The Role of Dispersal in the Long-Term Trajectory and Selection Pattern of a Secondary Sexual Trait in Pied Flycatchers

Master's Final Project

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1. Abstract

Dispersal, the tendency of animals to reproduce in a different place from where they were born, is common among animals. Dispersal entails costs that may induce life history trade-offs and thus affect the trajectory of phenotypes, including sexual traits. Here, using a 32-year dataset from an individual monitored population of pied flycatchers (*Ficedula hypoeluca*), we analyzed the temporal trends and phenotypic selection patterns of a heritable and sexually selected ornament in males, the forehead patch size, in relation to dispersal. We conducted these analyses from two complementary approaches related to the dispersal status of individuals, according to (1) breeding experience in the area i.e. recruits (born in the nest boxes) vs immigrants (unringed birds first capture breeders) (2) natal dispersal between the two habitat types (a pine and an oak forest) that exist in the study area. We found that the resident/immigrant status did not affect the forehead patch size trend. Also, phenotypic selection analysis (using the number of recruits as a fitness proxy) showed that there was no effect of the forehead patch size on selection regardless the resident or immigrant status. On the other hand, natal dispersal affected the forehead patch with philopatrics males of the pine forest having bigger forehead patches on average than the other groups. However, we did not find phenotypic selection of the forehead patch in relation to natal dispersal. Overall, these results suggest that fitness mediated by the dispersal decisions is unrelated to the forehead patch size.

Key words: selection, dispersal, sexual traits, long-term trajectories, pied flycatchers

2. Introduction

Sexual selection is a major driver of phenotypic variation (Andersson, 1982; Payne, 1984). In many species, individuals of one or both sexes exhibit conspicuous traits that are sexually selected. The production and maintenance of these traits involves costs, thus only high quality individuals may afford the cost associated with producing or maintaining enhanced version of sexual traits (Kilpimaa et al., 2004). However, the balance between the costs and benefits of expressing a trait is not constant, but rather may depend, among other factors, on environmental (local) conditions, on the familiarity or degree of adaptation to the breeding habitat (Kotiaho, 2001).

Natal philopatry, the tendency of adults to reproduce at their natal site, is common among animals (Greenwood, 1980; Greenwood & Harvey, 1982; Pärt, 1994). Nevertheless, not all individuals within populations remain philopatric, but some disperse to potentially unfamiliar environments. Although dispersal is an elemental factor in ecological and evolutionary patterns, the final factors that influence dispersal variation in natural populations remains unclear. Dispersal decisions may be affected by several factors, such as genetic composition (Jaenike & Holt, 1991; Doligez et al., 2009), early experience in the natal habitat (Davis & Stamps, 2004; Stamps et al., 2009) or by certain phenotypic and/or behavioral traits (Edelaar et al., 2008). Further, dispersal is often related to a range of costs such as those associated with the development of dispersal structures (Bell et al., 2005), the search for the optimal habitat (Hinsley, 2000), the loss of familiarity with the environment (Dickinson, 2009), the loss social rank (Vanderwerf, 2008), and the advantages of local adaptation (Tack & Roslin, 2010). Importantly, dispersal-mediated costs may induce life history trade-offs and thus affect the trajectory of phenotypes, including sexual traits as ornamental production and maintenance, and consequently the sexual selection and the evolution of populations

(Dieckmann et al., 1999; Bonte et al., 2011). Since the expression of a sexual trait is costly to produce or maintain, and dispersal imposes costs on individuals, it is expected that individuals resolve sexually mediated trade-offs in different ways to minimize overall costs (Bonte et al., 2011; Kinnison et al., 2003; Roff et al., 2003). If the differential action of selection on the expression of sexual traits is prolonged, the evolutionary trajectories of these traits are expected to differ between immigrants and philopatrics, which may also influence the trajectory of the phenotype in the population (Dieckmann & Doebeli, 1999; Bonte et al., 2011).

Here, we used a dataset collected from 1988 to 2020 from individual-based monitored population of pied flycatchers (*Ficedula hypoleuca*) to investigate whether phenotypic trajectory and phenotypic selection of a male sexual trait, the forehead patch size, is mediated by dispersal. The pied flycatcher is a small (11-13 g) long-distance migratory passerine, sexually dimorphic during the breeding season, that breed in natural tree cavities in temperate forest across Europe and winters in western Africa. Males arrive earlier than females to the breeding grounds (Potti, 1998; Potti & Montalvo, 1991; Lundberg & Alatalo, 1992), compete to establish a territory around a nesting site and try to attract a female (Dale & Slagsvold, 1990). Although pied flycatchers can reproduce in a wide variety of temperate forest, they prefer deciduous or mixed deciduous-coniferous forests over pure coniferous forests due to the scarcity of natural nest cavities and the prevalence of larger insects in the latter (Lundberg & Alatalo, 1981; Alatalo et al., 1985; Lundberg & Alatalo, 1992). However, the coniferous forest can be more attractive by adding artificial nest-boxes (Potti & Montalvo, 1990). Our study area is composed by two habitats, an oak forest, and a pine forest (see methods) between which they can disperse. Male pied flycatchers show conspicuous white forehead patches, an heritable and reliable indicator of individual quality that is both intra- and inter-sexually selected (Gustafsson, et al., 1995; Järvistö et al., 2013; Potti 1993; Potti & Merino 1996; Potti & Montalvo 1991a) as, for example, males with large forehead patches enjoy competitive and mating advantages both socially and through extra pair-paternity (Sanz, 2001; Canal et al., 2011; Järvistö, 2013). This study system provides thus an excellent opportunity to document the temporal dynamics of a sexual selected trait on different habitats, which may imply local adaptation (Camacho et al., 2019).

Based on previous knowledge, we expect directional, positive selection favoring larger forehead patches. However, the cost of express and maintain a sexual trait and, subsequently their reproductive success, may differ for immigrants and philopatric individuals. Thus, we analyze the trajectories and phenotypic selection of forehead patches from two complementary approaches, according to (1) breeding experience in the area i.e. recruits (born in the nest boxes) vs immigrants (unringed birds first capture breeders) (2) natal dispersal. In our study area, most pied flycatchers return to their natal patch to breed regardless of the habitat type, but over 25% of recruits change habitats (Camacho et al. 2013, 2016). Thus, four groups can be constituted based on whether individuals born and breed in the same or different habitat type (philopatrics of oak forest, philopatrics of pine forest, dispersals from oak forest to pine forest, dispersals from pine forest to oak forest). Overall, we predict a lower forehead patch expression and/or a negative selection, whether or not mediated by this sexual trait, on immigrants in relation to philopatric individuals. This is due to two non-mutually exclusive processes. First, immigrants (both related to the habitat patch or the population) lack crucial prior information about the local environment, including distribution of food resources or predation risk, which may confer them a reproductive disadvantage compared to philopatric individuals (Pärt, 1994; Slagsvold & Wiebe, 2018). Second, the genotype of immigrants may be poorly adapted to local environment at their destination and, therefore, their genetic contribution to the population may be limited compared to locally adapted philopatrics (Schluter, 2000; Hendry & Taylor, 2004; Nosil et al., 2005; Blondel et al., 2006).

3. Methods

Study area

Fieldwork was carried out between 1988 and 2020, in a wild population of pied flycatcher breeding in nest boxes near La Hiruela, in central Spain (41° 04′ N, 3° 27′ W). Sampling intensity was limited in years 2002 and 2003 and therefore, these years were excluded from analyses.

The study area and field protocol are described in detail in (Camacho et al., 2015, 2018; Potti et al., 2018). The study area consists in two habitats that differs ecologically: a mature deciduous oak forest and a mixed pine forest. The deciduous forest of oaks is a very heterogenous and well-structured habitat of 9.3 ha. It has a mean density of 460 trees ha^{-1} dominated by old oaks (*Querqus pirenaica*), but also a dense groundcover of *Erica arborea*, *Cistus laurifolius* and *Crataegus monogyna* (0.5–3 m high; mean cover 80 %) has evolved after the resource exploitation ceased over 50 years ago. The coniferous forest has 4.8 ha and it is a more homogeneous habitat constituted by a monoculture of Scots pines (*Pinus silvestris*) at a mean density of 200 trees ha^{-1} and scattered *Cupressus arizonica* and *Pinus pinaster* trees with spare shrubs of *Cistus laurifolius* and *Crataegus monogyna* (0.5-2 m of high; mean cover 5%) in the open areas (Camacho et al., 2015). Both areas are separated by 1.1 km. The movement between habitats is free, there is not physical barriers, but intermediated zones are unsuitable for pied flycatchers to settle and reproduce.

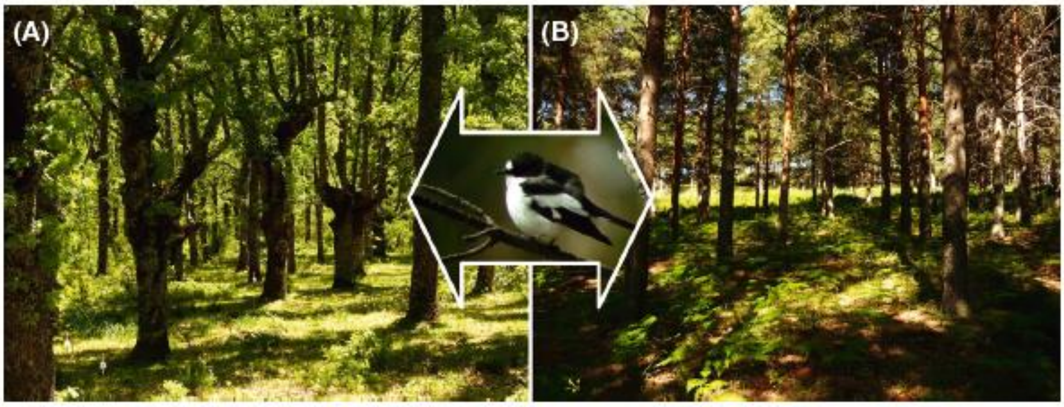

Image 1. Study system, a male pied flycatcher (Ficedula hypoleuca) and the study habitats: A) Deciduous oak forest, B) Mixed pine forest. From Camacho et al. 2013.

In total, there are 156 nest-boxes in the oak forest and 83 nest-boxes in the pine forest and their position has not changed since the beginning of the study. Nest boxes are placed at a mean distance of 30 m (SD 14.1) (Camacho et al., 2015).

Field work procedures

During the breeding period, from mid-April until early July, nest-boxes are regularly checked to determinate the exact laying dates, clutch sizes, hatching dates and numbers of fledged young. Adults were captured while incubating (females) or while feeding chicks (both sexes) with a trap installed inside the nest box on day 8-10 post-hatching (Potti et al. 2021). Individuals were marked with a numbered metal ring (males and females) and a unique combination of color rings (only males), weighted (± 0.1 g) and measured for tarsus length (± 0.01 mm), wing length (± 0.5 mm), dorsal coloration and forehead white patch (± 0.01 mm). The area of the forehead patch was calculated as patch height × width. Only a fraction of females (approx. 37%) express the forehead patch thorough their life and this expression (yes/no) is strongly related to age (only 6% of females express the patch at early ages; Potti et al. 2013). For these reasons, in this study, we only focus on the trajectory and selection of forehead patches in males.

Due to strong breeding fidelity of adults in the species, including the study population (Canal et al., 2014; Potti et al., 2013; Potti & Montalvo, 1991), the exact age of many birds was known (on average, 53% of breeding adults are born in the nestboxes; Potti & Montalvo, 1991b). Unringed birds first caught as breeding adults are considered hereafter as “immigrants”, while philopatric individuals that were first ringed as fledglings are referred hereafter as “residents”. Unringed breeders were aged as first-year or older based on plumage traits following ageing criteria described in Karlsson et al. (1986) and Potti and Montalvo (1991b).

All nestlings were ringed at the age of 13 days with metal rings, enabling us to establish their fate (returned/not returned) in the following years as a proxy of recruitment, to evaluate the number of recruits (reproductive success) and their natal dispersal (see below).

Dispersal patterns

In this study, natal dispersal is considered as a change in the forest plot (e.g. from the pine to the oak forest or vice versa) regardless the distance between the birth nest-box and the first breeding nest-box. Due to the small scale of the study area, and the migratory behavior of the bird, proximity to birth nest-box should not influence dispersal behavior. However, the structure of the forest type is different, which leads to differences in food availability, diet and population density, and may motivate dispersal.

Since, dispersal behavior after the first breeding period is very unlikely (<4%, Camacho et al., 2013) and because early experience affects breeding decisions (Camacho et al., 2016), we only focus on natal dispersal.

Based on the habitat of origin and first reproduction, natal dispersal was classified into 4 groups: oak forest philopatric birds (N=364), pine forest philopatric birds (N=174), oak to pine forest dispersers (N=75) and pine to oak forest dispersers (N=61).

In the study population (i) all nest boxes are sampled and recruitment rates are among the highest reported for the species (up to 22%, on average 14%; Canal et al., 2014; Potti et al., 2013; Potti & Montalvo, 1991a), (ii) non-systematic explorations of surrounding areas, as well as ring recoveries from other study populations of Iberian pied flycatchers, indicate that dispersal outside the study area is an extremely unusual event. (iii) mark-recapture analyses have shown that variation in the probabilities of survival (transition) and recapture do not change with time (Santoro et al., submitted). Therefore, we assume that our recruitment estimates are reliable and an unbiased sample of all recruits and that unringed birds captured as breeding individuals are immigrants from outside the study area.

Statistical analysis

Temporal trends in the forehead patch

Resident or Immigrant status analysis. We used Linear Mixed Models (LMM) to investigate the trend in the forehead patch size relative to the immigrant/resident status over the study period. We fitted a model, where we included the size of the forehead white patch as the response variable. As predictors we included breeding habitat type (two-levels class variable: oak or pine forest) to account for differences in habitat quality (Camacho et al., 2015), year of reproduction (a continuous variable to consider temporal component) and dispersal status (two-levels class variable: resident or immigrant) as well as their two-way interactions and the three-fold interaction. The three-fold interaction was included to investigate whether the forehead patch varies differently between residents and immigrants in each habitat over time. Because of the progressive increase in breeding density throughout the study period (see Camacho et al., 2019), we did not include density in the analyses to avoid collinearity problems with the variable of year. Further, male ages (two-levels class variable: yearling or older) and tarsus length, a common proxy of structural body size in this (Lundberg & Alatalo, 1992) and other passerines (Senar & Pascual, 1997), were included as fixed effects to account for age and size related differences in phenotypic expression. Male identity and the year of reproduction were included as random factors to account for the non-independence of samples from the same year or individual.

Natal dispersal status analysis. We used LMM to investigate the effects of natal dispersal on the trend of forehead patch size over the study period. As the only differences with the previous dispersal model, we included the variable natal dispersal (4 groups) instead of immigrant status. As the 4 levels of the natal dispersal variable already included information on the habitat of birth and breeding (see methods), breeding habitat was also removed from the models.

Selection analyses

Resident or Immigrant status analysis. To analyse patterns of selection on male forehead patch according to the immigrant status, we fitted Generalized Linear Mixed

Models (GLMMs) to the data on the annual number of recruits (as a surrogate of fitness). Using annual values instead of the lifetime number of recruits allowed us to maximize the sample size by keeping all individuals regardless of the presence of annual gaps in their capture histories. As predictors, we included the forehead patch size (centred and standardized by subtracting the mean annual patch size in the population divided by its standard deviation), its squared term to explore non-linear associations with fitness, the resident status (two class variable: resident or immigrant), year (as continuous variable to consider a temporal component on selection) and the two- and three-way interactions between the previous variables. As commented above, breeding density have increase throughout the study period, thus we did not include this variable in the analyses to avoid collinearity problems. In addition, we included three controlling variables in the model: (1) Breeding habitat type (two-level class variable: oak or pine) to account for differences in habitat quality (Camacho et al., 2015); (2) Breeding (egg laying) date, because it is a key predictor of reproductive success in this (Canal et al., 2012) and many other bird species (Newton, 2008); and (3) male age (two-level class variable: yearling or older), to account for age-related differences in performance, as described in this and other bird species (Evans et al., 2011; Lundberg & Alatalo, 1992; Nol & Smith, 1987). We included male and female identities as random intercepts since birds appear multiple times in the dataset and to control for the potential effects of female mates on the reproductive success of males. Breeding season identity (i.e. categorical year effect) was also included as a random intercept to account for the non-independence of samples from the same year and stochastic variation among years (see e. g. Evans & Gustafsson, 2017 for a similar approach).

Natal dispersal status analysis. To analyse patterns of selection on male forehead patch according to the natal dispersal, we fitted Generalized Linear Mixed Models (GLMMs) with the same fixes effects, interaction and random structure than the selection models above. As the only differences with the previous selection model, we included the variable natal dispersal (4 groups) instead of immigrant status. As the 4 levels of the natal dispersal variable already included information on the habitat of birth and breeding (see methods), breeding habitat was also removed from the models. We also exclude the square term of the standardized forehead patch size to simplify the model due to problems of convergence.

When analysing the selection on forehead patch, we used the corrected Akaike information criterion (AICc; Wagenmakers & Farrell, 2004) to sequentially compare the goodness-of-fit of different error distributions. These analyses showed that the most supported models, both when investigating selection on forehead patch based on immigrant and natal dispersal status, had a Conway-Maxwell-Poisson distribution and zero inflation. Therefore, we present the results based on these two models.

Extra-pair paternity occurs in this population (Canal et al., 2011; 2012) and might affect selection patterns. However, it is unlikely that extra-pair paternity causes a severe bias in our selection estimates for a number of reasons. First, a two-year molecular study indicated that the frequency of extra pair young (EPY) in the study population amounted to 11-20% (Canal et al. 2012), of which only males (ca. 50%) are considered in the present analysis. Second, the number of recruits per nest in the study population is on average 0.5 (Le Vaillant et al., 2021), further reducing the potential impact of EPY. Specifically, in the two-year study mentioned above, the total number of male recruits being EPY per year was n=5 and n=7, representing 12% and 6% of all recruits. Given the annual number of breeding males in the population (up to 170 males), the influence of these individuals on our analyses is expected to be small to negligible. Third, as shown by Charmantier & Réale (2005), the effect of relatively low frequencies of EPY (such as those in our population) on selection analyses are expected to be small.

Male pied flycatchers may postpone their first breeding attempt until their second year of life (Potti and Montalvo,1991b). Thus, to avoid underestimation of recruitment for the 2000 and 2001 cohorts due to the limited field effort in 2002 and 2003, we excluded those years from the selection analysis. For the same reason, all birds born in the last two years of study (2019 and 2020) were also excluded from the analysis.

Before interpreting the statistical results, we systematically performed model diagnostics statistics and data exploration to avoid misleading results based on statistical artefacts (e.g. by checking distributions of raw data, model residuals, multicollinearity) (Zuur et al., 2010). We found collinearity between years and population density, so we compare models and use years for the better adjust.

Statistical analyses were performed in R.4.0.3. For the linear mixed modelling we used the package lme4 (Bates et al., 2014), and for the generalized mixed modelling we used the package glmmTMB (Brooks et al., 2017). Significance of the fixed effects in the models was calculated with Type II Wald Chi-Square tests, using the function Anova (car package; Fox & Weisberg, 2011) on maximum likelihood models, while parameter estimates were calculated using Restricted Maximum Likelihood (Zuur et al., 2009). The representation of data was done using ggplot2 (Villanueva & Chen, 2019) and sjPlot (Lüdecke, 2018) packages.

4. Results

Temporal trends in the forehead patch

Resident - Immigrant status. We found that the male forehead patch increased over the study period similarly in immigrants and residents, regardless type of habitat (interactions: Resident status*Year of reproduction; Resident status*Habitat; Resident status*Habitat*Year of reproduction; Table 1). However, the forehead patch trend changed differently between habitats along the study period (interaction habitat*year of reproduction; Table 1). Specifically, the phenotypic trajectory of the forehead patch size of males in the pine forest showed a faster increased than the one from the males of the oak forest (Figure 1).

Natal dispersal status analysis. We found that in all groups there was an increase in forehead patch size over the years. Further, in the philopatric males of the pine forest this increment was greater than in the other groups (interaction Natal flow* Year of Reproduction; Table 2; Figure 2). In the oak forest, it seems that dispersers always had smaller forehead patch sizes than philopatrics over the study years, but they maintain the same trend of variation (Figure 2). In the pine forest, dispersers (from the pine to the oak forest) had larger forehead patches than philopatric males at the beginning of the study, but situation changed over the years and since 2011 dispersers, born in the pine forest, had smaller patches than philopatrics (Figure 2).

Selection analysis

Resident - Immigrant status. We found that the number of recruits decreased over the study period in both groups (Figure 3). The number of recruits was unrelated to the forehead patch size in relation to the resident/immigrant status over the study period (interactions: Forehead patch size* Resident status* Year of reproduction; Forehead patch size* Resident status* Year of Reproduction; Table 3; Figure 3). The age and size of the forehead patch over the years neither affected the fitness of males (Table 3). However, the number of recruits was higher in the pine forest than in the oak forest and decreased over the study period and with the advance of the breeding season (Table 3).

Natal dispersal status analysis. The size of the forehead patch, and its interactions with the natal flow over the years have no effect on the number of recruits (interaction Forehead patch size* Natal flow* Year of Reproduction; Table 4). However, the dispersal status over the years affected the number of recruits (Natal flow* Year of Reproduction; Table 4). Males that dispersed from the pine forest to the oak forest experienced a steeper decline in the number of recruits than the other groups during the study period (Figure 4).

5. Discussion

Using individual-based data collected during 32 years from a pied flycatcher population, we have investigated whether the phenotypic trajectory and/or phenotypic selection on the forehead patch, a sexually selected trait, differ between individuals with and without previous knowledge of the breeding habitat. We found that the forehead patch size increased similarly in residents and immigrant over the study period (Table 1).

However, the resident males from the pine forest experienced a greater temporal increase of the forehead patch than the other groups (oak residents and immigrants; Figure 1). Selection analysis showed that there was no effect of the forehead patch size on fitness regardless the resident or immigrant status (Table 3). In relation to the natal dispersal, we found that the pine forest philopatrics experienced the greatest growth of the trait throughout the study period (Figure 2). We did not find selection on the forehead patch size in relation to natal dispersal status over the study years (Table 4). However, regardless the forehead patch size, males dispersing from the pine to oak forest, the preferred habitat, were negatively selected (Table 4; Figure 4).

The forehead patch size increased over the study period similarly between residents and immigrants, without previous experience in the study population. As immigrants are expected to pay an additional dispersal cost in relation to residents (Bonte et al., 2011), a similar level of trait expression could occur thought a different resolution of life-history trade-offs i.e. reduced reproductive success. Under this scenario, the genetic contribution will be low to the population although the temporal phenotypic trait will be similar between residents and immigrants. However, selection analysis showed that residents are not negatively selected in relation to immigrants. Several non-mutually exclusive mechanisms may explain this pattern. First, it is possible the costs that an immigrant pays by showing a large forehead patch is expressed in other component of fitness as survival prospects (Cooke et al., 2019). Second, perhaps, only immigrants of high quality are able to reproduce in the population (Kilpimaa et al., 2004). Third, the cost of producing a signal increase in poor environmental conditions and that increase is expected to by higher in immigrants due to the additional costs related to dispersal (Møller and de Lope, 1994; Kotiaho, 2000). It is possible that conditions over the study period were not adverse enough to trigger detectable biological responses, thus all individuals could confront the cost of producing or maintaining a sexual trait regardless of the resident status and the signal expressed. However, this seems an unrealistic possibility as the study period cover 30 years and variables with potential effect on intra and inter-sexual competition as breeding density and climatic factors has varied during this period (Camacho et al 2016, Le Vaillant et al. 2021). Further work should investigate if selection on the forehead patch is mediated by environmental conditions. Fourth, selection may have fluctuated over the time, resulting in non-detectable overall pattern, as reported for laying date in this population (Le Vaillant et al., 2021) and other species (Grant, 2002). Fifth, we found that the forehead patch has increased at different rates in the two habitats (pine > oak) throughout the study period (Table 3). Thus, it is possible that immigrants disperse and reproduced in either the pine or oak forest based on the similarity of their own breeding habitat or their ability to express a phenotype similar to the phenotype of the habitat where they eventually reproduced (Blondel et al., 1993; Bonte et al., 2010). This would reduce the costs of dispersal and trait expression, thereby diluting differences in fitness according to the dispersal status.

When analyzing effects of natal dispersal on the forehead patch size, we found that the group of philopatric males in the pine forest showed a greater increase in the forehead patch size over the study period than the other groups. Indeed, this group passed to have the smallest patches at the beginning of the study to have the biggest patches at the end of the study period (Figure 2). As explained above, given the cost associated to dispersal and the relationship between the forehead patch and (intra- and inter) sexual contexts, we expected a lower reproductive success of dispersing individuals in relation to this sexual trait. However, the interactive effect of forehead patch and natal dispersal status had not effect on breeding success of individuals (Table 4). There are at least two non-mutually exclusive mechanisms, similar to those suggested for the resident/immigrant approach (explained above), that may explain this pattern: i) selection might be occurring on other fitness component and/or ii) environmental conditions were not adverse enough to trigger detectable biological responses. Interestingly, we found that natal dispersal decisions, regardless of the forehead patch size, affected the number of recruits over the study period (Table 4). Specifically, males dispersing to the oak forest, the preferred habitat (Lundberg & Alatalo, 1981; Alatalo et al., 1985; Lundberg & Alatalo, 1992), experienced a lower number of recruits over time (Figure 4). Thus, it is possible that dispersers from the pine to the oak forest are suffering an ecological "trap" (Schlaepfer et al., 2002). Perhaps, the differential increase in the intensity of competition for nest sites and food resources in the oak and the pine forest (Camacho et al. 2013) may be underlying this pattern. The concept of ecological trap is gaining renewed interest due to growing concern about the adaptive capacity of organisms in changing environments (Schlaepfer et al., 2002) so it would be interesting to test in further studies.

6. Conclusions

We found that temporal phenotypic change in forehead patch size was not affected by resident/immigrant status. Further, we found no selection on forehead patch size in relation to the resident/ immigrant status. Based on a natal dispersal approach, we found that philopatrics birds from the pine forest were the group experiencing the greatest growth in the trait throughout the study period, but it was not reflected in selection analyses. Overall, we have shown that the phenotypic trajectory of a sexual traits in native and dispersers is not mediated by phenotypic selection.

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8. References

Alatalo, R.V., Lundberg, A. & Ulfstrand, S. (1985). Habitat selection in the pied flycatcher *Ficedula hypoleuca*. Habitat selection in birds. *London: Academic Press*, *59*, 84.

Andersson, M. (1982). Sexual selection, natural selection and quality advertisement. *Biological Journal of the Linnean Society*, *17*, 375-393.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1-48.

Bell, J.R., Bohan, D.A., Shaw, E.M. & Weyman, G.S. (2005). Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research 95*, 69-114.

Blondel, J., Dias, P.C., Maistre, M. & Perret, P. (1993). Habitat heterogeneity and life-history variation of mediterranean blue tits (Parus caeruleus). *Auk 110*, 511-520

Blondel, J., Thomas, D., Charmantier, A., Perret, P., Bourgault, P., & Lambrechts, M. (2006). A thirty-year study of phenotypic and genetic variation of blue tits in mediterranean habitat mosaics. *Bioscience, 56*(8), 661.

Bonte, D., De Roissart, A., Vandegehuchte, M.L., Ballhorn, D.J., Van Leeuwen, T. & de la Pena, E. (2010). Local adaptation of boveground herbivores towards plant phenotypes induced by soil biota. *Plos One 5*, e11174.

Bonte, D., Van Dyck, H., Bullock, J., Coulon, A., Delgado, M., & Gibbs, M. et al. (2011). Costs of dispersal. *Biological Reviews*, *87*(2), 290-312.

Brooks, M., Kristensen, K., Benthem, K., Magnusson, A., Berg, C., & Nielsen, A. et al. (2017). glmmTMB Balances speed and flexibility among packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378.

Camacho, C., Canal, D. & Potti, J. (2013). Nonrandom dispersal drives phenotypic divergence within a bird population. *Ecology Evolution, 3*, 4841-4848.

Camacho, C., Canal, D. & Potti, J. (2015). Testing the matching habitat choice hypothesis in nature: phenotype-environment correlation and fitness in a songbird population. *Evolutionary Ecology*, *29*, 873-886.

Camacho, C., Canal, D. & Potti, J. (2016). Natal habitat imprinting counteracts the diversifying effects of phenotype-dependent dispersal in a spatially structured population. *BMC Evolutionary Biology*, *16*, 158.

Camacho, C., Canal, D. & Potti, J. (2017). Lifelong effects of trapping experience lead to age-biased sampling: lessons from a wild bird population. *Animal behavior, 130*, 133-139

Camacho, C., Martínez-Padilla, J. & Canal, D., Potti, J. (2019). Long-term dynamics of phenotype-dependent dispersal within a wild bird population. *Behavioral Ecology, 30*(2), 548-556

Camacho, C., Pérez-Rodríguez, L., Abril-Colón, I., Canal, D. & Potti, J. (2018). Plumage colour predicts dispersal propensity in male pied flycatchers. *Behavioral Ecology and Sociobiology*, *72,* 2.

Canal, D., Dávila, J. & Potti, J. (2011) Male phenotype predicts extra-pair paternity in pied 641 flycatchers. *Behaviour*, *148*, 691-712.

Canal, D., García-González, F. & Zsolt Garamszegi, L. (2021). Experimentally constrained early reproduction shapes life history trajectories and behavior. *Scientific Reports, 11*, 4442

Canal, D., Jovani, R., & Potti, J. (2012). Male decisions or female accessibility? Spatiotemporal patterns of extra pair paternity in a songbird. *Behavioral Ecology*, *23*(5), 1146-1153.

Canal, D., Serrano, D. & Potti, J. (2014). Exploring heterozygosity-survival correlations in a wild songbird population: Contrasting effects between juvenile and adult Stages. *PLoS ONE, 9*(8): e105020.

Charmantier, A., & Reale, D. (2005). How do misassigned paternities affect the estimation of heritability in the wild?. *Molecular Ecology*, *14*(9), 2839-2850.

Cooke, R., Bates, A., & Eigenbrod, F. (2019). Global trade-offs of functional redundancy and functional dispersion for birds and mammals. *Global Ecology And Biogeography*, *28*(4), 484-495.

Dale, S. & Slagsvold, T. (1990). Random settlement of female pied flycatchers *Ficedula hypoleuca*: significance of male territory size. *Animal Behavior*, *39*, 231-243.

Delgado, M.M., Penteriani, V., Revilla, E. & Nams, V.O. (2010). The effect of phenotypic traits and external cues on natal dispersal movements. *Journal of Animal Ecology*, *79*, 620-632

Davis, J., & Stamps, J. (2004). The effect of natal experience on habitat preferences. *Trends In Ecology & Evolution*, *19*(8), 411-416.

Dickinson, J. L., Euaparadorn, M., Greenwald, K., Mitra, C. & Shizuka, D. (2009). Cooperation and competition: nepotistic tolerance and intrasexual aggression in western bluebird winter groups. *Animal Behaviour 77*, 867-872.

Dieckmann, U. & Doebeli, M. (1999). On the origin of species by sympatric speciation. *Nature 400*, 354-357.

Doligez, B., Gustafsson, L., & Pärt, T. (2009). 'Heritability' of dispersal propensity in a patchy population. *Proceedings Of The Royal Society B: Biological Sciences*, *276*(1668), 2829-2836.

Edelaar, P., Siepielski, A., & Clobert, J. (2008). Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution*, *62*(10), 2462-2472.

Evans, S.R. & Gustafsson, L. (2017). Climate change upends selection on ornamentation in a wild bird. *Natural Ecology & Evolution*, *1*(2), 39-39

Evans, S., Gustafsson, L., & Sheldon, B. (2011). Divergent patterns of age-dependence in ornamental and reproductive traits in the collared flycatcher. *Evolution*, *65*(6), 1623-1636.

Fox, J. & Weisberg, S. (2011). Multivariate linear models in R. An R Companion to Applied Regression. *Los Angeles: Thousand Oaks*.

Grant, P. (2002). Unpredictable evolution in a 30-year study of darwin's finches. *Science, 296*(5568), 707-711.

Greenwood, P. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour, 28*(4), 1140-1162.

Greenwood, P., & Harvey, P. (1982). The natal and breeding dispersal of birds. *Annual Review Of Ecology And Systematics*, *13*(1), 1-21.

Gustafsson, L., Qvarnström, A., & Sheldon, B. (1995). Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature, 375*(6529), 311-313.

Hendry, A.P. & Taylor, E.B. (2004). How much of the variation in adaptive divergence can be explained by gene flow? - An evaluation using lake-stream stickleback pairs. *Evolution, 58*, 2319-2331.

Hinsley, S.A. (2000). The costs of multiple patch use by birds. *Landscape Ecology*, *15*, 765-775

Jaenike, J., & Holt, R. (1991). Genetic variation for habitat preference: Evidence and Explanations. *The American Naturalist*, *137*, S67-S90.

Järvistö, P.E., Laaksonen, T. & Calhim, S. 2013. Forehead patch size predicts the outcome of male-male competition in the pied flycatcher. *Ethology, 119*(8), 662-70.

Karlsson, L., Persson, K. & Walinder, G. (1986). Ageing and sexing in pied flycatchers, *Ficedula hypoleuca*. *Var Fagelvaild*, 45, 131-146

Kilpimaa, J., Alatalo, R., & Siitari, H. (2004). Trade–offs between sexual advertisement and immune function in the pied flycatcher (*Ficedula hypoleuca). Proceedings Of The Royal Society Of London. Series B: Biological Sciences*, *271*(1536), 245-250.

Kinnison, M.T., Unwin, M.J. & Quinn, T.P. (2003). Migratory costs and contemporary evolution of reproductive allocation in male chinook salmon. *Journal of Evolutionary Biology*, 16, 1257-1269.

Kotiaho, J. (2000). Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. *Behavioral Ecology And Sociobiology*, *48*(3), 188-194.

Kotiaho, J. (2001). Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biological Rev*iews, *76*, 365-376

Le Vaillant, J., Potti, J., Camacho, C., Canal, D., & Martínez-Padilla, J. (2021). Fluctuating selection driven by global and local climatic conditions leads to stasis in breeding time in a migratory bird. *Journal Of Evolutionary Biology*, 34(10), 1541-1553

Lüdecke D. (2018). sjPlot - Data visualization for statistics in social science. Available from: https://zenodo.org/record/1310947

Lundberg, A., Alatalo, R., Carlson, A., & Ulfstrand, S. (1981). Biometry, habitat distribution and breeding success in the pied flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica*, *12*(1), 68.

Lundberg, A. & Alatalo, R.V. (1992). The pied flycatcher. *Poyser, London*

Møller, A., de Lope, F., Moreno, J., González, G., & Pérez, J. (1994). Ectoparasites and host energetics: house martin bugs and house martin nestlings. *Oecologia, 98*(3-4), 263-268.

Newton, I. (2008). The migration ecology of birds. *Academic Press, London, UK.*

Nol, E., & Smith, J. (1987). Effects of Age and Breeding Experience on Seasonal Reproductive Success in the Song Sparrow. *The Journal Of Animal Ecology*, *56*(1), 301.

Nosil, P., Vines, T., & Funk, D. (2005). Reproductive isolation caused by natural selection against immigrants from divergent habitats. *Evolution*, *59*(4), 705-719.

Pärt, T. (1994). Male philopatry confers a mating advantage in the migratory collared flycatcher, *Ficedula albicollis*. *Animal Behaviour*, *48*(2), 401-409.

Payne, R. (1984). Sexual Selection, Lek and Arena Behavior, and Sexual Size Dimorphism in Birds. *Ornithological Monographs*, (33), iii-52.

Potti, J. (1998). Arrival time from spring migration in male pied flycatchers: individual consistency and familial resemblance. *The Condor, 100*(4), 702-708.

Potti, J., Camacho, C., Canal, D. & Martínez-Padilla, J. (2018). Long-term occupancy of nest boxes as a measure of territory quality for Pied Flycatchers. *Journal of Field Ornithology*, *89*(4), 337-347

Potti, J., Camacho, C., Canal, D., & Martínez-Padilla, J. (2021). Three decades of crimes and misdemeanours in the nest box life of european pied flycatchers *Ficedula hypoleuca*. *Ardeola*, *68*(2), 315-333.

Potti, J., Canal, D. & Serrano, D. (2013). Lifetime fitness and age-related female ornament signaling: evidence for survival and fecundity selection in the pied flycatcher. *Journal of Evolutionary Biology, 26*, 1445-1457.

Potti, J., & Merino, S. (1996). Decreased levels of blood trypanosome infection correlate with female expression of a male secondary sexual trait: implications for sexual selection. *Proceedings Of The Royal Society Of London. Series B: Biological Sciences*, *263*(1374), 1199-1204.

Potti, J. & Montalvo, S. (1990). Ocupación de áreas con nidales por el papamoscas cerrojillo (*Ficedula hypoleuca*). *Ardeola, 37*, 75–84.

Potti, J. & Montalvo, S. (1991a). Male arrival and female mate choice in pied flycatchers *Ficedula hypoleuca* in Central Spain. *Ornis Scandinavical, 22*(1), 45-54.

Potti, J. & Montalvo, S. (1991b). Return rate, age at first breeding and natal dispersal of pied flycatchers *Ficedula hypoleuca* in central Spain. *Ardea, 79*, 419-428

Potti, J. (1993). A male trait expressed in female pied flycatchers, *Ficedula hypoleuca*: the white forehead patch. *Animal Behaviour*, *45*(6), 1245-1247.

Roff, D.A., Crnokrak, P. & Fairbairn, D.J. (2003). The evolution of trade-offs: geographic variation in call duration and flight ability in the sand cricket, *Gryllus firmus*. *Journal of Evolutionary Biology, 16*, 744-753

Santoro, S., Fernández-Díaz, P., Canal, D., Camacho, C., Garamszegi, L.Z., Martínez-Padilla, J. & Potti, J. (Submitted). High frequency of social polygyny reveals little costs for females in a songbird. *Scientific Reports*.

Sanz, J.J. (2001). Experimentally reduced male attractiveness increases parental care in the 615 pied flycatcher *Ficedula hypoleuca*. *Behavioral Ecology, 12*, 171-6.

Schlaepfer, M., Runge, M., & Sherman, P. (2002). Ecological and evolutionary traps. *Trends In Ecology & Evolution, 17*(10), 474-480.

Schluter, D. (2000). Ecological character displacement in adaptive radiation. *The American Naturalist, 156*(S4), S4-S16.

Senar, J.E. & Pascua.l J. (1997). Keel and tarsus length may provide a good predictor of avian body size. *Ardea, 85*, 269-274

Slagsvold, T., & Wiebe, K. (2018). Immigrants and locally recruited birds differ in prey delivered to their offspring in blue tits and great tits. *Animal Behaviour*, *139,* 127-135.

Stamps, J., Krishnan, V., & Willits, N. (2009). How different types of natal experience affect habitat preference. *The American Naturalist*, *174*(5), 623-630.

Tack, A., & Roslin, T. (2010). Overrun by the neighbors: Landscape context affects strength and sign of local adaptation. *Ecology*, *91*(8), 2253-2260.

Vanderwerf, E.A. (2008). Sources of variation in survival, recruitment, and natal dispersal of the Hawai'i 'Elepaio. *Condo,r 110*, 241–250.

Villanueva, R., & Chen, Z. (2019). ggplot2: Elegant graphics for data analysis (2nd ed.). *Measurement: Interdisciplinary Research And Perspectives*, *17*(3), 160-167.

Wagenmakers, E., & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychonomic Bulletin & Review*, *11*(1), 192-196.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology Evolution*, 1, 3–14.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. &, Smith, G.M. (2009). Mixed effects models and extensions in ecology with R. *Springer, New York*.

9. Tables and Figures

Table 1. Resident/Immigrant status analysis: results of linear mixed models testing the resident status effects on the size of forehead patch along the study period between habitats. Parameter estimates and SE were calculates using REML models

Random effects	***Variance***	***Std. Deviation***			
ID male	152.513	12.35			
Year of Reproduction	9.593	3.097			
Residuals	64.641	8.04			
Fixed effects	***Estimate***	***Std. Error***	***Wald X^2***	***Wald df***	***P-value***
Intercept	50.166	12.695	-	-	-
Habitat (pine forest)	-45.152	13.543	0.1431	1	0.705
Dispersal stat (residents)	-0.744	8.803	0.078	1	0.779
Year of Reproduction	0.296	0.084	31.655	1	<0.001*
Age (Adult)	2.963	0.582	25.876	1	<0.001*
Tarsus length	-1.396	0.484	8.321	1	0.003*
Habitat (pine forest): Dispersal stat (resident)	4.267	18.115	1.395	1	0.238
Habitat (pine forest): Year Rep.	0.434	0.127	21.936	1	<0.001*
Dispersal stat (resident): Year Rep.	0.010	0.083	0.003	1	0.960
Habitat (pine forest): Dispersal stat (resident): Year Rep.	-0.057	0.169	0.113	1	0.736

Table 2. Natal dispersal status analysis: results of linear mixed models testing the natal dispersal status effects on the size of forehead patch along the study period. Parameter estimates, and SE were calculates using REML models

Random effects	***Variance***	***Std. Deviation***			
ID male	149.74	16.183			
Year of Reproduction	8.59	2.931			
Residuals	65.43	8.089			
Fixed effects	***Estimate***	***Std. Error***	***Wald X^2***	***Wald df***	***P-value***
Intercept	48.258	16.183	-	-	-
Natal flow:	-	-	6.730	3	0.081
Oak to pine forest	-11.670	19.596	-	-	-
Pine forest philopatrics	-51.238	14.878	-	-	-
Pine to oak forest	-2.375	19.917	-	-	-
Year of Reproduction	0.316	0.085	28.171	1	<0.001*
Age (Adult)	2.355	0.734	10.292	1	0.001*
Tarsus length	-1.362	0.694	3.851	1	0.049*
*Natal flow*Year Rep:*	-	-	12.727	3	0.005*
*Oak to pine forest*Year Rep.*	0.207	0.193	-	-	-
*Pine forest philopatric*Year Rep.*	0.507	0.147	-	-	-
*Pine to oak forest*Year Rep.*	0.004	0.211	-	-	-

Table 3. Selection models immigrants: results of Generalized Linear Mixed Models testing patterns of selection on male forehead patch according to the resident status over the study period.

Random effects	***Variance***	***Std. Deviation***			
ID Female	0.055	0.234			
ID Male	0.049	0.222			
Year of Reproduction	0.123	0.350			
Fixed effects	***Estimate***	***Std. Error***	***Wald X^2***	***Wald df***	***P-value***
Intercept	2.714	0.807	-	-	-
Forehead patch	-0.101	0.238	2.4622	1	0.117
Sqrt. forehead patch	0.074	0.194	0.787	1	0.375
Year of Reproduction	-0.015	0.008	3.796	1	0.051*
Dispersal status (Residents)	-0.024	0.409	1.938	1	0.164
Habitat (Pine Forest)	0.147	0.035	17.635	1	<0.001*
Age (Adult)	0.002	0.045	0.003	1	0.956
Laying date	-0.012	0.003	15.785	1	<0.001*
*Forehead patch*Dispersal stat (Resid)*	0.276	0.323	1.753	1	0.185
*Sqrt Forehead patch*Dispersal stat (Resid)*	-0.198	0.246	0.820	1	0.365
Forehead patch Year Rep.*	<0.001	0.002	0.198	1	0.656
Sqrt Forehead patch Year Rep.*	<-0.001	0.002	0.225	1	0.635
Dispersal stat (Resid) Year Rep.*	<0,001	0.002	0.584	1	0.445
Forehead patch Dispersal stat. (Resid)* Year Rep.*	-0.002	0.003	0.547	1	0.459
Sqrt . For. patch Dispersal stats (Resid).* Year Rep.*	0.002	0.002	0.532	1	0.466

Table 4. Selection models natal dispersal: results of Generalized Linear Mixed Models testing patterns of selection on male forehead patch according to the natal dispersal over the study period.

Random effects	***Variance***	***Std. Deviation***			
ID Female	0.069	0.263			
ID Male	0.041	0.204			
Year of Reproduction	0.123	0.351			
Fixed effects	***Estimate***	***Std. Error***	***Wald X^2***	***Wald df***	***P-value***
Intercept	2.519	0.810	-	-	-
Sqrt. forehead patch	0.107	0.276	0.414	1	0.520
Natal flow:	-	-	10.386	3	0.016*
Oak to pine forest	-0.879	1.268	-	-	-
Pine forest philopatrics	-0.421	0.734	-	-	-
Pine to oak forest	1.710	1.082	-	-	-
Year of Reproduction	-0.013	0.008	2.477	1	0.116
Age (Adult)	0.011	0.058	0.034	1	0.853
Laying date	-0.011	0.004	6.469	1	0.011*
Forehead patch: Natal flow:	-	-	1.221	3	0.748
Forehead patch: Oak-Pine	1.929	1.364	-	-	-
Forehead patch: Pine philopatrics	-0.624	0.609	-	-	-
Forehead patch: Pine-Oak	0.561	1.232	-	-	-
Sqrt. Forehead patch: Year Rep.	-0.001	0.003	0.131	1	0.717
Natal flow: Year Rep.	-	-	9.260	3	0.026*
Oak to pine forest: Year Rep.	0.009	0.012	-	-	-
Pine forest philopatric: Year Rep.	0.005	0.007	-	-	-
Pine to oak forest: Year Rep.	-0.017	0.009	-	-	-
Sqrt. Forehead patch: Natal flow: Year Rep.	-	-	3.569	3	0.312
Sqrt. Forehead patch: Oak-Pine: Year Rep.	-0-017	0.013	-	-	-
Sqrt. Forehead patch: Pine philop.: Year Rep.	0.006	0.006	-	-	-
Sqrt. Forehead patch: Pine-Oak: Year Rep.	-0.004	0.011	-	-	-

Figure 1. Forehead patch trend by habitat and resident status. Hir-Imm: Habitat La Hiruela (oak forest), Immigrants (not ringed before); Hir-Res: Habitat La Hiruela, Residents; Mt-Imm: Habitat Montes Claros (pine forest), Immigrants; Mt-Res: Habitat Montes Claros, Residents.

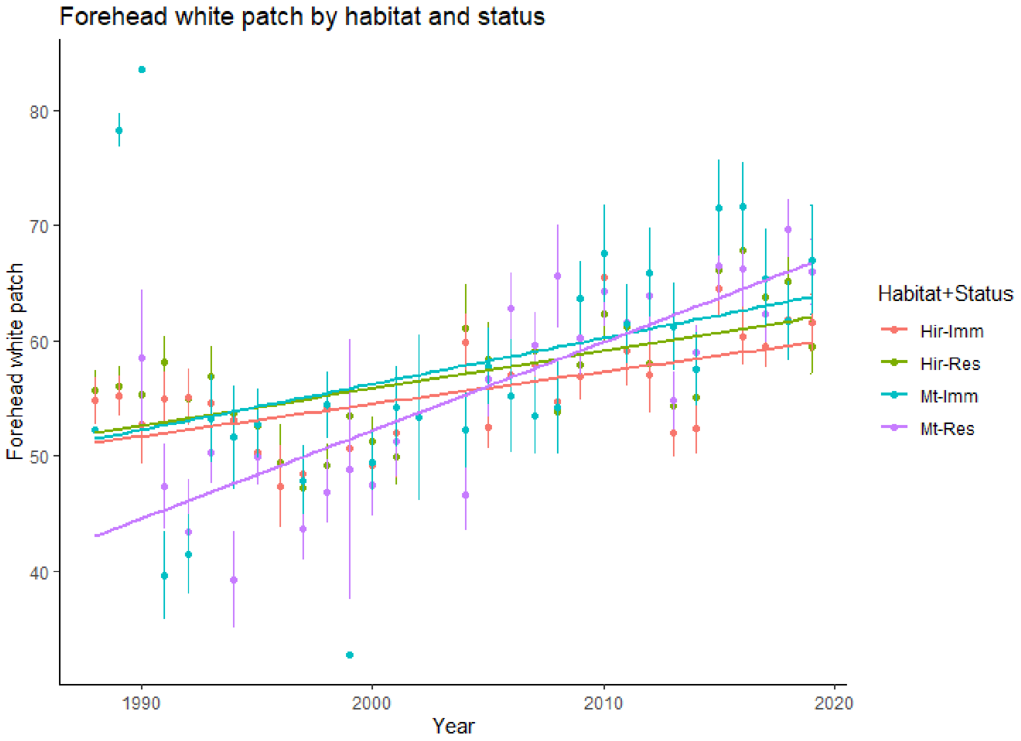

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Figure 2. Forehead white patch trend by natal dispersal. Hir-Hir: birds born in La Hiruela (oak forest) that breeds in La Hiruela; Hir-Mt: birds born in La Hiruela that breeds in Montes Claros (pine forest); Mt-Hir: birds born in Montes Claros that breeds in La Hiruela; Mt-Mt: birds born in Montes Claros that breeds in Montes Claros.

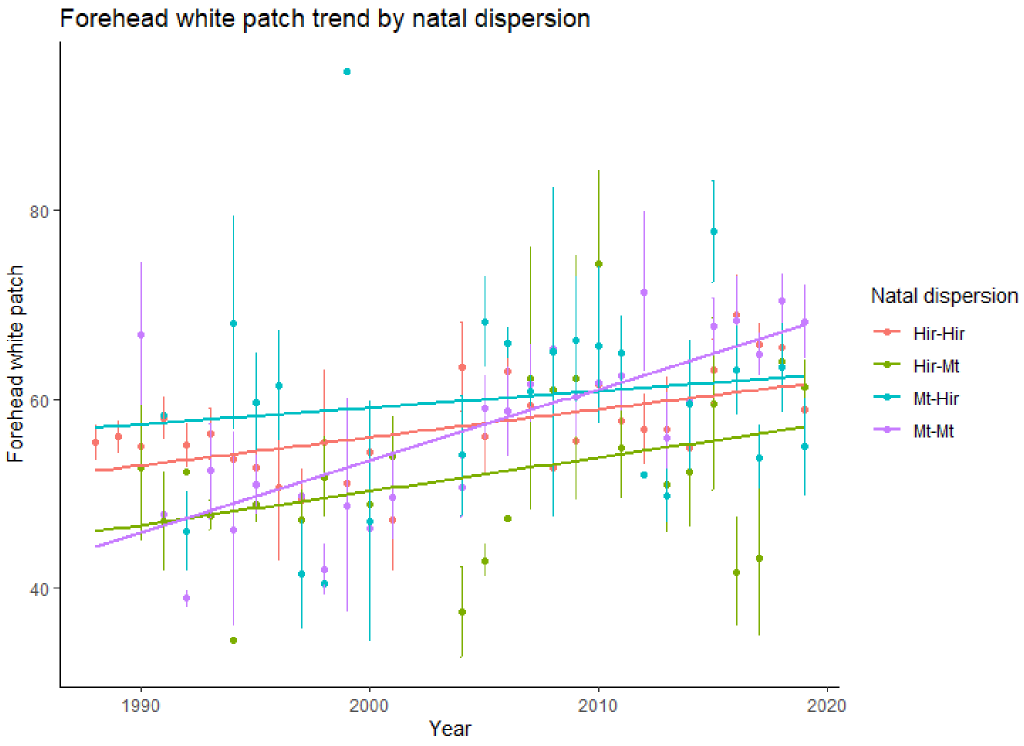

Figure 3. Number of recruits by resident status among years. I: immigrants; R: residents. (Year transformation: 90=1990, 100=2000, 110=2010)

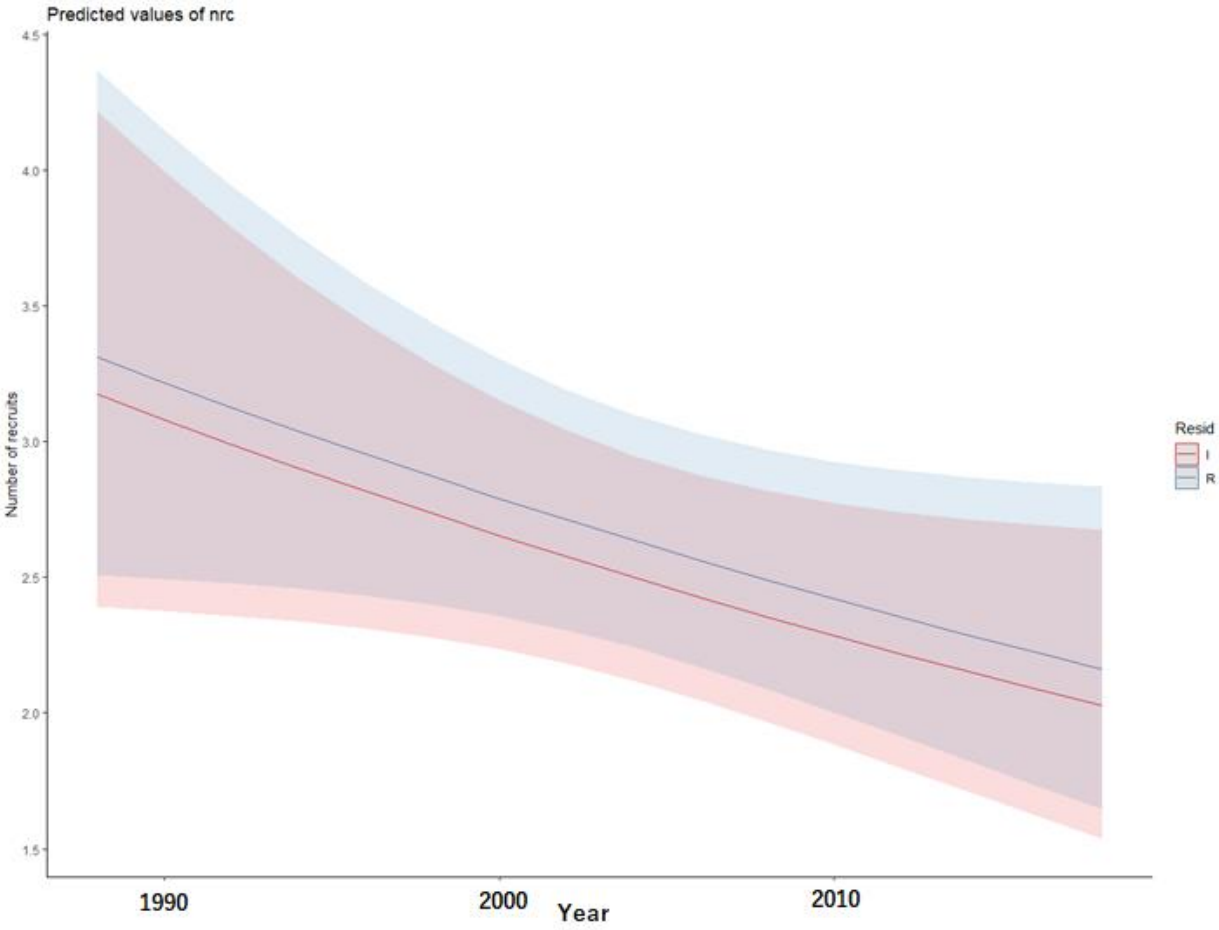

Figure 4. Number of recruits by natal dispersal among years. Hir-Hir: birds born in La Hiruela (oak forest) that breeds in La Hiruela; Hir-Mt: birds born in La Hiruela that breeds in Montes Claros (pine forest); Mt-Hir: birds born in Montes Claros that breeds in La Hiruela; Mt-Mt: birds born in Montes Claros that breeds in Montes Claros.