

Phenotypic plasticity in breeding plumage signals in both sexes of a migratory bird: responses to breeding conditions

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Abstract

Adaptive phenotypic plasticity may respond to present ambient conditions. Sexual and social signals in both sexes may express phenotype performance. Plumage signals that change discontinuously allow relating discrete variation to previous performance. Both sexes of the Pied flycatcher *Ficedula hypoleuca* present white patches on the wings and on the forehead, which constitute sexual and social signals. Forehead patches are moulted together with body plumage in Africa, while wing patches are partly moulted in Africa and partly in the breeding area soon after breeding. We studied individual inter-year changes (corrected for regression to the mean) in the size of forehead and wing patches of both sexes in 7 years for females or 6 years for males in two nearby study areas in central Spain. We found that initial signal extent strongly delimits the possible subsequent changes negatively. There is a negative association of male age with forehead patch changes. Cold and rainy springs are associated in females with decreases in both patch areas and vice versa, while no association with climate is observed in male wing patch changes. Cold pre-breeding conditions predict positive changes in female wing and male forehead patches. Breeding success is positively associated with forehead patch changes in females. Late-breeding males experience more positive changes in forehead patch size than early-breeding males. Some of these trends can be explained by variable costs of breeding in certain conditions for subsequent signal production and/or maintenance, while absence of trends in some cases may be explained by sex differences in costs of breeding and interactions with phenotypic quality of breeders.

Keywords: climate, phenotypic plasticity, sexual ornaments

Introduction

The widespread variability in phenotypes found within most populations studied is a result of genetic differences but also of phenotypic plasticity (Pigliucci 2001). Morphological, physiological or behavioural traits may vary within individuals across their lifetime as a function of environmental factors affecting the optimal phenotype (Piersma and Drent 2003, Bertossa 2011, Westneat et al. 2015). Thus, phenotypes may directly respond to information derived from factors like climate, food availability or social pressures (Milligan et al. 2009, Crozier and Hutchings 2014). However, this information may be filtered by changing performance in relation to environmental variation (Dreiss and Roulin 2010). Accordingly, reproductive performance in relation to phenotypic expression may be key in determining an optimal adjustment of traits to environmental conditions (Stamps 2007). Readjustments of the phenotype may occur continuously or in relation to important seasonal events or processes (Zimova et al. 2014).

Sexual and social signaling traits are ideal for studying phenotypic variation as they tend to be condition dependent and thereby express important performance attributes of phenotypes (Andersson 1994, Jennions et al. 2001). These traits have been intensely studied mainly in males due to their stronger expression in this sex (Garant et al. 2004, Saino et al. 2004). However, there is increasing evidence that social and sexual selection is also promoting the evolution of signals in females given the widespread social constraints operating also on successful female reproduction (Lyon and Montgomerie 2012). Sexual selection according to influential models is based on costs of producing or maintaining signals (Andersson 1994, Cotton et al. 2004). Plasticity in these signals could thus be based on changes in the impact of these costs on fitness. Adjustments could be based on costs of the present breeding effort. Thus, harsh

environmental conditions could increase the costs of signal production leading to downward adjustments in signal expression (Veiga and Puerta 1996). Moreover, reproductive costs could also deleteriously impact on subsequent trait expression (Gustafsson et al. 1995, Griffith 2000, Siefferman and Hill 2005). An indication of costly breeding could be breeding success, successful individuals having invested more resources in the current reproductive attempt. This should be especially important if signals reflect mainly production costs (Delhey et al. 2017).

Although continuous phenotypic change may be difficult to monitor, traits that change discontinuously may allow studying the association of discrete variation with previous performance of phenotypes. Plumage signals in birds are molted discontinuously after or before breeding and can be studied as plastic traits (Järvistö et al. 2016). Changes in expression are thus lasting and can be accurately estimated and subsequently compared for inter-year or inter-seasonal differences. The discontinuous yearly cycles of long-distance migrants may furthermore enhance the capacity to relate plasticity to environmental circumstances either on the breeding territories or on the winter quarters (e.g. Webster et al. 2002). Many signals are present in both sexes, although females may present less intense manifestations than males as a consequence of lower sexual selection pressures (Tobias et al. 2012). The limits of plasticity may be gauged by relating changes to initial values. A negative association of changes with initial expression may indicate that plasticity is constrained by presumed genetic limits.

The Pied flycatcher *Ficedula hypoleuca* has become a model organism for ecological and behavioral studies thanks to its adaptability to the conditions imposed by scientific studies (Lobato et al. 2008, Lehtonen et al. 2009a, b, Moreno et al. 2010, Cantarero et al. 2013, Moreno et al. 2013, Cantarero et al. 2014, Järvistö et al. 2015, López-Arrabé et al. 2015, Moreno 2015, López-Arrabé et al. 2018). It is a long-distance

migrant between its Western Palearctic breeding distribution and its African wintering range (Lundberg and Alatalo 1992). Both sexes present white patches on the wings and on the forehead, although female forehead patches are almost nonexistent in Northern populations (Morales et al. 2007, Morales et al. 2014, Cantarero et al. 2017). There is a large literature showing that these patches constitute sexual and social signals of differing importance according to the population being studied (Dale et al. 1999, Morales et al. 2007, Galván and Moreno 2009, Lehtonen et al. 2009a, Sirkiä and Laaksonen 2009, Lobato et al. 2010, Moreno et al. 2011, 2012, Järvistö et al. 2013, Moreno et al. 2014, Cantarero et al. 2015, Sirkiä et al. 2015, Cantarero et al. 2017, Plaza et al. 2018, Teerikorpi et al. 2018). Forehead patches are moulted together with body plumage in Africa, while wing patches are constituted by white patches on tertials, also moulted in Africa, and white bands on flight feathers, moulted in the breeding range during or soon after breeding (Lundberg and Alatalo 1992). The parts of wing patches moulted in the breeding respectively to wintering areas constitute roughly half of the total wing patch each (Cantarero et al. 2017). The expression of achromatic plumage in males varies across the breeding distribution, with males of Spanish populations exhibiting the largest white forehead and wing patches (Lehtonen et al. 2009a, Laaksonen et al. 2015).

Plastic changes in plumage signals can be considered as carry-over effects of environmental conditions experienced while breeding or during the winter (Järvistö et al. 2006, Hegyi et al. 2007b). Although costs of production of unmelanized plumage patches have not been studied and may be relatively small, costs of maintaining these signals in the presence of direct environmental insults like abrasion (Bonser 1995) or bacterial degradation (Burt et al. 2010), or in facing social pressures (Morales et al. 2014), could be considerable. White patches on flight feathers have probably stronger

implications for survival than white patches on foreheads due to their association with flight capability (Ruiz-de-Castañeda et al. 2012). On the other hand, contrasting dark and white plumage may affect detectability in the field in males (Slagsvold et al. 1995). Breeding in harsh climatic conditions positively affect reproductive costs and thereby positively affect subsequent signal production costs (Gustafsson et al. 1995), and the opposite could be true in benign climatic conditions. Breeding success could also affect future signaling either through the increased costs induced by a higher reproductive output or by affecting the cost/benefit balance of future breeding attempts.

Some studies have looked at plasticity of these patches in males in relation to environmental conditions during the winter or the breeding season both in the Pied flycatcher (Järvistö et al. 2016), and in its sibling species, the Collared flycatcher *Ficedula albicollis* (Hegyi et al. 2007a, Hegyi et al. 2007b), and in females in Collared flycatchers (Hegyi et al. 2008). However, no study has dealt with joint analyses of both forehead and wing patches in the two sexes in the same population (but see for age-dependence Evans et al. 2011). Here we have studied individual inter-year changes in the size of forehead and wing patches of both sexes in 7 (females) or 6 (males) years in two nearby study areas in central Spain where long-term studies of the species are being conducted (Moreno 2015, González-Braojos et al. 2017). Although other studies of plasticity in these traits have focused mainly on climatic conditions in the wintering range (Hegyi et al. 2007b, Järvistö et al. 2016), we are here mainly interested in potential carry-over effects of climate in the breeding area given the posited long-term impacts of prior breeding conditions for the subsequent development of these traits. We have previously shown with 25 years of data from one of the study populations (including most of the years covered by the present study) that laying date and breeding success were negatively affected by local temperatures while breeding, recruitment rate

likewise by minimum temperature prior to breeding in April (González-Braojos et al. 2017). Furthermore, temperatures during the nestling period affected male condition negatively (González-Braojos et al. 2017). Thus local climate during April (arrival and courtship), May (laying, incubation) and June (brood rearing) could affect condition and breeding output and thereby affect production costs of signals or reflect the potential costs and benefits of breeding in the area. On the other hand, reproductive success may reflect the costs of successfully raising broods to fledging.

We only consider the area of the patches as estimated from photographs as we have not used reflectance measurement equipment in the field. UV reflectance of white patches has been analyzed in other studies of the species (Lehtonen et al. 2009b, Sirkiä and Laaksonen 2009). In this study we focus on the area of these plumage patches as in other studies of the species (Galván and Moreno 2009, Lehtonen et al. 2009a, Lobato et al. 2010, Moreno et al. 2011, 2012, 2014, Cantarero et al. 2015, Laaksonen et al. 2015, Sirkiä et al. 2015, Cantarero et al. 2017, Plaza et al. 2018). Moreover, we have previously shown that area and UV reflectance of wing patches are positively correlated, at least in females (Cantarero et al. 2017). More than half of the females (56% in the study years) exhibit no measurable forehead patch in our populations.

In the present study, (1) we predict a negative association of patch size with subsequent changes as plasticity should be bounded. Furthermore (2), we explore the role of sex and age in determining constraints or adaptive value of signalling. We predict (3) that if breeding costs affect changes in signal extent to the next season, harsh climatic conditions while breeding should lead to patch decreases and vice versa. Furthermore (4), we expect that a high relative reproductive success and late breeding should lead to higher costs and therefore patch decreases.

Methods

General methods

The study was conducted during 2011-2017 for females and 2012-2017 for males in two nearby study areas in central Spain where long-term studies of pied flycatchers are being conducted (Moreno 2015, González-Braojos et al. 2017). Both the study areas in Lozoya (40° 58' N, 3° 48' W, 1400-1500 m altitude) and Valsaín (40° 54' N, 4° 01' W, 1100-1200 m altitude) are montane Pyrenean oak *Quercus pyrenaica* forests where 100 and 300 nest-boxes, respectively, have been erected (in 2001 in Lozoya, in 1991 in Valsaín). The two areas are separated by a mountain range reaching up to 2400 m so no individual has been recorded breeding in both areas in different years. Laying dates, hatching dates, clutch sizes and reproductive performance (hatching success, breeding success) are recorded and nestlings are measured and weighed 13 days post-hatch every year (for routine procedures in both study areas see González-Braojos et al. 2017). Breeding success is calculated as the proportion of eggs laid that result in fledged young.

Trait measurements

Most adults breeding in nest-boxes are captured with traps when nestlings attain 7-13 days of age, identified by their ring and measured (tarsus and wing lengths and mass according to standard procedures). In the years of the study, we took digital photographs of captured individuals from above of their forehead patch and of their extended right wing at a distance of approximately 10 cm and placing a ruler in contact with the head or wing for reference (see Lehtonen et al. 2009a for standardized procedures, Sirkiä and Laaksonen 2009, Laaksonen et al. 2015). Then, we determined the area of the wing and forehead patches by analyzing photographs with PhotoShop CS4 (version 11.0) according to Moreno et al. (2014). We did not measure patches when there was physical

damage or ongoing moult affecting their condition. We measured the whole wing patch as it is used as a single signal while wing-flicking (Curio 1960). Individual repeatabilities of traits among years were highly significant and of variable magnitude (Females, wing: $r=0.39$, $P<0.0001$; Females, forehead: $r=0.53$, $P<0.0001$; Males, wing: $r=0.53$, $P<0.0001$; Males, forehead: $r=0.64$, $P<0.0001$, see also Järvistö et al. 2016 for a northern population). Minimum age is estimated directly from rings if ringed as nestling, or indirectly by assuming that males older than 1 year (males of 1 year can be recognized by plumage) and females are two years old when first captured as breeders. This is based on the fact that 48% of local recruits in Valsaín and 40% in Lozoya are captured for the first time as breeders at two years, more than 20% at 3 years and less than 10% at one year (only 1.5% of male recruits in Lozoya).

The study deals with the absolute differences in patch size between successive years for individuals captured in more than one year. As experiments potentially affecting inter-year changes were conducted in both study areas in these years, only control individuals will be included. Thus, analyses include only inter-year changes when the individual in the year previous to the change was unmanipulated. As some individuals were captured more than twice, there are up to 5 measurements of the same individual leading to a maximum of 4 inter-year changes if all years are in a continuous sequence. The study is thus based on changes between subsequent years for 111 females (62 in Lozoya, 49 in Valsaín) and 74 males (38 in Lozoya, 36 in Valsaín). The numbers of individuals sampled twice, three, four or five times were 91, 16, 3 and 1 for females and 54, 12, 6 and 2 for males. Sample sizes may differ between traits due to ongoing wing moult in males.

Climate

Local climatic information was provided by the Spanish Meteorological Agency (AEMET). The station used is 9 km from the Valsaín study area (station at Segovia: 2465). Data from this station have been used previously the effects of weather on reproductive performance and local survival in the Valsaín population (González-Braojos et al. 2017). We assume that conditions in Lozoya are strongly correlated with those at Valsaín given the distance between both areas (20 km straight distance) and the habitat similarity between them. We have used as indicators of local climate the monthly averages for mean, maximum and minimum daily temperatures and mean daily precipitation for April, May and June. Adults arrive in the study area in the second half of April, lay eggs in the middle of May and nestlings fledge in the second half of June. Given the generally strong associations between climatic variables (more than 70% of correlations were higher than 0.50), they have been summarized through Principal Components analyses into two PCs. As the data set for females included one more year than for males, we have conducted separate PC analyses for females and males. For both data sets, PC1 was highly positively ($r > 0.80$) correlated with maximum temperature in April and May precipitation and negatively with May and June temperatures. High values of PC1 denote cold and rainy springs after a warm April. PC2 was negatively associated with minimum April temperatures and denotes cold conditions on arrival to the breeding grounds. PC1 and PC2 explained 89% (67 and 22% respectively) of variation in climatic variables for females and 92% (67 and 25% respectively) for males.

Statistical analyses

Given the important effect of regression-to-mean (RTM) effects when analyzing absolute changes in traits between sequential measurements (Kelly and Price 2005), we have corrected all changes following the method proposed by Berry et al. (Berry et al.

1984) as applied recently by Verhulst et al. (2013). The change from the baseline measure X_1 to follow up measure X_2 is adjusted for the regression to the mean effect to yield a corrected value D as follows:

$$D = \rho (X_1 - \text{mean}X_1) - (X_2 - \text{mean}X_2)$$

where

$$\rho = 2r(S_1S_2/S_1^2+S_2^2)$$

in which r is the correlation between X_1 and X_2 and S_1 and S_2 are standard deviations of the distribution of X_1 and X_2 . Thus, we will only describe effects on RTM-corrected changes between successive years. RTM-corrected changes are only a fraction of raw changes (0.50 and 0.55 on average for female wing and forehead patches respectively and 0.30 and 0.74 for male wing and forehead patches respectively).

Relative breeding date with respect to the population instead of absolute laying date was used to reflect the earliness-lateness in breeding which has been shown to have important associations with the breeding capacity of temperate birds. To that end we classified both females and males according to quartiles for each sex and year and for both areas pooled (area did not affect laying date when controlling for the strong effect of year), with the first quartile representing early birds, the two intermediate quartiles average birds and the last quartile late-breeding individuals. This factor was included in analyses. For breeding phenology in relation to environmental variables we analyzed climatic variables. We preferred a relative measure of breeding success to the absolute number of fledglings raised as there may exist individual optimization of clutch size, so absolute numbers do not reflect output with respect to capacity. Breeding success showed a highly skewed distribution towards high breeding success variables (more than 70% of individuals showing a success of 0.80 or higher). Thus a categorization was introduced whereby successful individuals were those with a breeding success of 0.80

or higher and unsuccessful individuals those with less than 0.80 success (a loss of one egg/chick or no loss).

We have conducted GLM analyses with the SAS statistical package (SAS Institute Inc., Cary, North Carolina,) of changes in both patches separately for females and males. Both patch sizes and their changes were normally distributed. We have included individual as random factor and degrees of freedom have been calculated according to the Satterthwaite method. As possible independent categorical factors affecting changes in trait expression we have considered study area, earliness in breeding (early, average, late) and breeding success category (successful/unsuccessful), and as independent covariables climatic factors for the initial season (PC1 and PC2), clutch size (unrelated to success), estimated age in the first year, wing length as an index of body size, initial trait expression and change in the other trait between the same years.

Results

Female wing patch

In small-patched females there was a tendency to show increases in the next year while the opposite was true in large-patched females (Table 1, Fig. 1a). There were significant effects of both climate PCs (Table 1). Cool and rainy conditions in May and June after a warm April were associated with patch reductions (Fig. 1b), while cold April conditions were linked to patch increments (Table 1).

Female forehead patch

In small-patched females there was a tendency to show increases in the next year while the opposite was true in large-patched females (Table 2, Fig. 2a). There was a significant negative association with climate PC1, with cold and rainy springs being associated with forehead patch decreases (Table 2). There was a significant effect of study area (Table 2), with a tendency for females in Valsaín to decrease their forehead

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patches and for females in Lozoya to increase theirs (Fig. 2c). This effect was significant ($F_{1,119}=7.87$, $P=0.006$, Table 2) despite the fact that females in Lozoya showed significantly larger patches than those in Valsaín (0.17 ± 0.01 versus 0.10 ± 0.01 cm², $F_{1,216}=14.9$, $p<0.001$), and should therefore increase less their forehead patches (Fig. 2a). Finally, successful females tended to increase their forehead patches more than unsuccessful females (Table 2, Fig. 2c).

Male wing patch

Small-patched males tended to show increases in the next year while the opposite was true in large-patched males (Table 3, Fig. 3). No other factor was significant (Table 3).

Male forehead patch

Small-patched males tended to show increases in the next year while the opposite was true in large-patched males (Table 4, Fig. 4a). There were significant effects of climate PC2, age and relative timing on changes in male forehead patch (Table 4). Cold conditions in April were associated with patch increments (Table 4). Older males showed a decrease in patch size (Table 4). Relative lateness in breeding was associated with patch increases and earliness with reductions (Fig. 4b).

Discussion

We have found a strong phenotypic constraint on expression of both patches in both sexes, so that initial signal extent delimits the possible subsequent changes negatively.

We also found a marked effect of locality on forehead patch changes in females, with the study area showing a population decline predicting patch reductions and vice versa.

Old males tend to reduce their forehead patches compared with young males. The most interesting associations of patch changes were with climate and with breeding

performance. In females cold and rainy springs (May and June) were linked to reductions in wing patch area . Cold conditions on arrival to the breeding grounds (April) were also related to wing patch increases in females and with forehead patch increases in males. With respect to reproductive performance, females with high breeding success experienced positive changes in forehead patch size more than unsuccessful females. Late-breeding males experienced forehead patch increases to the next year rather than early-breeding males. We will discuss these results in turn.

Several studies have previously shown that phenotypic plasticity is bounded for many continuous traits (Briffa et al. 2008, Schoepner and Relyea 2008, Kulkarni et al. 2009). Also for sexually selected traits phenotypic plasticity has been shown to be constrained (Nonaka et al. 2014, Pitchers et al. 2014, Wright et al. 2018), so that very large signals cannot increase further while very small signals cannot decrease incessantly. Thus, there is no point in studying within-individual phenotypic changes without taking into consideration potential limits on expression. A conclusion is that changes in continuous traits should preferably be statistically controlled for initial level of expression, even after correcting for RTM. This is supported by the fact that a large part of the changes experienced by individuals in signal expression in our study were linked to initial levels. Constraints on plasticity are due to the genetic architecture of traits which in turn has been selected by the ecological and social environment (Scheiner 2002, Foster et al. 2015).

Despite a similar climate, the two study areas differ with respect to conditions for breeding, with the population in Valsaín having experienced a protracted decline in breeding success in the last 25 years (González-Braojos et al. 2017). Conditions in Lozoya have not deteriorated in the last 18 years possibly because of the higher altitude at this locality (J. Moreno, unpubl. information). Lower population densities in Valsaín

means that competition for nest-boxes is much stronger at Lozoya (Moreno 2015). This in turn implies that signaling social dominance may be more important for both male and female fitness in Lozoya, as shown by the larger patches in Lozoya in both sexes. Despite females in Lozoya showing larger patches which should lead to negative rather than positive changes according to the strong negative association between initial expression and subsequent change, they still augmented more their patches than females in Valsaín. For males, there were no differences in trait changes between areas. This is difficult to explain if competition for cavities is stronger for males.

Sexual signals may experience a senescent decline along with other traits related to reproductive performance (Williams et al. 2006). On the other hand, terminal investment predicts that investment in sexual signals may increase over the lifetime (Kokko 1997). There is evidence both for age-dependent increases and declines in sexually selected traits (Velando et al. 2006, Galván and Møller 2009, Freeman-Gallant et al. 2010). In some cases, quadratic associations indicate that both increases of investment and senescent declines operate across the lifetime (Edler et al. 2012, Simons et al. 2016). In the closely related collared flycatchers, increases with age in ornamental plumage patches in both sexes have been shown (Hegyi et al. 2007,b, 2008, Evans et al. 2011), although female forehead patches were not considered in that study (probably because of its small extent). There is also evidence for age-dependent increases of the white forehead patch in male Iberian pied flycatchers (Galván and Moreno 2009). In our study, only males showed an indication of age-dependent changes in sexual signal expression and only with respect to forehead patches. Old males (more than 4 years) tended to reduce their forehead patches, while young males (1-2 years) tended to increase their expression. This result agrees with predictions from life-history theory, and indicates that forehead patch expression is affected by a general deterioration of

physical condition after 4 years in females (Sanz and Moreno 2000). Changes in both patches could be linked in relation with a common regulation of melanisation processes. However, no association between changes in the two patches was found in either sex (this study, see also Järvistö et al. 2016).

Two other studies have related within-individual changes in sexual signals to climatic conditions in *Ficedula* flycatchers. Hegyi et al. (2007b) found in collared flycatcher males that within-individual changes in forehead and wing patch size were predicted by the climate of their moulting season (winter and summer, respectively). Change in wing patch size was highest after summers with intermediate amounts of precipitation, while it was lower after very dry or very rainy years. There was also an indirect effect of previous winter climate on changes in wing patch size. Järvistö et al. (2016) focused on climate in Africa during the prenuptial moult of pied flycatcher males and did not consider conditions while breeding. None of these studies included females nor introduced breeding performance measurements taken prior to moult. Climate in the breeding range has been shown to affect reproductive performance in Valsáin (González-Braojos et al. 2017) and in Lozoya (unpubl. information). Warm conditions during incubation are associated with reductions in breeding success while during the nestling period they are linked to increases in breeding success (González-Braojos et al. 2017). The weather in April is also related to breeding success, with warm conditions at that time being followed by poor reproductive performance (González-Braojos et al. 2017). This is probably due to the fact that cold weather in April may mean a delayed caterpillar season and thus a better adjustment of the breeding schedule of pied flycatchers to the caterpillar peak (Sanz et al. 2003, González-Braojos et al. 2017). Thus a high winter NAO is linked to good nestling growth while high April temperatures predict poor recruit production (Sanz et al. 2003, González-Braojos et al. 2017). On the

other hand rainy conditions during incubation and nestling rearing and cold weather during nestling rearing are linked to reduced breeding success (González-Braojos et al. 2017).

Thus, warm conditions in April followed by rainy conditions in May and cold conditions in June represent mostly poor conditions for breeding. On the other hand, low April temperatures represent good conditions for breeding. Females respond to poor conditions for breeding (high PC1 meaning warm April weather followed by rainy conditions in May and cold conditions in June) by decreasing their white wing and forehead patches to the next year as carry-over effects. Warm conditions in April (low PC2 meaning unfavourable conditions for breeding output) are also followed by wing patch decreases in females and forehead patch decrements in males. This evidence accords well with the hypothesis of costs which predicts patch decrements after higher levels of breeding exertion (Gustafsson et al. 1995). Early breeding males are probably those suffering higher reproductive costs due to the costs of migrating early (Ruiz-de-Castañeda et al. 2009) and the stiffer competition for nest cavities at the beginning of the breeding season (Lobato et al. 2010). According to the cost hypothesis, we should expect these males to show patch decreases compared with late breeders as found for forehead patches. Moreover, this effect of relative timing of breeding should not be so strong in females which arrive later and show presumably lower levels of competition. No effect of timing was accordingly found in females.

Although some carry-over effects of climate can be explained by reproductive costs affecting subsequent patch moult, the absence of associations in some cases cannot be easily explained by costs. Thus, males show no trend of PC1 with respect to wing patches,. Furthermore, male wing patches show no significant carry-over effects related to breeding success. An alternative explanation for these absent trends is that

males are differently affected by climate than females. Males exert more effort early in the season (territoriality and courtship, where high PC1 indicates warm conditions) while females relatively more effort later on (where high PC1 indicates cold conditions). Thus, males may not be so strongly affected by poor conditions during incubation and nestling rearing as females.

If costs were to explain changes according to prior success, we should expect reproductively successful individuals to have spent more effort throughout the season by having raised a higher proportion of intended offspring. Thus, they should show decrements rather than increments in patches, contrary to our results for female forehead patches. However, this association may not be directly linked to an effect of reproductive effort as absolute clutch size has no significant effect on patch changes. Therefore, the positive success “effect” may be an effect of an unmeasured background variable related to individual female quality or condition. That is, unsuccessful females are those which are of poor quality, ill or in bad condition, and this background may also impinge on the future changes of patch sizes.

To conclude, conditions during breeding as expressed by local climate, relative timing of breeding and reproductive performance partly affect the moult of signals in both sexes occurring soon or months after the cessation of breeding activities. Our results do not suggest that conditions in the wintering areas are unimportant (see Järvistö et al. 2016 for evidence of their role), but rather that phenotypic plasticity also responds to conditions in the breeding areas Higher costs of breeding stimulate patch size decrements and vice versa, but patches seem also to be linked to sex differences in the temporal distribution of costs across the season and in the strength of the effects of individual quality.

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Ethical approval

Permissions for capturing and handling birds were provided by “Consejería de Medio Ambiente de Castilla y León” and “Consejería de Medio Ambiente de Comunidad de Madrid” for the Valsáin and Lozoya areas respectively. “Centro Montes de Valsáin” allowed us to work in Valsáin. The study was ethically approved by the Ethical Committee of CSIC.

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Figure Legends

Figure 1. Association of RTM-corrected change in wing patch area in females with (a) initial wing patch area ($r = -0.53$, $P < 0.001$) and (b) Climate PC1 ($r = -0.22$, $P = 0.023$).

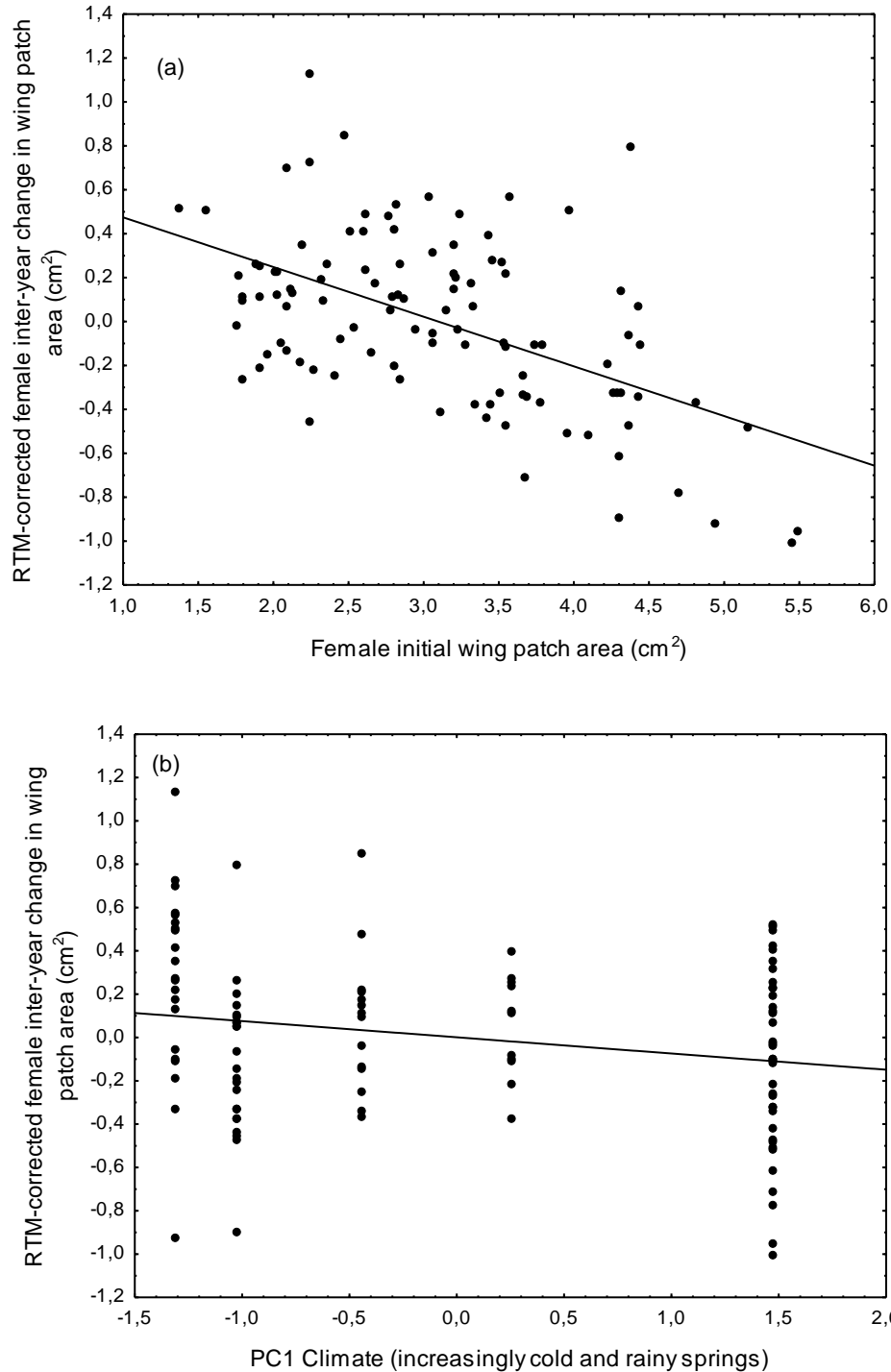
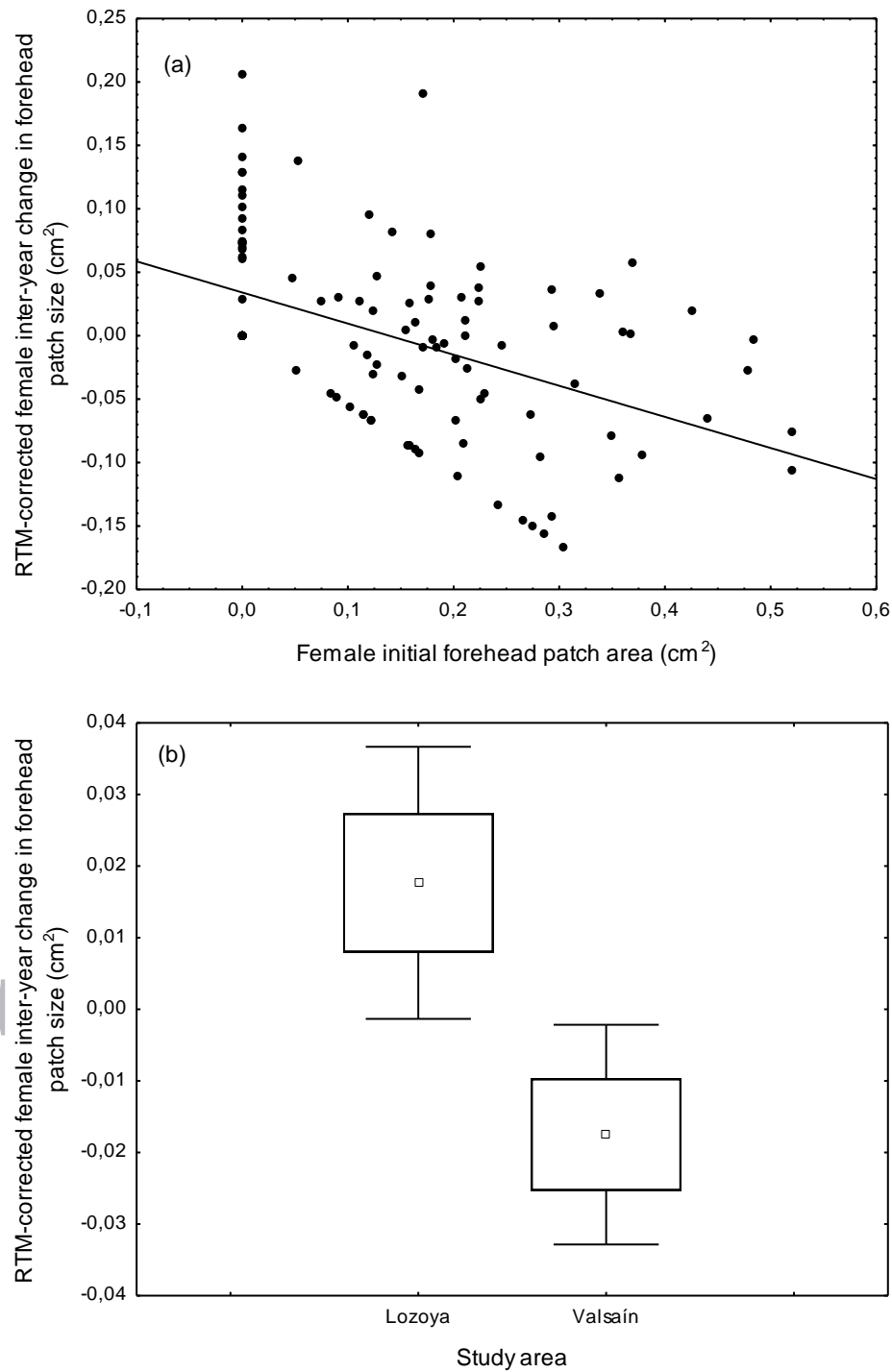


Figure 2. Association of RTM-corrected change in forehead patch area in females with (a) initial forehead patch area ($r = -0.48$, $P < 0.001$), (b) study area ($F_{1,119} = 7.87$, $P = 0.006$) and (c) breeding success ($F_{1,119} = 5.26$, $P = 0.024$). Boxes represent SE and whiskers represent 95 % CI.



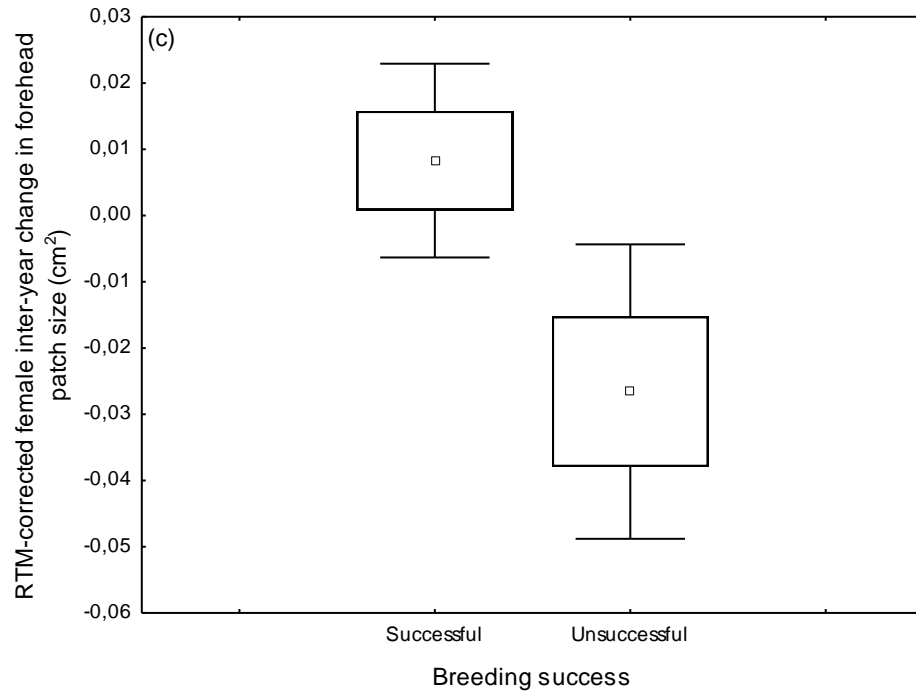


Figure 3. Association of change in RTM-corrected male wing patch area with initial wing patch area ($r = -0.55$, $P < 0.001$).

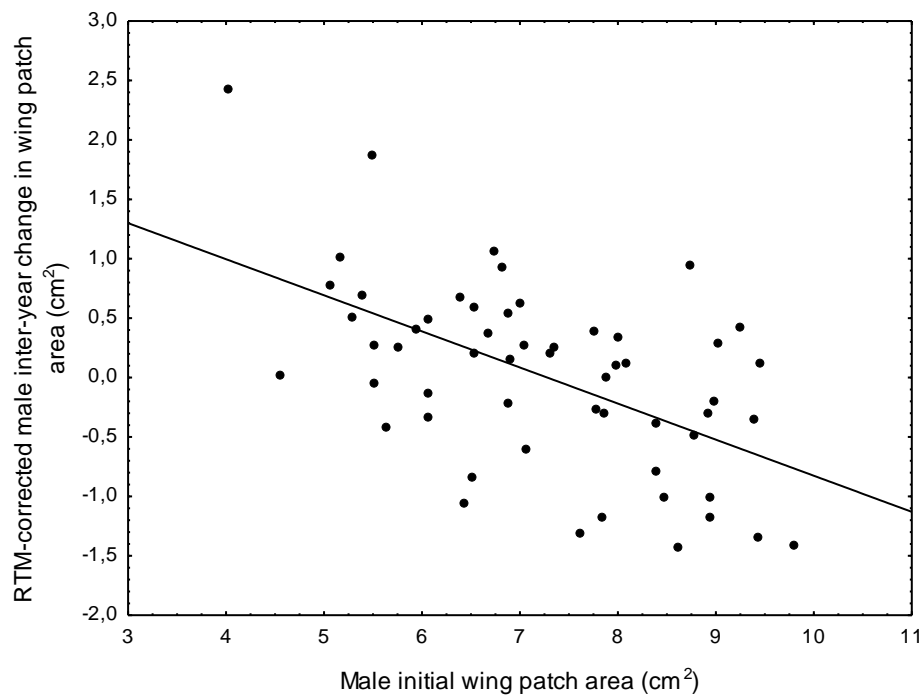


Figure 4. Association of RTM-corrected change in forehead patch area in males with (a) initial forehead patch area ($r = -0.44$, $P < 0.001$) and (b) relative timing ($F_{2,81} = 4.10$, $P = 0.020$). Boxes represent SE and whiskers represent 95 % CI.

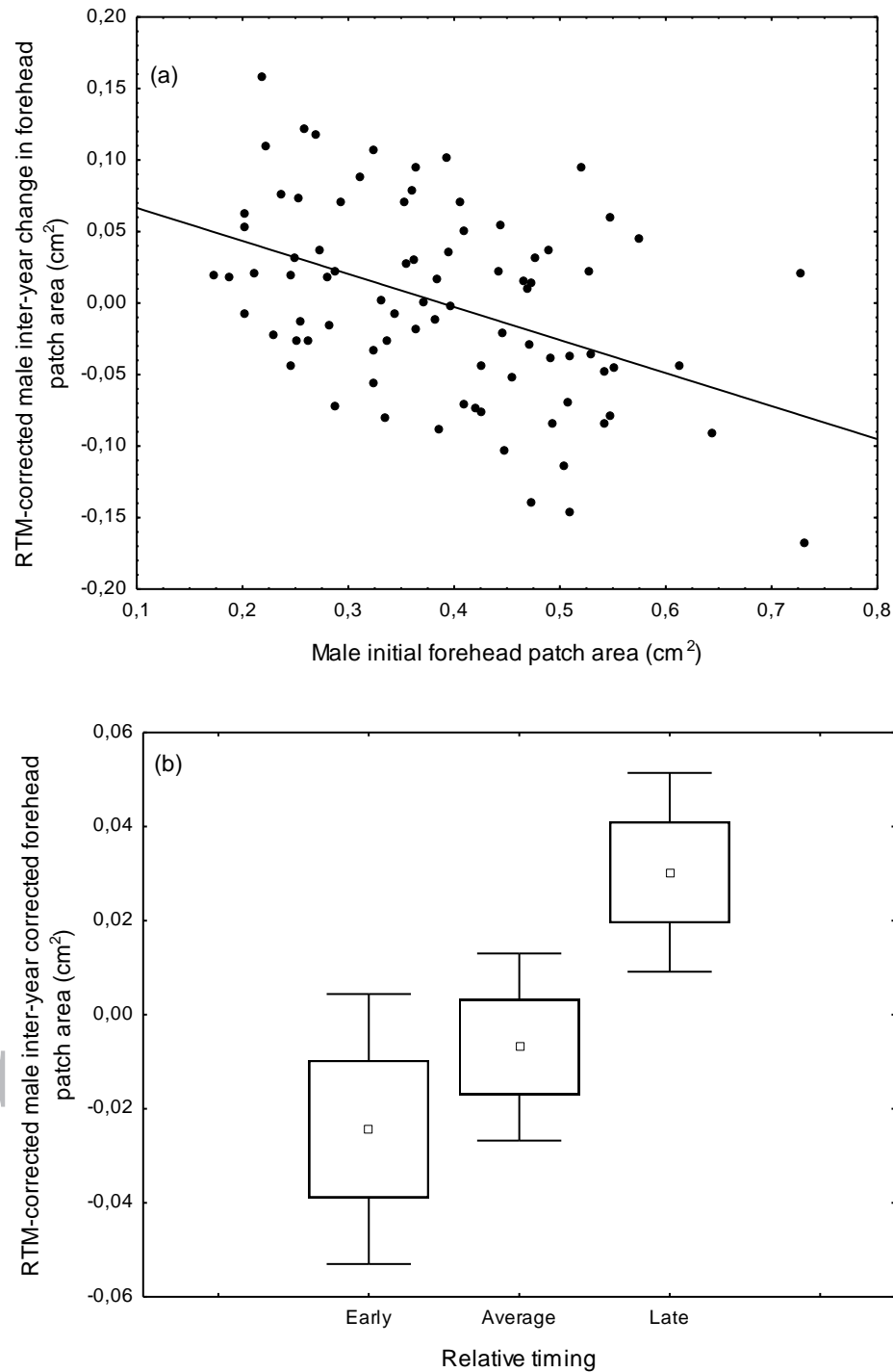


Table Legends

Table 1. GLM results for independent effects on RTM-corrected female inter-year change in wing patch with Denominator df computed using the Satterthwaite method (significant *P*-values are in bold).

		<i>Estimate</i> ± <i>SE</i>	<i>Num</i> <i>df</i>	<i>Den</i> <i>df</i>	<i>F</i>	<i>P</i>
PC1 Climate	Covariate	-0.062±0.027	1	89	5.17	0.0254
PC2 Climate	Covariate	0.090±0.034	1	89	7.17	0.0088
Clutch size	Covariate	0.061±0.046	1	89	1.79	0.1846
Estimated age	Covariate	0.319±0.336	6	89	0.79	0.5809
Wing length	Covariate	-0.001±0.017	1	89	0.00	0.9575
Forehead patch change	Covariate	0.521±0.458	1	89	1.30	0.2577
Initial wing patch area	Covariate	-0.262±0.037	1	89	50.72	<0.0001
Study area	Fixed	-0.137±0.074	1	89	3.45	0.0665
Relative timing	Fixed	-0.090±0.079	1	89	0.70	0.4983
Breeding success	Fixed	0.002±0.079	2	89	0.00	0.9786
Individual	Random	0.000±0.000	1	89	0.00	1.00

Table 2. GLM results for independent effects on RTM-corrected female inter-year change in forehead patch with Denominator df computed using the Satterthwaite method (significant *P*-values are in bold).

		<i>Estimate</i> ± <i>SE</i>	<i>Num</i> <i>df</i>	<i>Den</i> <i>df</i>	<i>F</i>	<i>p</i>
PC1 Climate	Covariate	-0.011±0.005	1	83.1	4.88	0.0299
PC2 Climate	Covariate	0.006±0.006	1	88.7	0.98	0.3240
Clutch size	Covariate	-0.013±0.008	1	87.8	2.48	0.1186
Estimated age	Covariate	-0.101±0.063	6	83.6	1.41	0.2221
Wing length	Covariate	-0.002±0.003	1	85.7	0.87	0.3530
Wing patch change	Covariate	0.011±0.015	1	73.3	0.47	0.4960
Initial forehead patch area	Covariate	-0.322±0.045	1	73.7	51.51	<0.0001
Study area	Fixed	-0.041±0.013	1	64.8	10.31	0.0021
Relative timing	Fixed	-0.007±0.015	2	84.9	0.35	0.7048
Breeding success	Fixed	0.037±0.014	1	88.9	6.95	0.0099
Individual	Random	0.001±0.001	1	89	0.06	0.4751

Table 3. GLM results for independent effects on RTM-corrected male inter-year change in wing patch area with Denominator df computed using the Satterthwaite method (significant *P*-values are in bold).

		<i>Estimate</i> ± <i>SE</i>	<i>Num</i> <i>df</i>	<i>Den</i> <i>df</i>	<i>F</i>	<i>p</i>
PC1 Climate	Covariate	0.146 ± 0.092	1	41	2.52	0.1199
PC2 Climate	Covariate	0.118 ± 0.089	1	41	1.77	0.1912
Clutch size	Covariate	-0.114 ± 0.136	1	41	0.71	0.4058
Estimated age	Covariate	0.3443 ± 0.883	4	41	0.21	0.9302
Wing length	Covariate	0.006 ± 0.057	1	41	0.01	0.9204
Forehead patch change	Covariate	-0.258 ± 1.591	1	41	0.03	0.8719
Initial wing patch area	Covariate	-0.287 ± 0.077	1	41	13.78	0.0006
Study area	Fixed	0.418 ± 0.214	1	41	3.83	0.0573
Relative timing	Fixed	-0.375 ± 0.276	2	41	1.19	0.3131
Breeding success	Fixed	0.045 ± 0.329	1	41	0.02	0.8925
Individual	Random	0.000 ± 0.000	1	41	0.00	1.00

Table 4. GLM results for independent effects on RTM-corrected male inter-year change in forehead patch area with Denominator df computed using the Satterthwaite method (significant *P*-values are in bold).

		<i>Estimate ± SE</i>	<i>Num df</i>	<i>Den df</i>	<i>F</i>	<i>p</i>
PC1 Climate	Covariate	0.003±0.005	1	36.4	0.36	0.5532
PC2 Climate	Covariate	0.013±0.006	1	62.9	5.18	0.0263
Clutch size	Covariate	-0.015±0.008	1	62.6	3.65	0.0606
Estimated age	Covariate	-0.189±0.056	4	31.3	2.96	0.0348
Wing length	Covariate	-0.003±0.003	1	63.5	0.66	0.4185
Wing patch change	Covariate	0.010±0.008	1	40.8	1.56	0.2188
Initial forehead patch area	Covariate	-0.271±0.054	1	59.1	25.10	<0.0001
Study area	Fixed	-0.015±0.015	1	48.6	1.02	0.3187
Relative timing	Fixed	-0.008±0.016	2	56.8	3.60	0.0337
Breeding success	Fixed	-0.005±0.017	1	46.7	0.08	0.7749
Individual	Random	0.001±0.001	1	57	1.43	0.0759