding cycle (Tobias et al. 2012). The implications of social status for incubation patterns should be considered in future studies.

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Compliance with ethical standards

Conflict of interest MP has received research FPI grant from Ministerio de Economia y competitividad. AC, JJC, and JM declare that they have no conflicts of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Permissions for handling birds were provided by "Consejería de Medio Ambiente de Castilla y León" (regional government with attributions on capture of wild birds). J. Donés, director of "Centro Montes de Valsaín" allowed us to work in the study area. The study was ethically approved by the Ethical Committee of "Consejo Superior de Investigaciones Científicas" (CSIC) and by the regional administration competent in matters related to animal protection in research according to Royal Decree 53/ 2013 (Dirección General de Producción Agropecuaria y Desarrollo Rural, Junta de Castilla y León).

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