PATTERNS OF SELECTION ON THE DORSAL COLORATION OF PIED FLYCATCHERS

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Abstract

Individuals in natural populations are constantly under selection and environmental factors, either exerting fixed or fluctuating pressures over time, are major drivers of this process. Long-term studies are needed to show the evolutionary dynamics of populations through changes in their phenotypic traits. Here, we analyze the phenotypic selection on the dorsal plumage color of pied flycatchers (*Ficedula hypoleuca*) by using individual based information collected from a long-term study over 26 breeding seasons. Number of fledglings and number of recruits were used as proxies of fitness on the analyses of selection on the plumage color. Our results show a stabilizing selection on the dorsal color as relatively dark phenotypes had more recruits than individuals with extremely brown or dark dorses. Selection did not vary over the study period nor with breeding density, which is considered an important environmental factor affecting reproductive success of individuals. Our findings provide valuable information about selective processes in natural populations. Future studies exploring the factors that drive selection on phenotypic traits should assess the relative importance of diverse (biotic and abiotic) agent of selection.

Keywords: *Ficedula hypoleuca*, phenotypic selection, dorsal color, breeding density, long-term study.

Introduction

Environmental changes, exacerbated under ongoing climate change, impose major challenges to natural populations (Alberti et al., 2017; Bussotti et al., 2014; Evans & Gustafsson, 2017; Gienapp et al., 2008; Mason & Unitt, 2018). Understanding the evolutionary mechanisms underlying local adaptation is essential to predict the evolutionary potential of populations and thus, their capacity of persistence under current scenarios of environmental change (Dreiss et al., 2012; Gomez-Mestre & Tejedo, 2003; Razgour et al., 2019).

Selection occurs when an individual expressing a particular phenotype has a fitness advantage compared with other individuals in the population (Hayward et al., 2018). Diverse factors boosting environmental and temporal variation may cause phenotypic distributions to vary both within and between generations (Wade & Kalisz, 1990). The expression of sexual traits is crucial for success in reproduction as they may indicate individual quality (Andersson, 1994; Cooney et al., 2019; Gil & Gahr, 2002; Webster et al., 1995). In the case of birds, the coloration of the plumage or the degree of expression of certain ornaments is known to be a reliable sign of the social status and/or of the physical and behavioral capabilities of individuals (Badyaev et al., 2001; Mateos-Gonzalez et al., 2011).

Environmental factors may vary in space and time, either in a predictable or erratic mode, playing a key role in phenotypic selection within populations (Garant, 2020). Abiotic factors such as precipitation and temperature are known to generate phenotypic changes in populations as a result of selective processes (Charmantier et al., 2008; Evans & Gustafsson, 2017; Garant et al., 2004; Gienapp et al., 2008; Kiss et al., 2020; Merilä & Hendry, 2014; Parmesan, 2006; Parmesan & Yohe, 2003; Remacha et al., 2020; Romano et al., 2019; Root et al., 2003). However, the effects of biotic factors such as predation, synchrony or population density within the population and the ecosystem, have rarely been quantified (Fisher et al., 2019; Reimchen & Nosil, 2002). In particular, population density may have a strong influence on the evolutionary trajectories of sexual traits because sexual selection is a density-dependence process, that is, density determines the probability and variability of potential mates and competitors (Carranza et al., 2020; Punzalan et al., 2010; Siepielski & Benkman, 2007; Steele et al., 2011). However, to our knowledge, only one study has quantified the selection on sexual traits during prolonged periods of time, while simultaneously considering the influence of environmental factors on the strength or direction of the selection (Evans & Gustafsson, 2017).

Here, we investigate in a pied flycatcher (*Ficedula hypoleuca*) population, the existence of selection on the dorsal plumage color of males and if so, if selection is mediated by breeding density, an environmental variable that may have important consequences on fitness due to its implications on competition (intra and inter-specific) for resources and mates. The pied flycatcher, a classical model species in evolutionary ecology (Camacho et al., 2018; Canal et al., 2011; Järvistö et al., 2016; Lamers et al., 2020; Lundberg & Alatalo 1992; Moreno et al., 2019; Sirkiä & Laaksonen, 2009), is a long-distance migrant passerine that breeds in the Western Palearctic and migrates to the wintering areas in the sub-Saharan regions. Males arrive earlier than females to the breeding grounds (Potti, 1998; Potti & Montalvo, 1991; Lundberg & Alatalo, 1992), establish a territory around a nesting site, and try to attract a female. Dorsal color in males varies substantially both within (Potti &

Montalvo, 2008) and between populations (Laaksonen et al., 2015), ranging from completely black males to brown individuals with an appearance similar to that of females (Drost, 1936; Lundberg & Alatalo, 1992). Previous works have shown that dorsal coloration is a signal of individual quality (Siitari & Huhta, 2002) as darker individuals establish earlier their breeding territories, have higher singing diversity and feed their fledglings at higher rates than browner males (Lampe & Espmark, 1994; Lundberg & Alatalo, 1992; Saetre et al., 1995). Based on these characteristics, we expect that selection favor black phenotypes over individuals with brownish plumages. In addition, we also analyze the effect of the temporal and/or environmental variation (breeding density) on the selection on dorsal color.

Methodology

Field work

Data were collected between 1988 and 2016 from a long-term study population of pied flycatchers breeding in nest-boxes in central Spain (La Hiruela, 41°04' N, 3°27' W). Sampling intensity was limited in the years 2002 and 2003 and therefore these years were excluded from further analyses. In total, we used data from 26 breeding seasons.

The study area is constituted by two plots located in two contrasting habitats: A deciduous forest mainly dominated by oaks (*Quercus pyrenaica*), but wherein other species like *Erica arborea*, *Cistus laurifolius* and *Crataegus monogyna* are widely distributed and a mixed coniferous plantation dominated by *Pinus sylvestris* located 1.1 km apart. Shrub cover is limited to open areas (see Camacho et al., 2015). In total, there are 239 nest boxes distributed over the two study plots: 156 in the oak and 83 in the pine forest.

Field work was carried out during the breeding season, which lasts from around the third week of April (when first males arrive from migration) to the first fortnight of July. All nests-boxes were regularly checked every 3 days, before the onset of egg laying, and on a daily basis, around hatching, to ascertain laying date, clutch size (typically 5-6 eggs), hatching date, and number of fledglings. Adults were captured while incubating (females) or while feeding nestlings (males and females) at the age of 8 days old by means of a nest box trap (Friedman et al., 2008). Birds were marked with a numbered metal ring and a unique combination of colors rings (only males). Adults were measured for tarsus length (with callipers, to the nearest 0.01 mm), wing length (with a ruler, to the nearest 0.5 mm), forehead white patch (to the nearest 0.01 mm), and weighted (with a spring balance, to the nearest 0.1 g) (Camacho et al., 2015; Canal et al., 2012). Unringed birds first caught as breeding adults were considered immigrants and aged as first year or older based on their plumage traits (Karlsson et al., 1986; Potti & Montalvo, 1991), whereas individuals ringed as fledglings (i.e. born in the study area) are referred hereafter as “residents”. The percentage of dorsal brown plumage was visually estimated in the field as the percentage of the area of head and mantle covered by non-black feathers (brownish, grey or white), excluding the rump and the white forehead patch (Camacho et al., 2018; Potti & Montalvo, 1991). Polygynous males, captured twice within the same year breeding in different nest-boxes, confirmed that the estimates of plumage color were consistent (Camacho et al., 2018).

We considered the number of fledglings and the number of recruits as proxies of reproductive performance. In male pied flycatchers, recruitment mostly occurs at the first and second year after birth. Pied flycatchers are highly philopatry and the study population shows the highest recruitment rate reported for the species to the date (13%, Canal et al., 2014; Potti et al., 2013; Potti & Montalvo, 1991). Personal observations from non-systematic explorations of surrounding areas indicate that dispersion outside the study area is an extremely rare event; thus, we are confident that our recruitment estimates are reliable.

Environmental variable

We considered breeding density as environmental agent of selection. Breeding density may have important effects on inter- and intra-specific competition and therefore, on individual fitness (Arcese & Smith, 1988; Both & Visser, 2000; Gustafsson, 1987; Wiggins, 1995). The nest boxes in the area are occupied by pied flycatchers, but also by other species as Blue tits (*Cyanistes caeruleus*), Coal tits (*Periparus ater*), Great tits (*Parus major*), Crested tits (*Lophophanes cristatus*), Eurasian nuthatches (*Sitta europaea*), and Short-toed treecreepers (*Certhia brachydactyla*). Therefore, breeding density was estimated annually as the proportion of nest boxes occupied by pied flycatchers or others hole-nesting species in relation to the number of total nest-boxes. In both study areas, nest box occupation by flycatchers has grown steadily (Figure 1, Camacho et al., 2019) and, as of 2020, the pinewood area is virtually saturated, while the oakwood still holds a surplus of unoccupied nest boxes.

Statistical analyses

Before interpreting the statistical results, we systematically performed several model diagnostics statistics (e.g., distribution of residuals or multicollinearity) to avoid misleading conclusions due to statistical artifacts. Based on these statistics, we realized that the distribution (Poisson) initially chosen for the selection models based on the number of recruits had a poor fit. Therefore, we run additional models with different distributions (Poisson, Conway-Maxwell-Poisson, binomial negative and binomial negative zero-inflation) to select the distribution that best fits our data (Supplementary material, table 1). Model selection was carried out following the AIC criteria (Burnham et al., 2002, see below). These analyses showed that Conway-Maxwell-Poisson was the best distribution for the recruit model. After these adjustments, the analyses did not show any obvious deviation from GLMM assumptions or any collinearity problems.

Previously to the analyses of selection, we analyzed if dorsal color, measured as the average dorsal color (i.e. percentage of non-black feathers in the mantle) each year in the population, varied over the study period. To this end, we fitted 3 linear models (LM) including as predictors either i) year: to explore the global trend of the plumage color in the population, ii) the interaction between year and inmigrant status: to analyzed if variation in the plumage color differed between resident or migrant individuals, or iii) the interaction between year and habitat: to analyzed if variation in the plumage color differed between the two habitats (deciduous and coniferous) of the study area (Figure 2A, 2B and 2C).

To analyze selection on the dorsal color, we run 16 models using the number of fledglings (Gaussian distribution) as a proxy of fitness (Table 1): 4 models included only the phenotypic trait. These models differed in their random structure (random intercept or random slope, formed by the standardized percentage of brown dorsal color of each individual and the year), and in the inclusion (or not) of dorsal color^2 (to test the existence of non-linear selection) for both types of random structure. Other 4 models (considering the different combinations of random structure and inclusion or not of the quadratic term) included an interaction between dorsal color and a temporal component (year as a continuous variable) and 4 models included an interaction between the dorsal color and the environmental factor (breeding density). Finally, 4 models included the interaction between the phenotypic trait, temporal and environmental factors. When analyzing the selection using the number of recruits as proxy of fitness, we repeated the process described above: we fitted 16 models (GLMM; Poisson of Conway-Maxwell distribution) covering different combination of effects (temporal, environmental and/or quadratic) and randoms structures. As male flycatchers may breed for the first time at the second year of age, and field effort was limited in 2002 and 2003, we excluded the years 2000 and 2001 from the analyses based on recruits.

In all the selection models we included habitat (oak vs. pine) as a fixed effect because the phenotype and reproductive success of pied flycatchers may differ between habitats (Camacho et al., 2013). Laying date was also included in all models as this is an important predictor of reproductive success in this (Canal et al., 2012) and other bird species (Newton 2008). The age of the male was also included as a covariate in the models due to the possible phenotypic variation that individuals may present with age. In addition, age is considered one of the most important predictors of fitness in this and other bird species (Lundberg & Alatalo, 1992; Evans et al., 2011; Nol & Smith, 1987). Individuals aged as five or more years old were grouped to avoid possible bias due to the small number of individuals exceeding this age. We included male and female identities as random factors to account for individuals (41% of males and 43% of females) appearing multiple times in the dataset and for the potential effects of females in the reproductive success of males. Year (treated as a categorical variable) was also included as a random factor to account for pseudo-replication and stochastic variation among years (see e. g. Evans & Gustafsson, 2017 for a similar approach).

The selection of models was performed using the Akaike Information Criteria for small samples (AIC) in a “smaller-is-better” form (Tables 1 and 2). Models that differed in more than 2 units in relation to the smallest AIC were not considered further (Burnham et al., 2002). Once selected the best model, the significance of the fixed effects was calculated with Type II (Type III in the presence of significant interactions) Wald Chi-Square tests on maximum likelihood models, while parameter estimates were calculated using Restricted Maximum Likelihood (Zuur et al. 2009). The package HLMdiag (Loy & Hofmann, 2014) and the VIF function (car package; Fox & Weisberg, 2019) were used for model diagnostics. We using the function Anova (car package; Fox & Weisberg 2019) to performed the Wald Chi-Square tests. We use the poly function of the stats package (R Core Team 2020) to add quadratic effects of plumage color in the models. GLMMs were performed using the function lmer of the ‘lme4’ package (Bates et al. 2015). All statistical analyses were performed in R version 4.0.1 (https://www. r-project.org).

Result

Temporal trend of the dorsal color at the population level

The average percentage of brown in the dorsal plumage decreased over the years in the study population (p=0.0133; Figure 2A). Variation in dorsal coloration was similar between immigrants and residents (interaction between year and status, p= 0.52919, figure 2B) and between habitats (interaction between year and habitat, p=0.55075, figure 2C).

Selection on the dorsal color: number of fledglings

The best selection models based on the number of fledglings (ΔAIC<2) were M1_P, M3_P, and M9_P (see Table 1). These models, fitted with a random intercept, contained the effect of dorsal color, his interaction with breeding density, and the effect of dorsal color^2, in addition to the other fixed variables in all models (habitat, laying date and male age). However, only the laying date had a significant effect on fledgling production reproductive success decreased over the season (Table 3).

Selection on the dorsal color: number of recruits

The best models based on the number of recruits (ΔAIC<2) were M9_R and M13_R (see table 2). These models, one fitted with a random intercept and the other with random slope, contained the effect of dorsal color^2 that indicating a non-linear selection on this phenotypic trait (Figure 3). Dark individuals with a low proportion of brown in their plumage had higher number of recruits than individuals with extreme phenotypes. Further, individuals breeding early and in the coniferous forest had higher reproductive success, whereas the age of individuals did not influence the number of recruits. Breeding density or year (as continuous variable) was not included in the top ranked models, thus their effects on fitness was not significant (Table 4).

Discussion

We have shown that relatively dark individuals have higher rate of recruits than extreme phenotypes, resulting in a stabilizing selection, altought this effect was not detected using another proxy of fitness (the number of fledglings). As a consequence, yearly mean values of brown dorsal color decreased in the population over the study period. These results were not influenced by breeding density or temporal factor.

Males with extreme dorsal phenotypes (higher dark and higher pale) had lower number of recruits than individuals with dark (but not extreme) phenotypes. Dark males are typically early breeders in the study population (Canal et al. submitted), thus they migrate and arrive to the breeding areas when environmental conditions may be adverse (e.g, harsh weather). Further, they are probably involved in intense inter-sexual disputes and mating displays to obtain and maintain high quality territories and females. Thus, it is possible that these highly demanding activities had a negative impact on parental investment, which could explain the low number of recruits of extremely dark phenotypes. In aggrement with this idea, individuals with experimentally enlarged forehead patches, another ornament involved in intra and inter-sexual competition in this species, suffered greater reproductive costs than control individuals (Qvarnström, 1997; Sanz, 2001). By contrast, the low reproductive success of males with a more female-like appearance (many pale grey/ash-brownish feathers) could be related to low quality of these individuals (Galván & Moreno, 2009; Lampe & Espmark, 1994; Potti & Montalvo, 2008; Siitari & Huhta, 2002; Sirkiä & Laaksonen, 2009) and/or their mates (via assortative mating).

Environmental factors may have a high influence on the local processes of selection (Evans & Gustafsson, 2017; Merilä & Hendry, 2014). In particular, high breeding density may increase selection due to increased competition among individuals in the population (Hayward et al., 2018). For example, on the red deer (*Cervus elaphus*) intraspecific competition caused by population density has crucial consequences on the phenotypic trajectories of individuals (Carranza et al., 2020). In that species, a high intraspecific density favors the development of extreme sexual characteristics, even though its production is associated with a lower individual survival, while in populations with low competition, intermediate phenotypes with lower associated costs are selected (Carranza et al., 2020). Further, environmental (ecological) factors may be subject to temporal variations, thus affecting the strength and direction of selection on phenotypes (Gosden & Svensson, 2008; Reimchen & Nosil, 2002; Siepielski & Benkman, 2007). For example, studies performed with damselfly (*Enallagma aspersum*) have shown that temporal factors modify the body size of the females, which leads to selective changes in the population in few generations (Steele et al., 2011). Opposite to these works, in our study population, selection on the dorsal color was not affected by breeding density and not varied over the study period. Our results contrast with those reported by Alatalo & Lundberg

(1984) in a Scandinavian population of pied flycatchers. They experimentally showed that the reproductive success (number of fledglings) of flycatchers breeding in areas with different breeding density, varied only in years with poor environmental conditions (low food availability). Perhaps in our study area breeding density is not high enough to boost selection on the dorsal color. Alternatively, other biotic factors (e.g. such as the availability of food, the presence of predators or the availability of females) but also abiotic factors (e.g. precipitation or temperature) not considered here, could be the true agents of selection that are acting in our population. Future research on these aspects is warranted.

Laying date was one of the most influential factors in the reproductive success in the study population as both number of fledglings and recruits decreased as the season advanced. The effect of breeding date in the reproductive success of temperate birds is well known (Newton 2008, Lundberg & Alatalo, 1992; Blums & Clark, 2004; Bull, 1995; Källander et al., 2017; Potti & Montalvo, 1991). In pied flycatchers, the diet of the nestlings is mainly based on butterfly caterpillars and moths (Moreno et al., 1995; Sanz, 1997) and early breeders match their nesting period with the peak of food (Jonzén et al., 2007), thus increasing the chances of offspring survival. By contrast, late in the season, nestling tends to suffer from food shortages, reducing the chances of survival (Both et al., 2006; Parsons et al., 1976; Perrins et al., 1973). Habitat also had an important effect in the number of recruits, whereas this factor had not effect in the number of fledglings. In particular, individuals breeding in the conifers forest, recruited more individuals (recruited nestlings/pair = 0.6843931) than those of oak forest (recruited nestlings/pair= 0.4864078). These differences may be due to greater selective pressures, increased presence of predators or reduced availability of food in the oak forest. Whereas the number of fledglings per pair was similar in both habitats (4.344374 vs 4.387283 in the oak and coniferous forest, respectively).

The results of the selection analyses varied according to the reproductive fitness component considered. In the case of the recruit models, males with a high (but not extreme) percentege of black were those enjoying higher reproductive success, while, when using fledglings as proxy of fitness, we did not find reproductive differences associated with plumage color. Perhaps, adverse environmental conditions, food availability or the presence of predators, were not strong enough over the study period to cause differences in the number of fledglings in relation to the dorsal color of males. However, these factors may have stronger effects after abandoning the nest (Wilkin et al., 2009). Strong selective factors operating during migration and/or soon after fledging may have increased the effects of dorsal color on individual survival up to recruitment in relation to the nesting stage.

Conclusions

We found a stabilizing selection on the dorsal coloration of males as relatively darkindividuals enjoyed higher fitness, measured as the number of recruits, than browner and darker individuals. Further, phenotypic selection did not varied over time or with breeding density, an environmental factor that was expected to be an important agent of selection because it determines the probability and variability of potential mates and competitors. It is possible that the environmental pressure caused by breeding density was not strong enough to boost fitness differences relative to the male dorsal color over the study period. Alternatively, other environmental factors could be shaping the phenotypic trajectory of the dorsal color. Biotic (predator density or food availability) and abiotic (precipitation or temperature) factors not considered here could be contributing (alone or in combination) to the trajectory of this phenotype. Future studies are warranted to investigate these possibilities.

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Tables and figures

Tables and figures

Table 1: Model of selection on dorsal color using the number of fledglings as proxy of fitness. These models included interactions (*), a quadratic term of the dorsal color as well as random intercept or random slope (between standardized brown dorsal color of each individual and the year) structure. For simplicity, control variables included in the models (i.e. laying date, habitat or age) are not shown. Models are ranked according to AICc values.

Models	Code	AIC	df	dAICc
Dorsal color, R. intercept	**M1_P**	**1171.189**	**9**	**0**
Dorsal color*Breeding density, R. intercept	**M3_P**	**1172.951**	**11**	**1.8**
Dorsal color + dorsal color^2, R. intercept	**M9_P**	**1173.187**	**10**	**2**
Dorsal color*Year, R. intercept	M2_P	1174.377	11	3.2
Dorsal color, R. slope	M5_P	1174.935	11	3.8
Dorsal color*Breeding density*Year, R. intercept	M4_P	1175.659	13	4.5
Dorsal color*Breeding density + dorsal color^2, R. intercept	M11_P	1175.938	13	4.8
Dorsal color*Breeding density, R. slope	M7_P	1176.578	13	5.5
Dorsal color + dorsal color^2, R. slope	M13_P	1176.935	12	5.8
Dorsal color*Year + dorsal color^2, R. intercept	M10_P	1177.657	13	6.5
Dorsal color*Year, R. slope	M6_P	1178.16	13	7
Dorsal color*Breeding density*Year, R. slope	M8_P	1179.328	15	8.3
Dorsal color*Breeding density + dorsal color^2, R. slope	M15_P	1179.581	15	8.5
Dorsal color*Breeding density*Year + dorsal color^2, R. intercept	M12_P	1180.501	16	9.5
Dorsal color*Year + dorsal color^2, R.slope	M14_P	1181.488	15	10.4
Dorsal color*Breeding density*Year + dorsal color^2, R.slope	M16_P	1184.171	18	13.2

Table 2: Model of selection on dorsal color using the number of recruits as proxy of fitness. These models included interactions (*), a quadratic term of the dorsal color as well as random intercept or random slope (between standardized brown dorsal color of each individual and the year) structure. For simplicity, control variables included in the models (i.e. laying date, habitat or age) are not shown. Models are ranked according to AICc values.

Models	Code	AIC	df	dAICc
Dorsal color + dorsal color^2, R. intercept	**M9_R**	**5916.397**	**11**	**0**
Dorsal color + dorsal color^2, R. slope	**M13_R**	**5916.745**	**13**	**0.4**
Dorsal color*Year + dorsal color^2, R. intercept	M10_R	5918.573	14	2.2
Dorsal color*Year + dorsal color^2, R. slope	M14_R	5919.936	16	3.7
Dorsal color*Breeding density + dorsal color^2, R. intercept	M11_R	5920.263	14	3.9
Dorsal color*Breeding density + dorsal color^2, R. slope	M15_R	5921.327	16	5.1
Dorsal color*Breeding density*Year + dorsal color^2, R. intercept	M12_R	5921.341	17	5.1
Dorsal color, R. intercept	M1_R	5921.969	10	5.6
Dorsal color*Breeding density*Year + dorsal color^2, R. slope	M16_R	5922.456	19	6.3
Dorsal color, R. slope	M5_R	5923.545	12	7.2
Dorsal color*Year, R. intercept	M2_R	5925.508	12	9.1
Dorsal color*Breeding density, R. intercept	M3_R	5925.594	12	9.2
Dorsal color*Year, R. slope	M6_R	5927.182	14	10.9
Dorsal color*Breeding density, R. slope	M7_R	5927.375	14	11.0
Dorsal color*Breeding density*Year, R. intercept	M4_R	5928.974	14	12.6
Dorsal color*Breeding density*Year, R. slope	M8_R	5930.666	16	14.4

Table 3: Results of the GLMM of the M3_P model for recruits (see table 1). This model was the most saturated model between the two top ranked models, thus significance of the effects was estimated in this model to be conservative. Parameter estimates and SE were calculates using REML models.

	Estimate	Std. Error	Wald X^2	Wald test df	P
(Intercept)	1.26E+00	3.36E-02			
Dorsal color	-7.73E-04	6.25E-03	0.0169	1	0.8966
Breeding density	1.45E-02	9.76E-03	2.196	1	0.1384
Habitat	2.05E-02	1.51E-02	1.8495	1	0.1738
Male age	1.72E-05	5.52E-03	0	1	0.9975
Laying date	-1.22E-02	9.98E-04	148.3871	1	**<2e-16**
Dorsal color x Breeding density	-1.57E-03	6.47E-03	0.0587	1	0.8086

Table 4: Results of the GLMM of the M13_R model for recruits (see table 2). This model was the most saturated model between the two top ranked models, thus significance of the effects was estimated in this model to be conservative. Parameter estimates and SE were calculates using REML models.

	Estimate	Std. Error	Wald X^2	Wald test df	P
(Intercept)	0.914544	0.096919			
Dorsal color	0.725095	0.873871			
Dorsal color quadratic	-2.140299	0.726968	10.0921	2	**0.006435**
Habitat	0.200113	0.036264	30.4509	1	**3.42E-08**
Male age	-0.003538	0.012893	0.0753	1	0.783781
Laying date	-0.015039	0.003577	17.6719	1	**2.63E-05**

Figure 1: Variation in breeding density (number of occupied nest boxes –either by pied flycatchers or other species- with respect to the total number of nest boxes) over the study period.

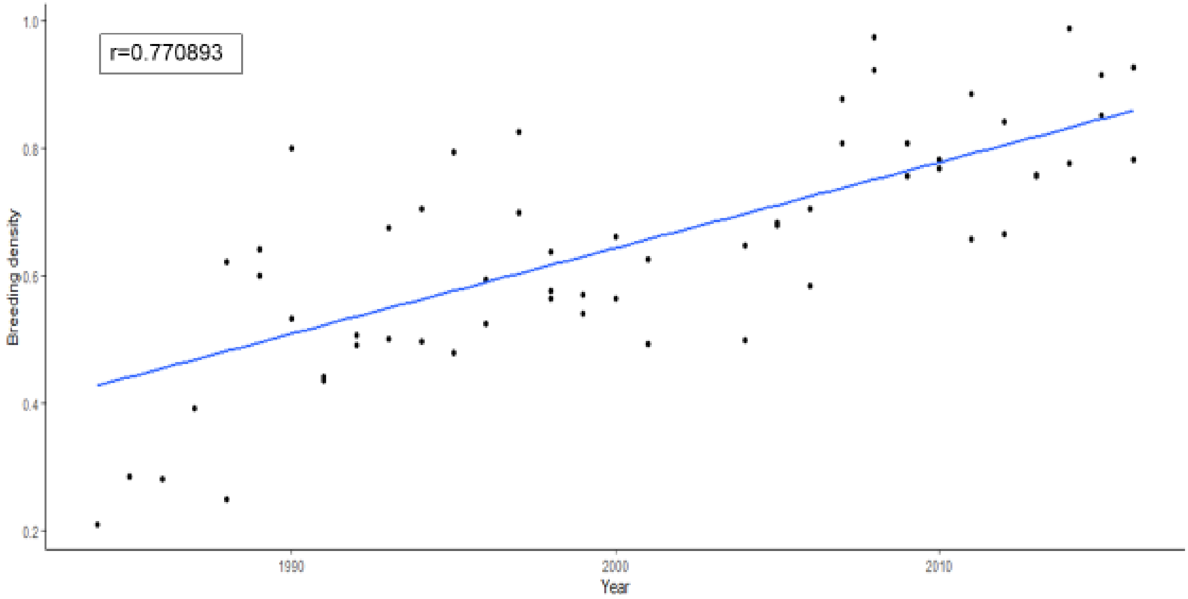
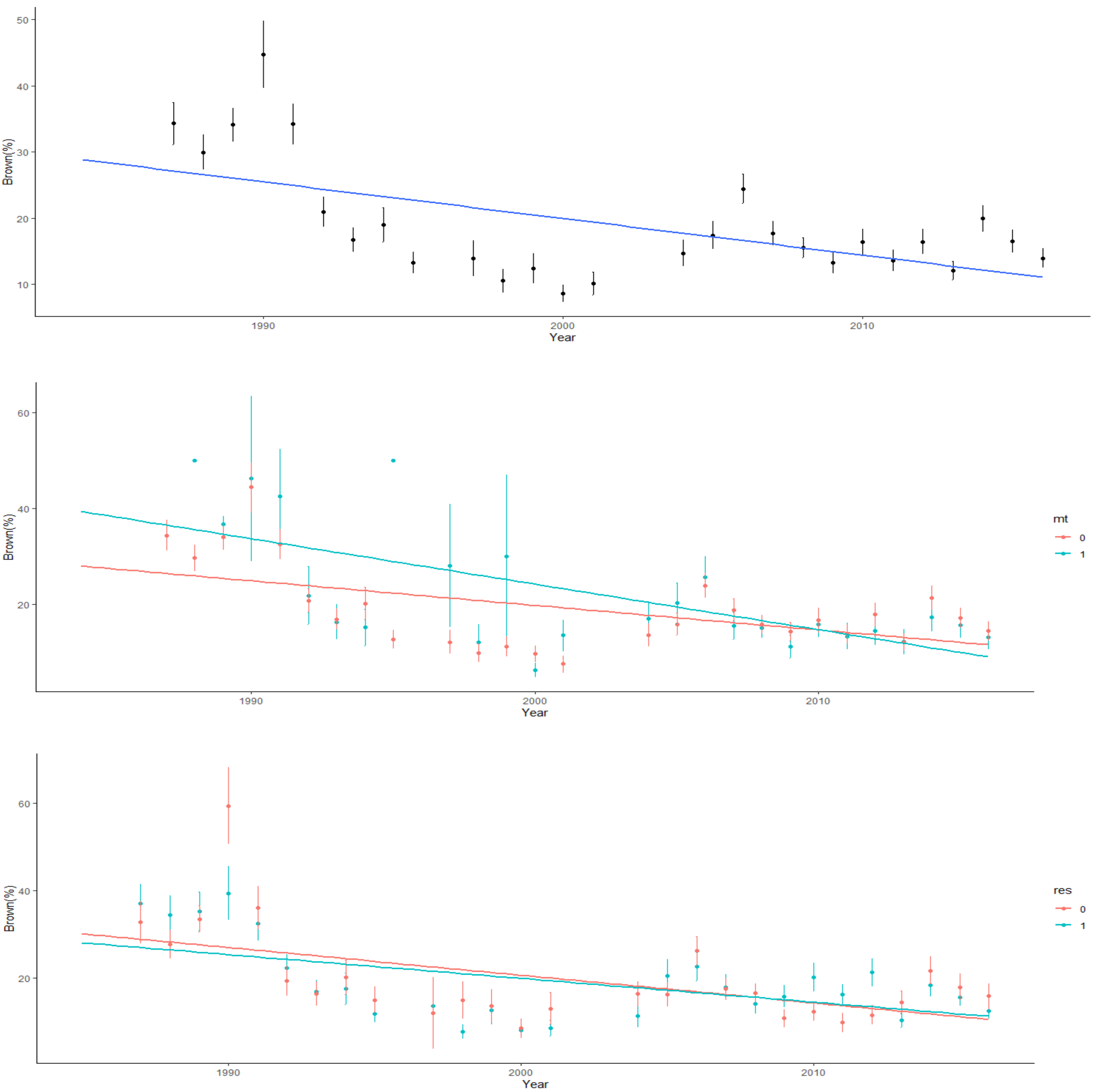


Figure 2: Temporal trend in the dorsal color of males: A) at the population as a whole, B) between resident (Blue) and migrant individuals (Red) and C) between habitats, mixed coniferous plantation (Blue) and deciduous forest (Red). Dots indicates annual means of the dorsal color in the population whereas bars indicate the standard error of the percentage of brown in each year.



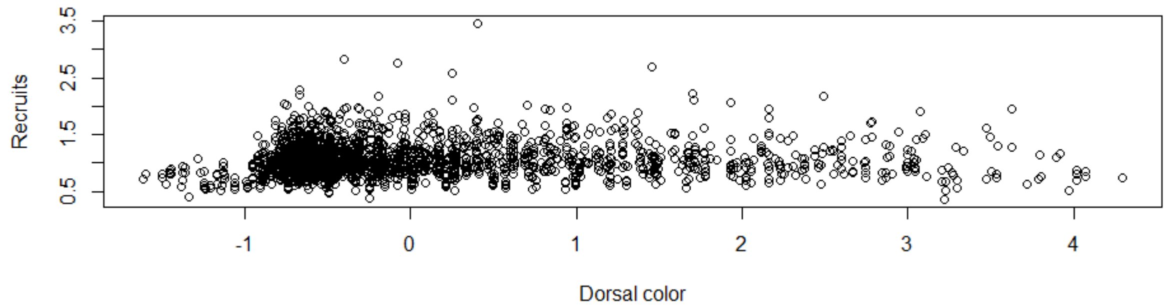


Figure 3: Stabilizing selection on the dorsal coloration of pied flycatcher males. Velues in the X-axis correspond to the standardized brown values: -1 indicates high percentages of black in the dorsal color, while 4 indicates individuals with a high percentage of brown in relation to the average population of each year. The represented data come from applying the fitted function of the stats package to the results of the M13_R model (Table 2).

Supplementary material

Table 1: Results of the selection of the distribution of errors for the models of the recruits.

	df	AIC	ΔAIC
Poisson de Conway-Maxwell	12	5919.899	0.0
Poisson	12	6037.441	117.5
Negative binomial zero-inflation	13	6433.681	513.8
Negative binomial	13	6708.392	788.5