

The female wing patch in collared flycatchers (*Ficedula albicollis*)

A sign of quality or merely a genetic correlation?



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Summary

The evolution, function and maintenance of male secondary sexual traits are well understood. However, little attention has been paid to sexually selected traits in the most choosy sex (often females) and female ornamentation is often assumed to be a non-adaptive by-product of selection for ornamentation in males. A recent debate challenges this view on female ornamentation, since some evidence suggests that females may also advertise their qualities as predicted by sexual selection theory. The wing white is a sexually selected trait in male collared flycatchers displayed in male-male competition and in courtship for females. However, female flycatchers also possess a less conspicuous version of the trait. Here we show that the size of a female's wing white increases with age (as in males) and that the size of the trait is positively correlated "female quality" and reproductive performance. Moreover, females with less wing white paired up more often with polygynous males (associated with significant fitness costs). Additionally, collared flycatchers mate assortative with respect to their wing patches. We suggest that female wing white functions as a signal under sexual selection.

Introduction

Since Darwin (1871), the evolution, the function and the maintenance of male secondary sexual traits have caused a persistent debate among evolutionary biologists (Andersson 1994). For instance, Maynard Smith (1991) pointed out that "no topic in evolutionary biology has presented greater difficulties for theorists". However, nowadays the large body of empirical and theoretical work, as well as the long academic discourse have lead to a better understanding of the function and evolution of male secondary sexual traits (Andersson 1994). Andersson (1994) concluded that the main mechanisms behind the evolution of male secondary sexual traits are in the majority of cases male-male competition and female choice of the most ornamented males. Consequently females enjoy benefits from their choice as predicted by "the good genes model" of sexual selection. Alternatively, male traits can also indicate direct benefits (Heywood 1989) to females such as territory quality (Gottlander 1987) or good parental care (Grant and Grant 1987).

However, little attention was paid to sexual selected traits in the choosy sex, mostly females. They are often assumed to be non-adaptive by products of selection for ornamentation in males (Lande 1980). In this idea of genetic correlation, the different trait magnitude was explained by different sex-dependent gene-expression. Lande's influential model (1980) neglected adaptive functions of females' ornaments and were until the late 90ies the widely accepted theoretical framework to explain female ornamentation in respect to sexual selection.

Nevertheless, the effects of female ornamentation on competition over non-sexual resources (e.g. food) were known since the early 80's (West-Eberhard 1983). However, it needed till the 90's to involve sexual selection theory in the debate and to challenge the common view on female ornamentation. Males as breeding partners can be seen as sexual resource and under certain circumstances this resource can become limited. In this case females would be expected to compete for the males like they compete for other limited, non-sexual, resources. Moreover, the fact that sexual selection is acting on males, does not preclude sexual selection on females (Amundsen 2000). Indeed, theorists have realized a long time ago that mutual mate choice is also present in species with common sex-roles (Andersson 1994) and there is no reason for the chosen sex to be completely indiscriminate and accept every mating, when mating is costly.

If males are choosy, one could assume that females, the choosiest sex, will also advertise their genetic quality as predicted by the "good genes model" or direct benefits such as parental care.

Some studies investigating female ornamentation failed to find evidence for a signalling function of sexually selected traits, although exactly the same trait was known to signal viability (Norris 1993) or parasite-resistance (Møller 1993) in males. Additionally, the possibility of female secondary sexual traits indicating direct benefits was experimentally tested in the bluethroat (*Luscinia s. svecica*) (Smiseth and Amundsen 2000). The study failed to detect a relationship between female ornamentation and feeding rate. Considering the fact that males of these species prefer to mate with colourful females (Amundsen 1997) this result is rather puzzling.

On the other hand, evidence for females signalling parasite resistance was found in an experimental cross-fostering study in the barn owl (*Tyto alba*) (Roulin *et al.* 2000). Moreover, an experimental approach in the rock sparrows (*Petronia petronia*) demonstrated that males decrease their attendance at the common nest, when the females ornaments size was experimentally decreased (Pilastro *et al.* 2003). Another experiment on zebra finches revealed that males can detect and show a preference for more fertile females (Jones *et al.* 2001). Non-experimental or aviary-based evidence was found mainly in birds in the 90's (for a review see Amundsen 2000).

Regarding indication of direct benefits, evidence for females signalling good parental abilities was found in the yellow-eyed penguins (*Megadyptes antipodes*) (Massaro *et al.* 2003). In this species carotinoid derived, intense plumage and eye colours predicted parental quality in both sexes. As expected consequence the penguins mates assortativ in respect to these traits. Finally the most convincing evidence for females advertising their phenotypic quality was found in female Eastern Bluebirds (*Sialia sialis*). Sieffermann & Hill (Evolution 2005) were able to demonstrate experimentally, that structural coloration, which indicates competitive ability and reproductive success in males, is dependent of the nutritional state of the females. Furthermore, the coloration predicts the date of the onset of egg laying as well as maternal provisioning rate and different measures of reproductive success.

In our study species the Collared Flycatcher (*Ficedula albicollis*), the males' possess a white wing patch. This wing patch is due to the black plumage coloration very conspicuous and is displayed during courtship flights towards females and during aggressive encounters towards male competitors. Moreover the size of the wing patch is thought to be sexually selected through extra pair paternity (Sheldon & Ellegren 1999) and has been shown to be condition dependent and to predict viability (Török *et al.* 2003).

Females possess a reduced version of this trait, which is, due to the duller coloration of the females, less conspicuous. I examined in this project the question if the trait could function as a signal under sexual selection. Therefore I addressed three questions:

Does the size of the wing patch reflect different aspects of female phenotypic quality?

Is the wing patch correlated measures of reproductive success?

Does the size of the trait impact mating dynamics?

Materials and Methods

Data collection

The data were collected by investigating a population of collared flycatchers (*Ficedula albicollis*), nesting in boxes, on Gotland in southern Sweden. In the years 1980 to 2005, during each spring, breeding data (onset of egg laying, clutch size, number of hatched offspring, and number of fledged offspring) were collected by checking all boxes regularly. Moreover all birds, nestlings and adults likewise, were measured, weighted and ringed following a standard protocol (Gustafsson 1989; Pärt and Gustafsson 1989; Pärt and Qvarnström 1997). The female wing patch size and all other morphological traits were measured during incubation or offspring feeding. Since the width of the white wing patch changes due to feather position, we measured the length of the depigmented area starting from the tip of the primary coverts. Patch length on each feather was measured with callipers to the nearest 0.1mm. Total patch size was calculated by summarizing the Patch length of the primaries 1 to 5.

Defining the mating status

The female mating status was defined regarding their mate. If a male was caught at just one nest, the respective female was classified as monogamously mated female. In case we caught a male feeding more than one brood, the respective females were classified as primary (early onset of egg laying) or secondary females (later onset of egg laying). Females where we did not catch the respective male were classified as single females. This group contains females that did not receive enough assistance from males to allow us to catch them. Consequently secondary females, without male assistance, as well as some widow females are classified as single females. However, the number of widow females appears to be small: Preliminary observations of colour ringed individuals revealed, that 80% of single females were observed with males that were later caught feeding chicks of another (their primary) female (Pärt, Qvarnström and Gustafsson, unpublished data). Since the classification of the mating status relied on capturing polygynous males at both nests, we probably misclassified some primary females as monogamously mated, if the males did not provide any assistance at their secondary female's nest. Defining the pairing status in this manner implies that the different pairing statuses are characterised by a degradation of paternal care: Monogamous females

receive most paternal help, primaries more than secondaries and single females' offspring receives least parental care.

Data processing and statistical analyses

To control for differences due to annual fluctuation I took residuals from a linear regression on the year previous to my statistical analyses and used these residuals for further data analyses. In this manner, I controlled all indicators of individual quality (lay date, clutch size, body weight, and body condition), the number of fledged young, as well as the female patch size itself for annual fluctuations. Controlling both, indicators of quality and the patch size for annual variation is justified, since a certain year can have different influences on different traits. To ensure the most accurate values I was using the entire database to calculate residuals for the onset of egg laying and the clutch size but excluded experimentally manipulated broods for analyses of reproductive success.

For analysis including bodyweight I included all females which were measured during incubation. When analysing assortativ mating I restricted the analyses to females collared flycatchers that were paired up conspecifics. Moreover the analyses of assortativ mating is the only one where I was not operating with the residuals, as above described, since I expect the years to have the same effects on the same trait, even in males and the females.

In the analysis of the mating status I considered breeding attempts of the same female in different years as independent data points, since repeated pairings with the same male are extremely rare, amounting to 1% of the total population (Kruuk *et al.* 2001).

As a measurement of body condition I took the residuals of a linear regression of bodyweight on tarsus length. The bodyweight was previously corrected for annual variation in the above described manner. For this and all other analyses including bodyweight I excluded all females which were not measured during incubation.

In order to control for age effects on the ornament size, I split the females in one year old birds (later referred as "yearlings") and birds with the age of two years or older (later referred as "adults"). To pool the bird in these two groups is justified by the aging effects on the trait size (Figure 1), with the only significant change of the trait magnitude between yearlings and older birds. The exact age was known for most of the birds, due to the ringing as juveniles. However, if I was lacking this information, I excluded bird with uncertain ages if they were caught for the first time. Individuals which were, due to repeated captures in consecutive years, undoubtedly classifiable as older bird remained in the database for the following analyses. Finally I corrected for aging effects on the patch size by taking the residuals of a model including the age in the above described manner.

All analyses were performed using Jmp 5.0.1

Results

The female wing patch is an indicator of some aspects of female quality. The patch size increases with age. The significant change in size takes place between yearlings (returning the first time for breeding) and two year old birds. After the age of two there are no more changes in the size of the wing patch (Figure 1).

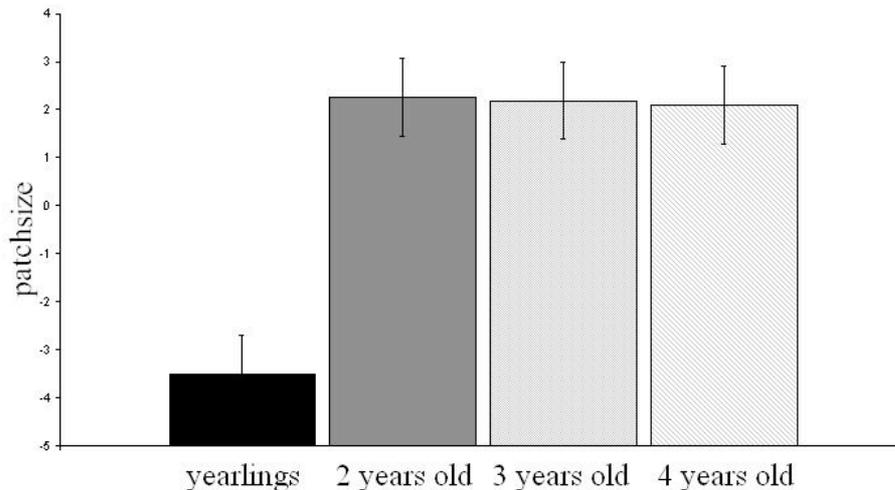


Figure 1 The patch size during life of female collared flycatchers (*Ficedula albicollis*). Presented is the mean patch size of 57 females over the first 4 years of their life. The only significant change occurs between the age of one and two years (ANOVA; $N=57$; $F=12,3$; $p<0,0001$). Error bars indicate the standard deviation.

Females with bigger patches start egg laying earlier and lay bigger clutches. However, there was no correlation with other aspects of female quality such as body weight or body condition. When controlling the patch size for age effects, none of the previously found correlations can be detected (Table 1).

Table 1 Female ornament and female quality correlation in collared flycatchers (*Ficedula albicollis*) The table shows correlations of different aspects of female quality with the female ornament. First as linear regression of the ornament with the quality parameter and second as a linear regression, when the trait size was previously corrected for age effects.

Quality parameter	Slope	N	P
Lay date	-0,066	6821	<0,0001
Lay date (corrected for age effects)	0,008	5662	0,49
Clutch size	0,007	6899	<0.0001
Clutch size (corrected for age effects)	<0,001	5735	0,83
Body weight	0,003	2049	0,25
Body weight (corrected for age effects)	-0,004	1637	0,26
Body condition	0,005	2044	0,11
Body condition (corrected for age effects)	-0,002	1635	0,57

Breeding couples with big patched females produced more fledged young in the breeding season than couples with relatively small patched females. The same trend was found when the patch size was corrected for age related changes (Figure 2).

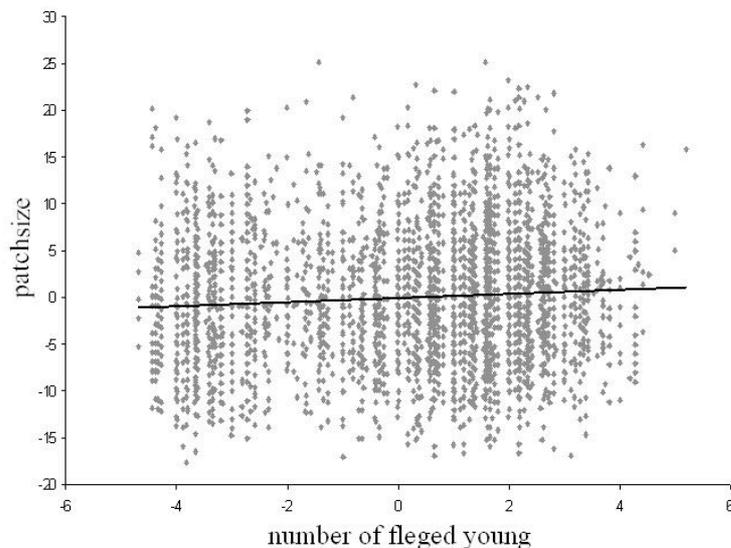


Figure 2 The patch size in female collared flycatchers (*Ficedula albicollis*) correlated with the females' reproductive success. Shown is a linear regression between patch size and the number of fledged young as a measure of reproductive success. There is a positive correlation between patch size and reproductive success ($p < 0,0001$; slope=0,02; N=3977). Even when controlling the patch size previously for age related changes a trend is found ($p = 0,053$; slope=0,012; N=3129)

Investigating the mating dynamics, I found assortative mating between males and females with respect to their wing patches. Bigger patches males mate assortatively with bigger patches females. When dividing the females in yearlings and adults, there is the same significant pattern for adult females and a trend that even among yearling females and males mate assortatively (Figure 3).

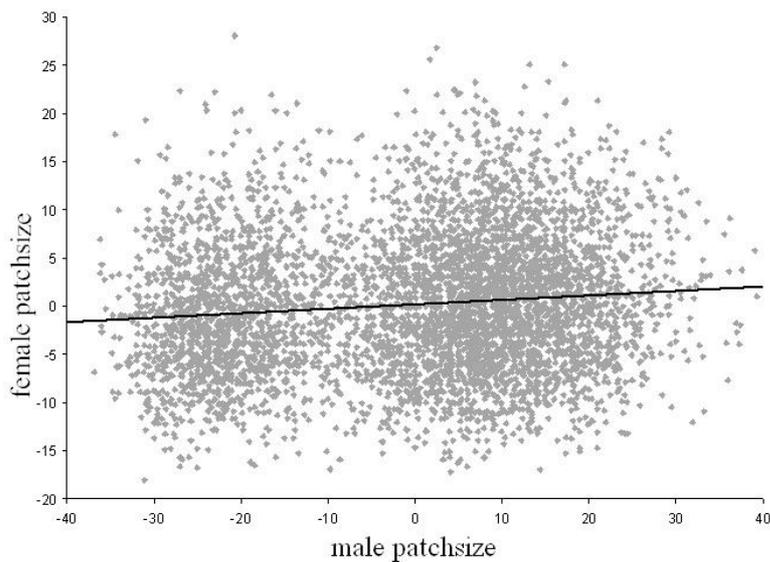


Figure 3 Assortative mating in collared flycatchers (*Ficedula albicollis*) Illustrated is positive assortative mating with respect to females and males ornament sizes ($p < 0,0001$; slope=0,055; $N=5456$). When splitting the females in yearlings and adult birds the same trend is present for yearlings ($p=0,095$; slope=0,016; $N=1484$). Moreover there is significant assortative mating detectable for adult females ($p < 0,0001$; slope=0,035; $N=3048$)

Moreover the female wing patch predicts the pairing status of its possessor: Females with bigger patches ended up more often in a favourable mating status namely as monogamous or primary female. When splitting the females with respect to their age in yearlings or adult birds the significant difference between monogamously paired females and single females remains stable, but within the adult birds no difference can be found (Figure 4).

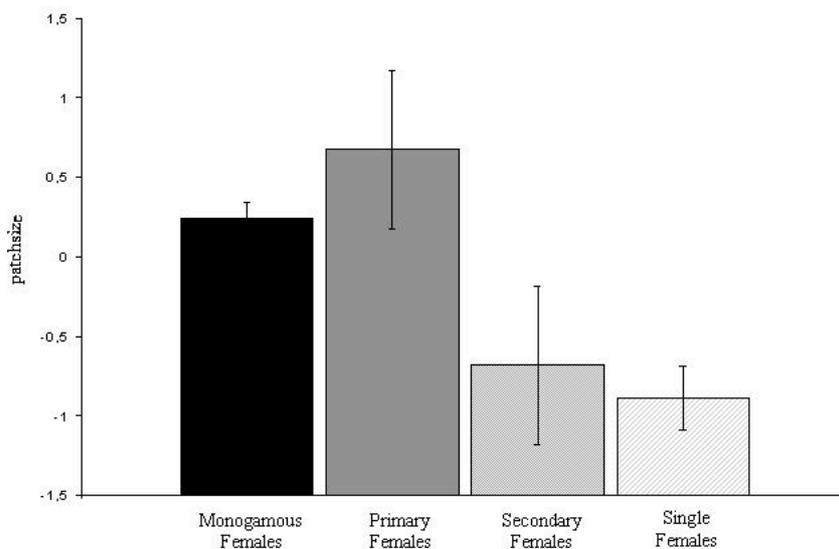


Figure 4. Patch size of female collared flycatchers (*Ficedula albicollis*) and their respective mating status. Females in different pairing situations differ significantly in their patch sizes (one-way ANOVA; $p < 0,0001$; $F=9,88$; $N=6399$). The same pattern is found for yearlings (one-way ANOVA; $p=0,02$; $F=3,15$; $N=1773$) but not for adult birds (one-way ANOVA; $p=0,17$; $F=1,68$; $N=3557$) Error bars indicate the standard deviation.

Discussion

In order to gain a better understanding of female ornamentation, it is crucial to investigate the prerequisites for sexual selection, on the very same ornaments, which are sexually selected for in the males. To enable indicator models of sexual selection to work, in respect to female ornaments, we need to demonstrate that females vary in quality and furthermore that this variation is honestly reflected by the ornament. In my study object, the female collared flycatcher, I could demonstrate that the size of wing patches reflects differences in several aspects of female quality like age, the onset of egg laying and the clutch size (Table 1). The fact, that the strengths of these effects (estimates $-0,066$ and $0,007$ for lay date and clutch size, respectively) are very small is expected for highly fitness related traits like these. Analysing the change of the patch size over the first 4 years I found a very interesting pattern. The significant change in size takes place between yearlings (returning the first time for breeding) and two year old birds. After the age of two there are no more changes in the size of the wing patch (Figure 1). This pattern is consistent with the pattern observed for male wing patches. As a consequence of the fact that older birds are known to arrive and breed earlier as well as laying bigger clutches I corrected for these age related changes in the plumage trait to examine the possibility of signalling other but phenotypic qualities. As a result of removing this aspect of phenotypic quality the previous existing correlation does no longer exist. Consequently, the most important differences in individual quality, which might be signalled by that patch size, are age related phenotypic qualities.

For some other aspects of quality I failed to detect correlations with the ornament. However, it has been argued that this is not surprising, since plumage traits are determined during the winter moult when the passerine flycatchers are over wintering in Africa and all our measures of body weight and body size are taken during the breeding season in the summer. In males, for instance body weight predicts competitive ability and reproductive success solely at the time of arrival at the breeding grounds (Anna Qvarnström, pers. comment). On the other hand, it is a fair, intuitively justified, assumption to use the body weight and the body condition (in our case representing fat storage corrected for body size, see methods) during incubation, when it is beneficial for the incubating females to possess big fat storages.

Further, I found a correlation between reproductive success and the female ornament expression, when using the number of fledged young as a measure of reproductive success. This result remains a trend even when controlling the patch size for age effects (Figure 2). Since reproductive success is highly fitness related this result supports the idea that females

with larger patches, indeed have a higher fitness. However, the measure of reproductive success in a certain year is highly confounded by paternal care. On the one hand, this fact makes it critical to imply high female quality as a cause for this increase reproductive success. On the other hand the differential allocation hypothesis tells that breeding individuals allocate parental effort to the attractiveness of their breeding partners. Since collared flycatchers face a trade-off between current and future reproduction (Gustafsson & Sutherland 1988) and high parental effort decreases the size of secondary sexual traits in the males (Gustafsson *et al.* 1995), males breeding with a highly ornamented and as a result very attractive female could adjust their investment and invest more in current reproduction. This is far from being unlikely, since plasticity in reproductive decisions of female collared flycatcher have recently been demonstrated (Qvarnström *et al.* 2000). To find experimental evidence for the adjustment of paternal care to the expression of the female ornament an experimental approach would be necessary. However, my results indicate through this comparative evidence that experiments addressing this question are promising. The adjustment of male breeding strategies with respect to female ornamentation has been experimentally investigated in Rock Sparrows (Pilastro *et al.* 2003). Pilastro *et al.* were able to show decreased brood defence when the ornament was decreased but they failed to find changes in male feeding rates. Further investigations of these questions are needed to get a better understanding of the possible signalling functions of female ornaments.

Although, ornament-quality and ornament-reproductive success correlations are important to point out the possible benefits male-mate choice and differential allocation of parental effort, we have to keep in mind that they can not be interpreted as conclusive evidence for an adaptive function of the female ornament. The competing explanation of female ornaments as correlated response to the selection in males (Lande 1980, 1987) can still cause the very same pattern if the ornament is condition dependent, as it has been shown for the males (Gustafsson *et al.* 1995; Török *et al.* 2003). This could be possible without any direct selection on the female's trait, just as a matter of inheriting the same attributes as the male trait due to a genetically correlated response (Amundsen 2000). Nevertheless such a genetic correlated response could be the starting point for direct selection on the ornament and a signalling function in male-mate choice and/or female-female competition (Amundsen 2000).

With the present study I was able to point out that, in the collared flycatchers, males who assess female quality by inspecting their ornaments and choosing the most ornamented would, on average end up with an older more experienced female, which breeds earlier, lays bigger clutches and has a higher reproductive success.

To find evidence mutual sexual selection in the collared flycatcher I investigated mating dynamics namely assortativ mating and different mating statuses. In case of mutual sexual selection one could assume to find assortativ mating in respect to the ornaments of both sexes. I was able to demonstrate that assortativ mating in respect to the wing patches occurs (Figure 3). However, one could argue that this pattern is caused by age assortativ mating facilitated by the fact that older birds arrive earlier at the breeding grounds. To control for this age assortativ mating I split my focal females in yearlings and adult birds. Still I was able to detect a trend to assortativ mating and significant assortativ mating, respectively in these two groups (Figure 3). To find this result in both of these groups presents strong evidence that mutual sexual selection occurs in this species.

Finally I analysed the pairing statuses of the female collared flycatcher. For females it is extremely important to get as much paternal care as possible. However, some males pair up with more than one female. Consequently these females have to share his paternal care. Mostly the first females, a male pairs up with, gets more paternal care than the second. This is a gradual effect with some secondary females receiving as much parental care as the primary females and other secondary females do not get any assistance. It has been shown that primary and secondary females produce 15% less offspring compared to monogamously paired females and consequently suffer severe fitness reduction through polygyny (Qvarnström et al. 2003, Gustafsson & Qvarnström 2006). As a result there should be a heavy selection pressure acting on females to pair up monogamously.

My results show, that larger patched females, in deed end up more often in the favourable pairing situation as monogamously mated (Figure 4). This pattern can not be generated by sexual selection on the males only and is explainable solely through mutual sexual selection including male-choice and/or female-female competition. Taking these results into account and applying sexual selection theory one would expect that female collared flycatchers advertise their qualities in the same manner as males do. The different ornament magnitude, compared to males, can be easily explained by the different strengths of the selection pressures on the two sexes, with the males facing stronger sexual selection pressure than the females (Amundsen 2000).

With my results I showed, that mutual sexual selection occurs in the collared flycatcher. Moreover I pointed out possible benefits of male-mate choice for the most ornamented female. Finally the finding of assortativ mating with respect to the ornament suggests that the female ornament, the wing patch, is used either as a cue for male-mate choice, or as a status patch in female-female contest competition.

However, to clarify that the female wing patch is used as a signal under sexual selection, like in the males, experimental evidence is required.

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