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Eco-Evolutionary Consequences of Dispersal Syndromes during Colonization in a Passerine Bird

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ABSTRACT: In most animal species, dispersing individuals possess phenotypic attributes that mitigate the costs of colonization and/or increase settlement success in new areas (dispersal syndromes). This phenotypic integration likely affects population dynamics and the direction of selection, but data are lacking for natural populations. Using an approach that combines population dynamics, quantitative genetics, and phenotypic selection analyses, we reveal the existence of dispersal syndromes in a pied flycatcher (*Ficedula hypoleuca*) population in the Netherlands: immigrants were larger, tended to have darker plumage, bred earlier, and produced larger clutches than local recruits, and some of these traits were genetically correlated. Over time, the phenotypic profile of the population gradually changed: each generation advanced arrival and breeding and exhibited longer wings as a result of direct and indirect selection on these correlated traits. Although phenotypic attributes of immigrants were favored by selection during the early phase of colonization, observed phenotypic changes were similar for immigrants and local recruits. We propose that immigrants facilitated initial population establishment but that temporal changes likely resulted from climate change–induced large-scale selection. This study highlights that newly established populations are of nonrandom composition and that phenotypic architecture affects evolutionary population trajectories.

Keywords: animal model, dispersal syndrome, **G** matrix, heritability, *Ficedula hypoleuca*, response to selection.

Introduction

Dispersing animals often represent a nonrandom subset of the population and differ consistently from less dispersive individuals in suites of correlated morphological, physiological, behavioral, and/or life history traits (dispersal syndromes; Clobert et al. 2009). Dispersal polymorphisms are especially prevalent in species that live in spatiotemporally heterogeneous or ephemeral habitats and hence need to regularly colonize new areas to persist through time. In birds, for example, highly dispersive, aggressive, explorative and/or larger individuals lead the range expansion by displacing heterospecific or conspecific competitors in new habitats, while opposite phenotypes are found in core areas (Duckworth and Badyaev 2007; Skjelseth et al. 2007; Duckworth 2008; Liebl and Martin 2012). Insects also offer dramatic examples of dispersal syndromes, with wing dimorphism being frequent (Roff and Fairbairn 2007) and dispersal tendency being related to physiological (Haag et al. 2005) and morphological (Simmons and Thomas 2004; Legrand et al. 2015) individual differences.

Dispersal syndromes are considered to be adaptive, with divergent selection or phenotypic plasticity favoring the functional integration of traits that maximize the fitness of individuals with different life history tactics (Ronce and Clobert 2012). Because dispersal and colonization are multistage processes, a different combination of traits should be favored at different stages of these processes. For instance, in newly colonized habitats initial population densities are usually low, and hence traits that allow individuals to benefit from low densities will be favored (e.g., *r*-type life history traits, high dispersal) while other combinations of trait values will be favored once local densities have increased (e.g., *K*-type life history traits, low dispersal; Travis and Dytham 2002; Phillips 2009; Burton et al. 2010). The phenotypic means of newly established populations is thus expected to change over time. Whether this reflects an evolutionary change (i.e., a genetic change that occurs between generations) depends on the mechanism underpinning syndromes. To simplify, if syndromes result from adaptive phenotypic plasticity occurring within a generation—for example, when dispersive phenotypes are adjusted to postnatal conditions (Nicolaus et al. 2022*b*)—no

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genetic change is expected (i.e., the syndrome is not heritable). In contrast, if the local performance of different dispersive genotypes changes over time—for example, through negative density-dependent selection on colonizer attributes—genetic change is expected.

Studies evaluating the eco-evolutionary dynamics of dispersal syndromes have often linked dispersal to single independent traits. However, individuals are phenotypically integrated complex units, and dispersal tendencies are expected to be integrated with many phenotypic characteristics that can greatly complicate our measurements of phenotypic selection and our predictions of population evolutionary responses. While **G** matrices (matrix of genetic inheritance of traits and their genetic correlations) were long considered a description of genetic constraints that hinder population evolutionary responses (Lande and Arnold 1983; Blows and Hoffmann 2005), it is now established that **G** matrices can evolve under selection, although their dynamics for evolution are still uncertain in natural populations (Jones et al. 2004, 2014; Arnold et al. 2008; Roff and Fairbairn 2012). Hence, we expect that dispersal syndromes could change the trajectories of evolutionary responses available to populations and affect the rate of evolutionary changes. Making exact predictions is difficult because we currently lack knowledge on, for instance, how correlational selection may shape genomic architecture (Svensson et al. 2021) or whether exposure to novel environments changes the genetic variance and covariance of dispersal-related traits (Sgrò and Hoffmann 2004; Bonte and Dahirel 2017).

This study aimed at evaluating the eco-evolutionary consequences of dispersal syndromes during colonization using a multitrait approach. We focused on a migratory pied flycatcher population that was first established in 2007 in the Netherlands by mostly birds of unknown origin. Ringed immigrants (4% of population in 2007/2008) originated mostly from an area ~20 km away, but also from farther away (extremes are >100 km within the Netherlands and >600 km for an immigrant of British origin). Pied flycatchers are mandatory secondary nest cavity breeders that use the presence of heterospecific nonmigratory competitors (mostly great tits [*Parus major*]) as a means of localizing suitable breeding areas (Seppänen and Forsman 2007) despite intense competition for access to nest sites (Samplonius and Both 2019). European passerine populations, including flycatchers, have been shown to suffer from trophic asynchrony with their breeding environment as a consequence of anthropogenic climate change (Sanz et al. 2003; Both et al. 2006; Visser et al. 2006). One emerging idea is that directed dispersal can help flycatcher populations find breeding habitats with more suitable phenology (Burger et al. 2013; Lamers et al., unpublished manuscript), and consequently colonization of new habitats is expected to be of increasing importance for the persistence of species in a rapidly changing world. Based on this knowledge, we hypothesized that (1) initial colonization will be performed by individuals that can better compete with prior resident species (i.e., larger and darker individuals; Sandell and Smith 1991; Ducrest et al. 2008) and can establish quickly (individuals with high fecundity and short life span; Réale et al. 2010) and (2) over time and increasing densities, population composition and phenotypic profile will change because the performance of dispersers/colonizers is expected to be density dependent. For example, in western bluebirds (*Sialia mexicana*), the benefits of aggression in colonization success is balanced by a fecundity cost at high density, explaining why after initial colonization the proportion of aggressive types decreases rapidly (Duckworth 2008). In our population, dispersers/colonizers that are more aggressive (Nicolaus et al. 2022*b*) may experience higher mortality through interactions with heterospecifics if population buildup leads to increased competition for nest sites (Samplonius and Both 2019). Using 12 years of phenotypic data, we first investigated whether the population means of seven traits change after initial colonization and whether these changes reflect within-individual effects (indicating plasticity) and/or between-individual effects (indicating evolutionary changes or transgenerational nongenetic effects; Duckworth et al. 2018). We then tested the existence of dispersal syndromes by quantifying whether dispersers and local birds differ in their suite of correlated traits. Subsequently, we used our multigenerational pedigree to establish the genetic basis of trait variation and covariation (**G** matrices), which is essential to predict the evolutionary trajectory of traits. Last, we performed phenotypic (correlational) selection analyses and estimated predicted responses to direct and indirect selection on correlated traits to establish whether syndromes affect the rate of microevolutionary change (Lande and Arnold 1983; Brodie 1992).

Methods

Study Species

The pied flycatcher is a long-distance insectivorous migratory passerine, wintering in sub-Saharan western Africa and breeding in temperate and boreal forests across Europe. Flycatchers readily accept nest boxes for breeding and are found in habitat types ranging from deciduous forests to coniferous habitats.

Study Sites

Our study was performed in Drenthe in the Netherlands (52°49′N, 6°25′E). The study population was established in 2007 and consists of 12 spatially distinct study plots in three larger forested areas, carrying 50 or 100 nest boxes each (1,050 boxes in total; see fig. S1). Distances between adjacent plots ranged from 2.6 to 7 km, and the distance between the most distant plots was 18 km in the north-south direction and 12 km in the east-west direction (fig. S1). Before the start of the study in 2007, nest boxes were absent from 10 of 12 areas and local breeding densities were very low, estimated to be ~15% prior to nest box establishment, compared with 5 years after, based on bird counts in the area (Both et al. 2017). Colonizers were mostly of unknown origin. Plots in our area vary in vegetation, ranging from totally deciduous (mostly *Quercus robur*) to totally coniferous (mostly *Pinus sylvestris*; Nicolaus et al. 2019).

Data Collection

Since 2007 and from the beginning of April onward, arrival of males and females was monitored at least once every other day (Both et al. 2016). After observed pair formation, pairs were visited at least once every 3 days to determine the onset of egg laying (flycatchers lay one egg per day) and daily from the day before the expected hatch date until hatching. Females were often caught during incubation. At day 7 (hatch date = day 0), we caught parents using a spring trap; measured their tarsus length, wing length (primary eight counted from inside), and body mass; and ringed them (if unringed). In our population, males exhibit large variation in dorsal darkness as well as in white wing patch size. Therefore, we categorized caught males into seven color groups (Drost score; from 1 [jet black] to 7 [fully brown]; Drost 1936) and visually estimated the percentage of white in their tertial feathers. For unringed first-time-caught birds, minimum age (distinction between first-year and older birds) was estimated on the basis of plumage characteristics (Jenni and Winkler 1994). Nestlings were weighed and ringed at day 7 and measured again at day 12 (weight, tarsus, and primary eight; data not used here). Young fledge after about 15 days, and later checks informed us about their fledging success (data not used here). Because on average 92% of female (range: 84%–98%) and 82% of male (range: 72%–92%) local breeding birds are caught and formally identified with their ring number (unknown parent identity mostly caused by nest failure before catching), we were able to determine bird local survival between years and an accurate composition of the population (in terms of immigrant birds and local recruits; Both et al. 2017). We defined as "immigrant" a bird that is breeding in our population but was not locally ringed (originally unringed or ringed outside our study plots at >20 km) and as "local" a bird that was born in our study area and found breeding later in life back within this area (i.e., philopatric to its natal area even if it dispersed within our plots [up to 18 km]). Note that an immigrant bird keeps this status all its life and that the first cohorts of local birds are direct descendants of immigrants.

Statistical Analyses

Temporal Phenotypic Changes. To characterize and explain temporal change in population phenotypic means, we analyzed temporal variation in life history (arrival date, laying date, and clutch size), morphological traits (tarsus and wing length), and male coloration (Drost score and percentage of white in the central tertial) using general linear mixed models (GLMMs) with Gaussian errors. Year (2007–2018) was fitted as a continuous covariate while correcting for age (age and age^2; de la Hera et al. 2014) and, when needed, for sex (factor with female used as reference) and observer effects (factor, 4–31 observers depending on trait measured). Bird status (immigrant vs. local, the former used as reference category) and year × status and year × sex were fitted as additional covariates. To simplify the models, the latter interactions were kept only if significant. All continuous covariates were centered on the grand mean of the data set. Birds for which age at first capture was not scored were excluded from the analyses (~250 records). Proportion of white on the tertial (tertial) was arcsine square root transformed to meet normality. In all models, bird identity and year were fitted as random effects. Hence, year was fitted both as a fixed and as a random effect in the same models because year as a fixed effect estimates the population-level coefficients (intercept and slope of the temporal changes) while year as a random effect accounts for year-specific differences in trait values (and nonindependency of data collected in the same year). As the second step and to unravel the underlying mechanisms of temporal phenotypic changes, we separated the effect of year into within- and between-year effects using a centering technique (van de Pol and Wright 2009). For each individual, we calculated its mean year value (mean year; between-individual effect) and for each observation the deviation from its mean year (delta year; within-individual effect indicating plasticity) that we fitted as new covariates.

Preliminary analyses revealed that the tarsus values of one observer (ID1 present from 2007 to 2018) decreased linearly with time. To correct for this within-observer change effect, we compared the tarsus of birds that have been measured in the same year by ID1 and C. Both (also present from 2007 to 2018). Using C. Both as a reference (this observer shows consistent tarsus values, with high repeatability), we added the year-specific mean differences between these two observers to ID1's tarsus values.

Analyses gave the same results whether ID1's tarsus values were corrected or not (not shown), implying that our findings did not hinge on how the data were corrected.

All GLMMs were constructed in R (ver. 3.4.3; R Development Core Team 2017) using the glmer function of the lme4 package (ver. 1.1-27.1; Bates et al. 2015). We used the sim function of the arm package to simulate values of the posterior distribution of the model parameters (fixed effects [β] and variance components [σ^2]; ver. 1.5-02; Gelman et al. 2012). We extracted 95% credible intervals (CrIs) around the mode on the basis of 1,000 simulations using the MCMCglmm package (ver. 2.33; Hadfield 2010). The statistical significance of fixed effects was assessed on the basis of these 95% CrIs. We consider an effect to be significant in the frequentist's sense when its associated 95% CrI does not overlap with zero.

Quantitative Genetics Analyses. We used restricted maximum-likelihood (REML) models with a pedigree based on social matings (animal models) to estimate (co)variance components of each trait. We ran the animal models for a pedigree that includes, when pruned to retain only links to the individuals with trait measurements (Morrissey and Wilson 2009), 3,270–3,770 records for unisex traits, with 870–952 maternities and paternities, and 1,984–2,258 records for sex-specific traits, with 396–516 maternities and paternities (see table S4). Maximum pedigree depth was five generations. Mean maternal sibship size ranged from 1.17 to 1.39 and mean paternal sibship size ranged from 1.20 to 1.48, with a pedigree-wide mean pairwise relatedness of 0.0002–0.0003 (see table S4). The social pedigree was built using all information about individuals marked in our nest boxes between 2007 and 2018 and based on the assumptions that (i) immigrants are unrelated to each other and to resident birds, (ii) the social parents are also the genetic parents, and (iii) the occurrence of extrapair paternity (<5% in this species; Brommer et al. 2010) has little effect on the estimate of heritability (Charmantier and Réale 2005). Starting with univariate models, we first used a fixed effects structure that included age, age^2, and sex for traits common to males and females and individual identity, year, and observer as random effects, thereby partitioning the phenotypic variance (V_P) not explained by fixed effects into among-individual (V_I), among-year (V_{YEAR}), among-observer (V_{OBS}), and within-individual (V_R) variance components ($V_P = V_I + V_{YEAR} + V_{OBS} + V_R$). Then we decomposed V_I into its additive genetic (V_A) and permanent environmental (V_{PE}) components ($V_P = V_A + V_{PE} + V_{YEAR} + V_{OBS} + V_R$). This last model was constructed by including additive genetic merit (or breeding value) as an additional random effect. Adjusted ratios r, pe^2, and h^2 were calculated as the proportion of V_P corrected for fixed effects and explained by V_I, V_{PE}, and V_A, respectively. As a second step, we ran multivariate models to estimate the covariances for among-individual (COV_I), within-individual residual (COV_R), additive genetic (COV_A), and permanent environment (COV_{PE}) terms. This information was used to subsequently calculate the among-individual (r_P), within-individual residual (r_R), additive genetic (r_G), and permanent environment (r_{PE}) correlations between the traits (i.e., establishing the existence of a syndrome). Additionally, to compare whether syndromes differ between immigrant and local individuals, phenotypic matrices (immigrants are by definition of unknown pedigree, thus genetic matrices are not estimable) as well as r_P and r_R were estimated for these two groups separately. All traits were standardized over all individuals for non-sex-specific traits or over all individuals of the same sex for sex-specific traits (by subtracting the [sex-specific] population mean from each individual's observation and dividing it by the [sex-specific] population's standard deviation). The statistical significance of random effects was derived from the Akaike information criterion (AIC; with a difference of ≥2 in AIC between models indicating better support of the data; Burnham and Anderson 2002). All models were implemented in ASREML (ver. 4.1; Gilmour et al. 2015).

Phenotypic Selection Analyses and Predicted Response to Selection. To quantify the strength of linear selection acting on the combination of traits and predict response to selection, we first attempted to estimate the direct genetic covariance between the breeding values of the traits and fitness in multivariate animal models (Price 1970; Morrissey et al. 2010). However, because of a lack of model convergence, we switched to phenotypic selection analyses, from which we calculated selection gradients and estimated predicted responses to selection. This was achieved by analyzing variation in the relative annual number of recruits and in the relative annual adult survival probability in relation to the standardized traits (to obtain linear selection gradient β) and their interaction (to obtain correlational selection gradients; Lande and Arnold 1983; Brodie 1992). Relative annual number of recruits was defined as the number of recruits produced by a parent for a given breeding season divided by the annual mean of the population and the relative annual survival probability as probability for an adult individual to survive until the next year divided by the annual mean probability of the population. Traits were standardized by subtracting the (sex-specific) annual population mean from each individual's observation and dividing it by the (sex-specific) annual population's standard deviation. In preliminary analyses, quadratic effects of standardized traits were also fitted (to test for nonlinear selection gradients); however, since they were never significant, we removed them to simplify the analyses. In these analyses, unpaired nonbreeding males were not included. A large fraction of young does not recruit locally in their first year, and because our measurement of reproductive fitness is a summation of all recruits observed as breeders, we calculated selection until the breeding season of 2016, which then included recruits up to 2018. When selection analyses were done on females or males separately, we used annual measures of fitness relative to the annual mean of the females or males and standardized traits within sex.

Second, to test whether the strength of selection acting on the studied traits differs between the early colonization phase compared with the later settlement phase, we analyzed variation in the relative annual number of recruits and in the relative annual survival probability of individuals in relation to the standardized trait, phase (colonization vs. settlement) and the interaction between standardized trait and phase. The two phases were defined on the basis of the change in the population trajectory, which occurred in 2011 (i.e., switch to nearly zero growth rate; fig. 1). Interactions between standardized traits were not fitted, as the first step did not reveal any evidence for correlational selection (see table S5). Yearly selection gradients were also calculated and are presented in table S6. We further analyzed whether direction and strength of selection acting on the studied traits generally differs between immigrants and local recruits. To that purpose, we analyzed variation in the relative annual number of recruits and in the relative annual survival probability of individuals in relation to individual status (immigrant vs. local). Because the proportion of local breeders was low during the colonization period, we could not test the interactive effect of status × period on relative fitness. Predicted responses to selection based on the multivariate breeder's equation are presented in table S12.

We used a generalized linear model with Gaussian errors for all selection analyses. All models were constructed in R (ver. 3.4.3) using the glm function of the lme4 package (ver. 1.1-27.1; Bates et al. 2015). Estimates are given with their 95% confidence interval (CI). The statistical significance of selection gradients and correlational

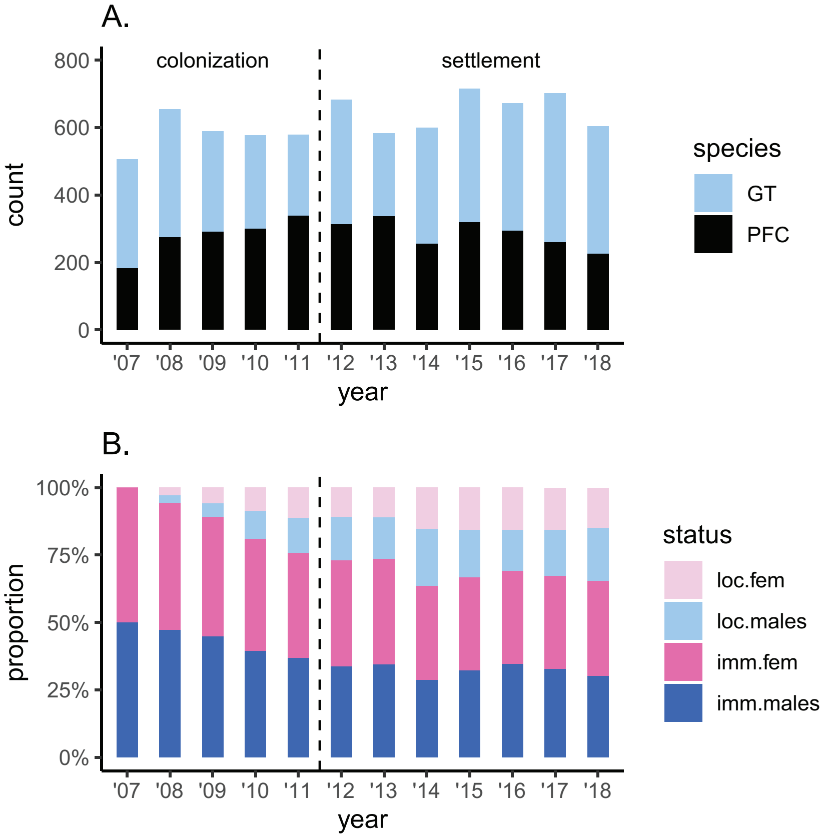

Figure 1: Temporal population change in the annual number of breeding pairs of great tits (GT) and pied flycatchers (PFC; *A*) and in the proportion of female ("fem") and male ("males") immigrants ("imm.") versus locally born ("loc.") flycatchers (*B*) in a Dutch population between 2007 and 2018.

section gradients were assessed on the basis of these 95% CIs (as detailed above).

Ethical Treatment of Animals. All research presented here was conducted in accordance with all applicable Dutch laws and under the license of the Animal Experimentation Committee of the University of Groningen (AVD105002017822).

Results

Population Buildup

Nest box provisioning resulted in at least tripling the number of breeding pairs in the first year compared with preceding years (Both et al. 2017). During the first 5 years after establishment (2007–2011; hereafter, "colonization"), the number of pied flycatchers occupying nest boxes increased by >1.5 fold (from 183 to 292 pairs; fig. 1*A*), with immigrant birds representing 88% of the total population on average (fig. 1*B*). During that period, great tits were abundant, particularly during the first year of colonization (occupying 64% of the boxes). In the following 7 years (2012–2018; hereafter, "settlement"), the density of breeding birds stabilized around 287 breeding pairs of flycatchers (range: 226–338 pairs; 68% of immigrants) and 364 pairs of great tits (range: 245–441 pairs; fig. 1). Flycatchers in our population produced 6.3 eggs (SD: 0.8; $n = 2{,}447$ nests; 2007–2018) from which they locally recruited 0.4 young (SD: 0.7; $n = 2{,}259$ nests including failed ones; 2007–2016).

Temporal Population Phenotypic Changes

Three out of seven traits exhibited a significant temporal change after initial colonization, independent of age effects. Over the years, males advanced arrival, local females advanced laying date, and all birds increased wing length (table 1; fig. 2*A*–2*G*). Partitioning the year effect revealed that in all cases, observed significant temporal changes were caused by significant between-individual effects (table 1), even if plasticity occurred sometimes too: for example, for wing length both delta year and mean year were significant, with estimates exhibiting nonoverlapping CrIs.

Dispersal Syndrome

For most studied traits, immigrants differed significantly from locals in their morphological and life history traits: immigrants were significantly larger (longer tarsus and wing) and tended to be darker (lower Drost score; table 1; fig. 2*H*). Female immigrants tended to arrive earlier, bred earlier, and produced larger clutches (table 1; fig. 2*H*). Mark-recapture analyses showed that annual apparent survival rates of immigrant females were lower than those of local females (0.34 [95% CI: 0.32 to 0.36] vs. 0.42 [95% CI: 0.39 to 0.46]) and lower than those of males (0.47 [95% CI: 0.45 to 0.49]; table S2). Trait means of immigrants and locals varied in concert (additive effects of year and status), except for laying date (interactive effects of year and status; table 1). If bird status was defined at a finer-scale resolution (i.e., distinguishing between birds that stay or move between the two main parts of the study area; see fig. S1), results showed that phenotypic differences were observed only between birds moving on a larger spatial scale (from outside to the study area, ≥20 km) and the rest of the breeding population (birds either staying or moving between parts of the study area, <20 km; table S3). It thus confirmed that the considered scale (immigrant vs. local) was appropriate. Similarly, to verify that the effect of status existed independently of age effects, we ran (1) sex-specific models, as we have shown that the percentage of correctly aged individuals is higher for males than females (87% for first-year males, 91% for adult males, 76% for first-year females, and 94% for adult females; Both et al. 2017), and (2) models with age fitted as a factor (young vs. old) to reduce the uncertainty of age effects for birds that entered the population >2 years old. Note that tarsus length reaches its asymptotic length 2 weeks after hatching, and therefore any misclassification of age could not affect its results. In all cases, results remained qualitatively very similar (not shown), indicating that the effect of status exists independently of age effects. Only for tarsus did sex-specific analyses reveal that the effect of status was driven by females (effect of status [95% CI]: males, 0.001 [−0.001 to 0.005]; females, −0.008 [−0.013 to −0.003]).

Quantitative Genetics of Life History and Morphological Traits

We first ran univariate animal models to partition the phenotypic variance in the studied traits not explained by fixed effects into permanent environmental and genetic variance components. The analyses revealed that morphological and coloration traits exhibited relatively high and significant repeatability and heritability estimates compared with life history traits (fig. 3*A*, 3*B*; table S7)—that is, they have a higher potential to evolve under selection.

Second, we ran multivariate animal models to estimate the covariances and correlations of traits at the between-individual (r_P) and within-individual (r_R) phenotypic level. We then partitioned r_P into additive genetic (r_G) and permanent environment (r_{PE}) correlations. Results showed that many traits were correlated at the phenotypic level: birds with larger wings possessed larger tarsus, and individuals

Table 1: Model summary of general linear mixed models of temporal changes in population mean phenotypic traits

Fixed effect	df	β (95% CrI)	df	β (95%CrI)	df	β (95%CrI)	df	β (95%CrI)
		A. Tarsus length (*n* = 4,820)		B. Wing length (*n* = 4,821)		C. Female arrival (*n* = 1,924)		D. Male arrival (*n* = 1,835)
Intercept	1	**1.735 (1.728 to 1.741)**	1	**5.81 (5.78 to 5.83)**	1	**24.21 (23.38 to 25.76)**	1	17.44 (16.26 to 18.74)
Age	1	**.002 (.000 to .003)**	1	**.03 (.03 to .04)**	1	**−1.44 (−1.83 to −1.11)**	1	−1.67 (−1.88 to −1.13)
Age^2	1	.000 (−.001 to .001)	1	**−.01 (−.01 to .00)**	1	**.44 (.34 to .62)**	1	.31 (.16 to .43)
Sex[a]	1	.000 (−.001 to .000)	1	**.16 (.14 to .16)**	...	...	...	...
Status[b]	1	**−.004 (−.007 to −.001)**	1	**−.02 (−.03 to −.01)**	1	.55 (−.14 to 1.37)	1	.04 (−.82 to .55)
Year	1	**.001 (.000 to .002)**	1	**.01 (.01 to .02)**	1	−.17 (−.53 to .15)	1	**−.44 (−.78 to −.07)**
Observer	31	...	31	...	4	...	4	...
Mean year	1	**.0007 (.0001 to .0012)**	1	**.0109 (.009 to .012)**	1	**−.17 (−.28 to −.04)**	1	**−.48 (−.58 to −.35)**
Delta year	1	**.0025 (.0014 to .0033)**	1	**.0198 (.015 to .026)**	1	.43 (−.13 to 1.01)	1	.20 (−.25 to .78)
		E. Laying date (*n* = 2,287)		F. Clutch size (*n* = 2,285)		G. Drost score (*n* = 2,265)		H. % white tertial (*n* = 2,132)
Intercept	1	34.63 (33.75 to 36.23)	1	**6.43 (6.27 to 6.52)**	1	**6.38 (6.28 to 6.47)**	1	**.79 (.77 to .82)**
Age	1	−1.03 (−1.28 to −.72)	1	**.16 (.13 to .21)**	1	**−.24 (−.28 to −.19)**	1	**.02 (.02 to .03)**
Age^2	1	.30 (.20 to .41)	1	**−.04 (−.05 to −.02)**	1	**.05 (.04 to .07)**	1	−.01 (−.01 to .00)
Status[b]	1	.89 (.05 to 1.33)	1	**−.09 (−.16 to −.01)**	1	.08 (−.03 to .19)	1	.00 (−.01 to .02)
Year	1	−.02 (−.34 to .34)	1	.01 (−.03 to .05)	1	.00 (−.02 to .02)	1	.00 (−.01 to .01)
Year × status	1	**−.24 (−.44 to −.01)**	...	...	...	...	1	...
Observer	...	...	...	...	27	...	27	...
Mean year	1	.06 (−.04 to .14)	1	.01 (−.01 to .01)	1	−.01 (−.02 to .02)	1	.00 (.00 to .00)
Delta year	1	.14 (−.44 to .47)	1	.09 (.02 to .12)	1	−.01 (−.06 to .05)	1	−.01 (−.02 to .00)
Mean year × status	1	−.24 (−.44 to −.01)	...	...	...	...	...	...
Delta year × status	1	−.55 (−1.34 to .08)	...	...	...	...	...	...

Note: Phenotypic variation in traits of pied flycatchers is regressed as a function of age, age^2, year (from 2007–2018), bird status, year × status, and observer. Traits considered are tarsus length (pt. A), wing length (pt. B), female arrival date (pt. C), male arrival date (pt. D), laying date (pt. E), clutch size (pt. F), Drost score (pt. G), and proportion of white in the second tertial (arcsine square root transformed; pt. H). Tarsus length and wing length are also corrected for sex. In all main models, bird identity and year are fitted as random effects. Below the main models, the decomposition of the year effect into within-individual (delta year) and between-individual (mean year) effects is shown. In these models, bird identity is fitted only as a random effect. Estimates (β) are presented with their 95% credible intervals (CrIs) and are shown in boldface type if significant. Degrees of freedom are also indicated.

[a] Sex (female vs. male): female is used a reference category.

[b] Status (immigrant vs. local recruit): immigrant is used as a reference category.

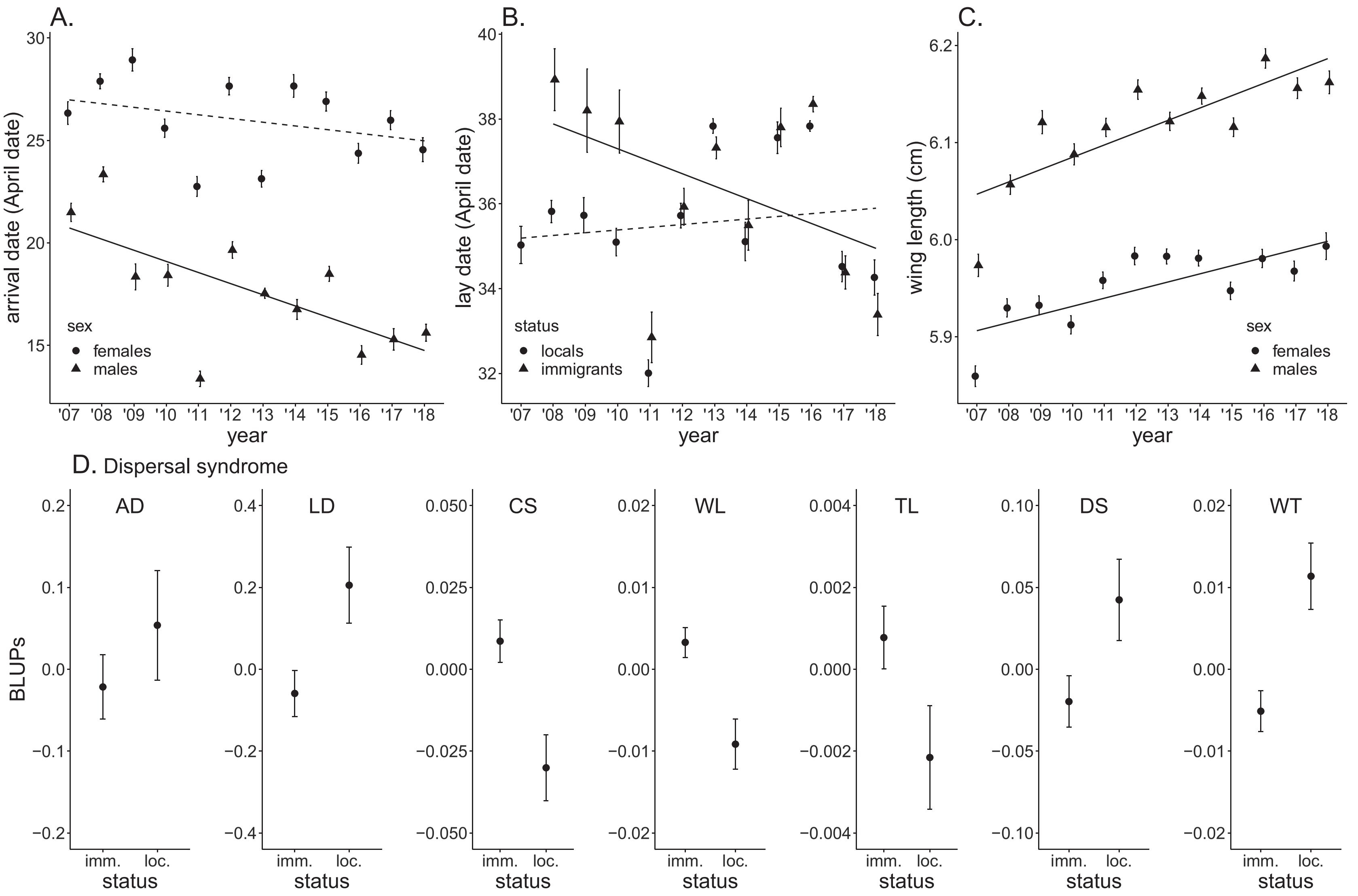

Figure 2: *A–C*, Mean population change in three phenotypic traits of pied flycatchers since colonization (2007–2018). Means of raw data are presented with their associated standard errors. *D*, Dispersal syndrome: differences between immigrants ("imm.") and locals ("loc.") in arrival date (AD), laying date (LD), clutch size (CS), wing length (WL), tarsus length (TL), Drost score (DS), and percentage white in tertial feathers (WT). For graphic purposes, best linear predictors (BLUPs) of mixed models controlling for age and sex effects are plotted (excluding the interaction status). Solid and dashed lines represent significant and nonsignificant trends, respectively. Only if migration status showed an interaction with year do we show their estimates separately.

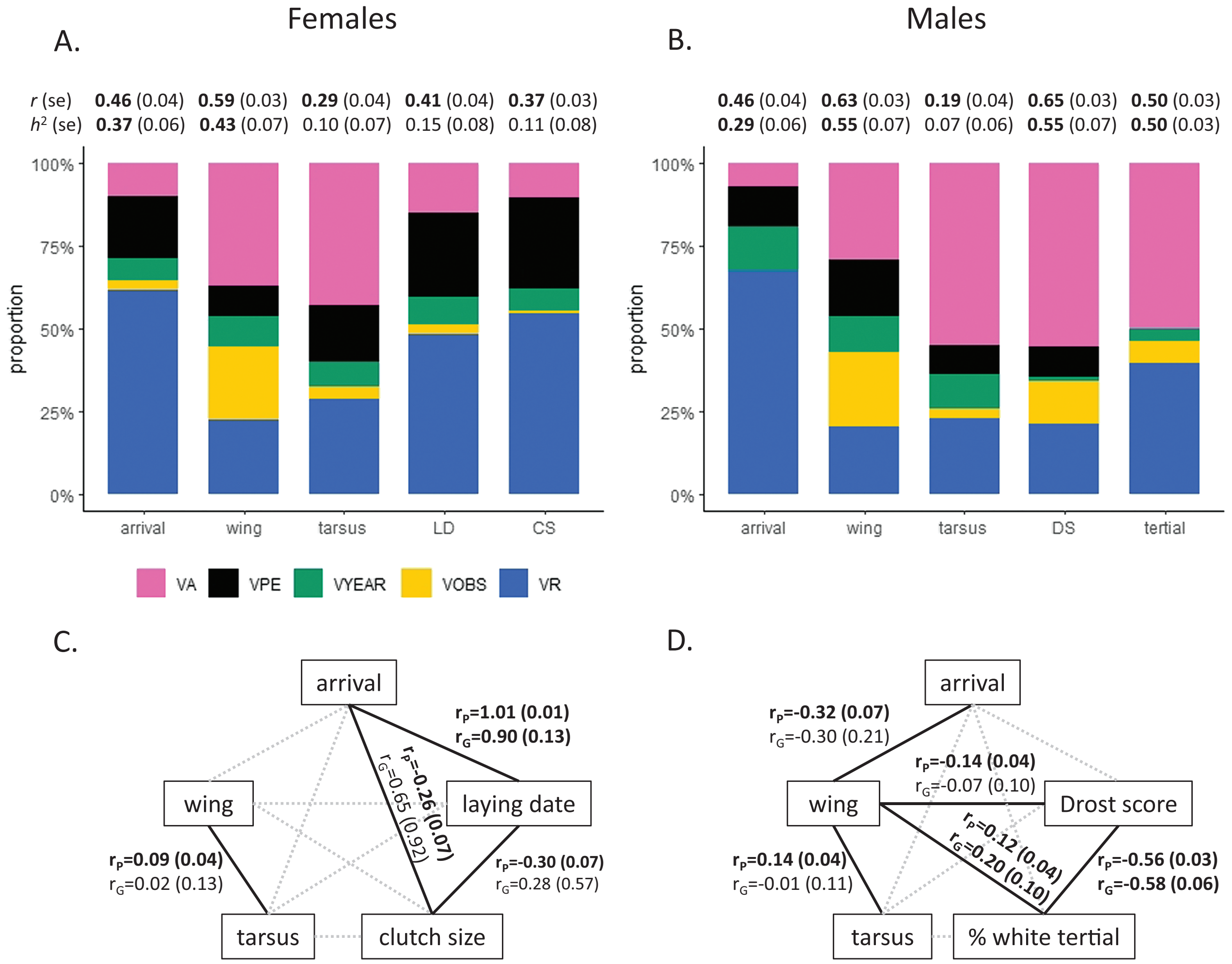

Figure 3: Quantitative genetics of morphological, life history, and coloration traits in female and male pied flycatchers. *A*, *B*, Phenotypic variance in wing length, tarsus length, arrival date, laying date (LD), clutch size (CS), Drost score (DS), and tertial is decomposed into additive genetic (V_A), permanent environment (V_{PE}), among-year (V_{YEAR}), among-observer (V_{OBS}), and within-individual (V_R) variance components. Repeatability (r) and heritability (h^2) estimates are indicated above the graphs and are shown in boldface type if significantly different from zero (table S5). *C*, *D*, Matrices of between-individual phenotypic (r_P) and genetic (r_G) correlations for morphological, life history, and coloration traits. Significant correlations are denoted by boldface type and solid lines. Nonsignificant correlations are denoted by gray dotted lines. All estimates are reported with their associated standard errors.

with longer wings, especially males, arrived earlier, were darker, and had more white in their tertial feathers (fig. 3*C*, 3*D*; tables S8–S10). Early-arriving females bred earlier and produced larger clutches (fig. 3*C*; table S8). Fewer correlations, however, remained significantly different from zero at the genetic level (arrival and laying in females, wing length and tertial, Drost score and tertial in males; fig. 3*C*, 3*D*; tables S8–S10). For arrival and wing length, although estimates of r_P and r_G were very similar, splitting r_P into r_G and r_{PE} resulted in estimates accompanied with large standard errors (tables S8–S10). Furthermore, the phenotypic correlational structure of immigrant and local recruit phenotypes appeared to be qualitatively similar (table S11), implying that immigrants and local recruits were distributed along the same syndrome in the population. Overall, these analyses showed that timing of arrival and breeding, wing length, and plumage coloration were phenotypically and genetically integrated.

Phenotypic Selection

We found no support for the existence of correlational selection (table S5). Instead, selection appeared to be clearly directional toward early arrival and early breeding: birds that arrived and bred earlier in the season produced relatively more recruits and survived relatively

Table 2: Phenotypic selection analyses of morphological and life history traits in all sexes (pt. A), females (pt. B), and males (pt. C)

	Recruits β (95% CI)	Survival β (95%CI)
A. All:		
Intercept	.92 (.92 to 1.08)	1.00 (.93 to 1.07)
Tarsus	−.04 (−.04 to .13)	−.04 (−.11 to .03)
Period[a]	−.10 (−.10 to .10)	.00 (−.09 to .09)
Tarsus × period[a]	.00 (−.11 to .10)	.04 (−.05 to .12)
Intercept	1.00 (.93 to 1.07)	1.00 (.94 to 1.06)
Wing	.07 (−.04 to .10)	**.10 (.01 to .14)**
Period[a]	.00 (−.10 to .10)	.00 (−.08 to .08)
Wing × period[a]	−.05 (−.09 to .10)	−.09 (−.15 to .02)
Intercept	1.00 (.91 to 1.09)	1.00 (.92 to 1.08)
Arrival	**−.14 (−.23 to −.04)**	**−.22 (−.29 to −.14)**
Period[a]	.00 (−.11 to .11)	.00 (−.09 to .09)
Arrival × period[a]	−.02 (−.13 to .09)	**.12 (.03 to .21)**
B. Females:		
Intercept	1.00 (.88 to 1.12)	1.00 (.89 to 1.11)
LD	**−.22 (−.34 to −.10)**	−.11 (−.22 to .00)
Period[a]	.00 (−.15 to .15)	.00 (−.14 to .14)
LD × period[a]	.00 (−.15 to .15)	.05 (−.09 to .18)
Intercept	1.00 (.88 to 1.12)	1.00 (.89 to 1.11)
CS	.09 (−.03 to .21)	.01 (−.1 to .12)
Period[a]	.00 (−.15 to .15)	.00 (−.14 to .14)
CS × period[a]	.01 (−.14 to .16)	.01 (−.12 to .15)
C. Males:		
Intercept	1.00 (.86 to 1.14)	1.00 (.89 to 1.11)
DS	.10 (−.04 to .24)	−.04 (−.16 to .07)
Period[a]	.00 (−.17 to .17)	.00 (−.13 to .13)
DS × period[a]	−.07 (−.24 to .09)	.09 (−.05 to .22)
Intercept	1.00 (.86 to 1.14)	1.00 (.89 to 1.11)
Tertial	**.21 (.06 to .35)**	−.04 (−.15 to .08)
Period[a]	.00 (−.17 to .17)	.00 (−.13 to .13)
Tertial × period[a]	**−.25 (−.41 to −.08)**	.00 (−.13 to .13)

Note: Variation in the relative annual number of recruits and relative annual adult survival is studied in relation to standardized traits (tarsus length, wing length, arrival date, laying date [LD], clutch size [CS], Drost score [DS], and percentage of white in tertial; wing length and arrival are standardized within sex). Estimates of fixed effects are reported with their 95% confidence intervals (CIs). Significant selection gradients and interactions are denoted by boldface type.

[a] Period (0 = colonization; 1 = settlement): colonization is used as a reference category.

better (tables 2, S6). Females laying larger clutches produced relatively more recruits but did not survive better (tables 2, S6). Interestingly, selection on early arrival, longer wings, and more white in tertial feathers (characteristics of immigrants) was stronger during colonization than settlement (table 2; fig. 4). Tarsus length and male plumage characteristics did not appear to be under directional selection (table 2). Strength and direction of selection on morphology and arrival did not differ between sexes (tested but not shown), but fitness differed between local recruits and immigrants. Compared with immigrants, local recruits produced 16% more recruits and had a 33% higher chance of returning for females and 7% for males (effect of status on difference in relative number of recruits [95% CI]: females, 0.16 [−0.01 to 0.33]; males, 0.16 [0.01 to 0.31]; effect of status on relative survival [95% CI]: females, 0.33 [0.18 to 0.49]; males, 0.07 [−0.04 to 0.19]).

Discussion

This study aimed at evaluating the eco-evolutionary consequences of dispersal syndromes for a newly established wild pied flycatcher population. As expected, dispersal syndromes were detected in this population, with most traits being correlated at the phenotypic level and partly at the genetic level, and changes in the population phenotypic trait means occurred after initial colonization. Part of the observed population changes were attributed to directional (but not correlational) selection on dispersal-related traits, which suggests that dispersal syndromes a priori do not impose an evolutionary constraint. Furthermore, phenotypic attributes of immigrants (earlier arrival for females and longer wings) were favored during the early but not the later years of colonization, implying that immigrant traits may facilitate initial settlement. Intriguingly, with the exception of laying date, both immigrants and local birds exhibited similar phenotypic changes over the 12 years, implying that the population changes could not be solely caused by colonization processes and that additional mechanisms were in play. We discuss below the implications of these findings for the dynamics and evolutionary trajectories of the population.

This study first confirmed the existence of a dispersal syndrome in pied flycatchers: immigrants/colonizers exhibited longer wings and tarsi, and males had darker coloration. These dispersal-related differences support studies in passerines, where long wingspan is usually associated with improved flight performance (Lockwood et al. 1998; Fiedler 2005; Förschler and Bairlein 2011; Vagasi et al. 2016), high dispersal tendency (Skjelseth et al. 2007), and earlier arrival at the breeding grounds (Potti 1998; Bowlin 2007; Choi et al. 2010; Teplitsky et al. 2011). Additionally, darker plumage coloration is typically associated with higher levels of aggression (Ducrest et al. 2008), a behavior that may benefit immigrants that need to compete with prior resident species and/or conspecifics to acquire territory in new areas (Ahola et al. 2007; Samplonius and Both 2019). Indeed,

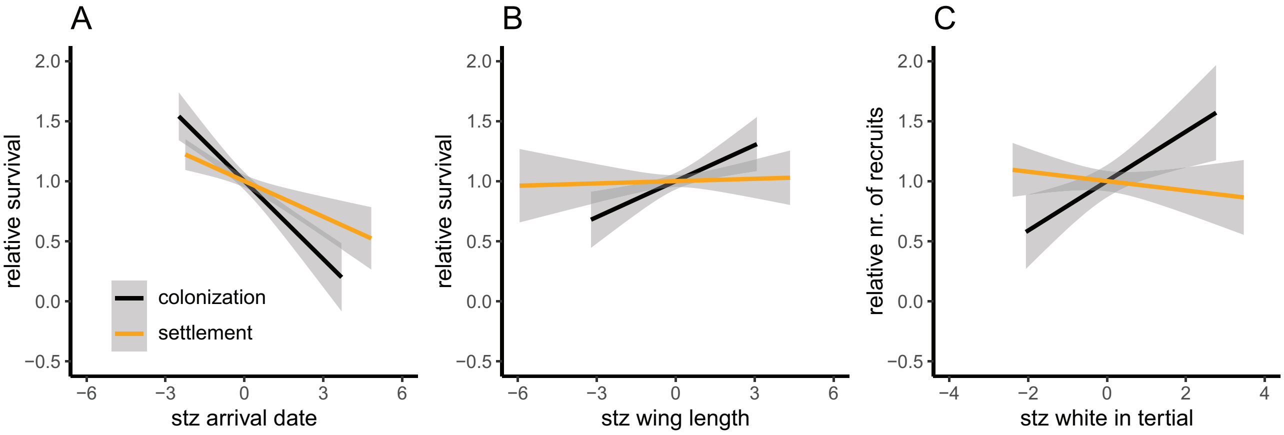

Figure 4: Viability phenotypic selection acting on wing length (*A*) and arrival date (*B*) and fecundity selection acting on plumage coloration (*C*) were stronger during colonization than during settlement in a Dutch pied flycatcher population. Regression lines are presented with their associated standard errors (gray shade).

light-colored pied flycatcher males have been found to entice less aggression from territorial males and hence more easily establish a breeding territory close to other males (Slagsvold and Saetre 1991; but see Huhta and Alatalo 1993). Thus, the lighter color of local males may be beneficial in established populations with a higher density. We also found that dispersal is part of *r*/*K* life history tactics, with high dispersal being associated with high fecundity (larger clutch size) and low survival (here, lower apparent adult survival and lower number of recruits; Réale et al. 2010). Such differences in fitness between locals and immigrants corroborates the idea that immigrants and their offspring are either more likely to die at an early age or more likely to permanently disperse outside the natal sites (e.g., through genetic [Doligez et al. 2009] or maternal [Duckworth et al. 2015] effects). The lower apparent survival of immigrant females further suggests that this larger dispersal tendency may persist in later life in females. The results of the current study complement the earlier finding that more dispersive individuals are more generalist in their diet (Nicolaus et al. 2019) and more aggressive (Nicolaus et al. 2022*b*)—that is, they possess phenotypic attributes and life history tactics that facilitate settlement in novel environment.

Additionally, although dispersal syndromes have been suggested to be a result of genetic integration (Duckworth 2012; Korsten et al. 2013), we were not able to show strong genetic correlations among traits. Genetic correlations, when detected, were much less than 1, implying that they are unlikely to represent an absolute constraint of trait-independent evolution. In most other cases, significant genetic correlations were not detected, which indicates either that other nongenetic mechanisms underlie some of the observed phenotypic correlations (Duckworth et al. 2018) or that selection simply does not favor certain trait genetic covariances (as no correlational selection was detected here). Alternatively, genetic correlations exist, but we were not able to reveal them. Lack of statistical power is an important issue in studies of genetic correlations (Roff 1997), and it may be hard to formally tease apart permanent environmental and additive genetic sources of phenotypic correlations.

We expected to find changes in mean phenotype after initial colonization, due to an increasing fraction of locally born individuals possessing certain trait combinations over time. Indeed, we found directional changes in mean phenotype in three out of seven traits that were due not just to phenotypic plasticity but also to the result of among-individual differences. However, we think these were unrelated to the colonization process because (1) trends were observed in both immigrants and locals and (2) the trend in wing length was in the opposite direction than expected: locals had shorter wings, but wing length increased over the years. Rather than the result of a local colonization process, we consider the observed trends in mean phenotype the likely result of large-scale selection on earlier breeding phenology and wing length, likely in response to climate change. Global warming is indeed expected to cause the optimal breeding windows of insectivorous passerines to advance (Visser and Both 2005) and thus to select for traits (here, wing length) that facilitate early breeding (Potti 1998; Bowlin 2007; Choi et al. 2010; Teplitsky et al. 2011). Other studies of migratory passerines found similar patterns of wing length increase that coincide with climate-related changes (Hüppop 2012; Weeks et al. 2020). These studies generally argue that such an increase represents (1) an adaptive response to longer northward migration distances (Møller et al.

2010; Hüppop 2012) and/or (2) a compensatory adaptation to maintain migration (Weeks et al. 2020) because increasing temperatures are expected to cause a reduction in body size and an increase in the metabolic cost of flight (Bergmann 1847; Gardner et al. 2011; Sheridan and Bickford 2011; but see Siepielski et al. 2019). However, these explanations are unlikely here because, to our knowledge, there is no evidence that northern pied flycatcher populations have longer wings or that structural body size is shrinking (this study). Alternatively, longer-winged individuals migrate faster and hence arrive earlier (Teplitsky et al. 2011) or are better adapted to a faster rate of spring phenology (Hahn et al. 2016; but see Zimova et al. 2021) and hence the selection for earlier arrival does indirectly select for longer-winged individuals.

A unique element in our study is that we considered seven phenotypic traits simultaneously, their correlations on the phenotypic and genetic level, and their covariation with fitness. Using such a multivariate approach enabled us to show that most of the selection was on the timing of arrival and breeding, traits with relatively low repeatability and heritability. Although the temporal trends in these traits were partly due to between-individual effects, we cannot unequivocally conclude that the observed change is genetic. Even with our relatively large pedigree and sample size (e.g., 3,770 individuals, 951 maternities, 953 paternities; table S4), we could not estimate the direct covariation between the breeding values of these traits and fitness. However, the trend toward longer wings, together with the weak directional selection on this trait in the settlement phase and its (potentially genetic) correlation with arrival and laying phenology, suggests that evolutionary change for earlier phenology has led to an indirect change in wing length. Our estimated responses to selection indeed showed that population phenotypic temporal changes were better explained when indirect selection on correlated traits was included (table S12). Although our estimated responses to selection do not incorporate or report uncertainty and thus should be treated with care (Stinchcombe et al. 2014; Pujol et al. 2018), they suggest that genetic correlations potentially speed up the rate of microevolution (table S12).

In conclusion, we have shown that dispersers in our population represented a nonrandom sample of the population and that their phenotypic characteristics likely facilitated initial settlement. Our finding more generally implies that data collected on newly established populations are likely to be biased toward a specific subset of individuals (e.g., with *r*-type life history strategy, larger body size, and competitive behavioral phenotype; for similar findings on amphibians, see Phillips et al. 2006). Hence, ignoring dispersal syndromes and/or focusing on too-short time windows (early or late phase of settlement) could lead to misinterpretation of biological patterns regarding, for example, population evolvability, productivity, or community structure and ecosystem processes. We further conclude that the observed phenotypic changes in our population were not solely the result of phenotypic plasticity but involved direct and indirect selection (likely linked to climate change) on correlated traits. Overall, our study pleads for the need for longitudinal studies and highlights the importance of considering consistent individual differences and the architecture of phenotypes to better understand and predict population evolutionary potential, population response to selection, and population dynamics.

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Statement of Authorship

All authors saw and approved for submission the final version of the manuscript, and all persons entitled to authorship have been named. M.N. and C.B. designed the study, all authors collected data, R.U. managed the database, and M.N. analyzed the data, produced the figures, and wrote the manuscript with input from all authors.

Data and Code Availability

All data supporting the results and R code are available via the Dryad Digital Repository (https://doi.org/10.5061/dryad.p5hqbzkqn; Nicolaus et al. 2022*a*).

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