Quantifying heritability of the environment using animal models: a case study.

Gabriel Munar-Delgado[1]*, Marion Nicolaus[2], Christiaan Both[2], Pim Edelaar[3]

[1]Department of Biodiversity, Ecology and Evolution. Faculty of Biological Sciences, Complutense University of Madrid; Madrid, Spain.

[2]Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands

[3]Department of Molecular Biology and Biochemical Engineering, University Pablo de Olavide; Seville, Spain.

*Corresponding author. Email: gabriel.munar@gmail (GMD)

Abstract

Evolutionary ecology has traditionally studied how natural selection shapes the phenotypes of individuals in response to their environment, which increases population fitness. It is also well known how habitat choice can affect individual local adaptation. However, recent work has highlighted the incompleteness of the link between habitat choice and its evolutionary consequences. By treating the selected habitat as an extended phenotype, the evolutionary focus can be shifted to how the extended phenotype evolves to match the organisms' phenotypic traits. Theoretical approximations suggest that animal models could be used to estimate the heritability of the extended phenotype, providing insights into its evolutionary dynamics. Here we use data from a long-term study of a pied flycatcher population (*Ficedula hypoleuca*) to test the use of animal models for the estimation of the heritability of an extended phenotype i: the vegetation around the nest box. We also applied animal models to different subsets of the population (based on philopatric status) to test which mechanism might be causing the inheritance of the extended phenotype, if any. We also ran simulations to randomize the nest box and its surrounding vegetation for the different population subsets, thereby eliminating the effect of habitat choice, and used the animal models to identify the sources of variation of the extended phenotype. We confirmed that animal models can be used to estimate the local habitat heritability in natural populations and found a significant habitat heritability for our pied flycatcher population. Moreover, subset analysis and subset randomization both indicated that the observed heritability was caused by philopatry. Thus, we propose that animal models can be used to estimate the heritability of the extended phenotype and also to disentangle the mechanism(s) causing its inheritance. By acknowledging that organisms can influence the habitat they experience to increase their adaptation and by focusing on the evolution of extended phenotype, we should be able to better understand how population adaptation increases and how it evolves.

Key words: additive genetic variance, animal model, extended phenotype, habitat inheritance, habitat choice, philopatry

Introduction

Traditionally, adaptation has been seen as the process of natural selection shaping populations to match pre-existing environmental templates (Darwin, 1859; Schluter, 2001). Consequently, the causal relationship of adaptation has been considered as unidirectional: the environment affects the organisms, but not the other way around. However, recent studies have synthesized and highlighted how organisms can affect their local environment by either adjusting or selecting it to match their ‘phenotypic templates’ (Edelaar et al., 2019, 2023; K. Laland et al., 2016). When individuals within a population differ in the environments that best match their own characteristics (Bolnick et al., 2002), their local performance will vary across distinct environments. Under such circumstances, natural selection should favor mechanisms that facilitate individuals to select environments that best match their phenotypes (Davis & Stamps, 2004), or to modify them (Callahan et al., 2014). Thus, the causal relationship between organisms and their environment in adaptation terms can be bidirectional, the organism and the environment can each be changed to match the other (Edelaar et al., 2023; K. N. Laland & Sterelny, 2006).

To highlight the capacity of organisms to adjust their environment, the adjusted environment has been called an ‘extended phenotype’ (Dawkins, 1982). The extended phenotype has traditionally referred to the expression of the genotype in the external environment, any change made in the environment by the organism that affects its own fitness. An example of this is the nest of birds. Birds adjust their local environment by constructing a nest which, in fact, affects their reproductive success. Thus, natural selection should favor the most successful nests and if the bird building capacity is heritable, the extended phenotype (the nests) is expected to evolve. On the other hand, extending this logic, the habitat selected by the organism has also been recently approached as an extended phenotype since it (partially) depends on the organism (Edelaar et al., 2019; Munar-Delgado et al., 2023) and potentially affects fitness. Following the nest example, when a bird selects a nest site (such as a nest cavity), and its characteristics affect reproductive success, the outcome is similar to that of nest building, and nest site selection is expected to evolve. In this paper we focus on the selected habitat as an extended phenotype which can be inherited and therefore have its own evolutionary dynamics (Edelaar et al., 2023).

Following the traditional view, quantitative genetics has traditionally focused on the adaptive evolution of phenotypic traits, estimating their heritability and evolutionary potential. However, recently, Munar-Delgado et al. (2023) have suggested that by approaching the habitat as a potential extended phenotype it is feasible to apply the quantitative genetics perspective and use animal models to estimate its heritability. Animal models are mixed models widely used in quantitative genetics to estimate the heritability of phenotypic traits (Kruuk, 2004; Lynch & Walsh, 1998). In conventional application of these models, the environment may be fitted as an independent covariate to control for its effects on the phenotypic trait (i.e., to model phenotypic plasticity). However, when we consider that the environment is an extended phenotype and it is instead fitted as a dependent variable in the animal model, its heritability can also be estimated (Gervais et al., 2020, 2022; Järvinen et al., 2017; Munar-Delgado et al., 2023). Additionally, Munar-Delgado et al. (2023) showed how the heritability of phenotypic traits increases via phenotypic plasticity when they are affected by a heritable extended phenotype. So even if the focal trait is a phenotypic trait and the habitat inheritance is not of primary interest itself, not taking into consideration that the habitat is heritable could bias the interpretation of estimates of phenotypic trait heritabilities. Thus, applying this quantitative genetic methodology to environmental traits influenced by the organism should help to: i) understand if and how environments are heritable and ii) disentangle the evolutionary dynamics between the chosen habitat and other phenotypic traits.

In this study, we applied animal models to estimate the heritability of the environment using an extensive dataset from a long-term study of a pied flycatcher (*Ficedula hypoleuca*) population. The dataset contains pedigree information and information about each individual’s local habitat, which was defined as the composition of the tree vegetation around the nest box used as a breeding adult. By treating the vegetation composition as an individual's extended phenotype, we can estimate its heritability. We expect to be able to apply animal models to estimate the heritability of breeding site vegetation composition.

We also investigated the mechanism involved in any habitat heritability. If the chosen habitat is heritable, it can be inherited via different habitat choice mechanisms: direct genetic habitat choice, plastic habitat choice and matching habitat choice (Akcali & Porter, 2017; Ravigne et al., 2004).

Direct genetic habitat choice refers to habitat choice directly mediated by preference alleles. This process is able to drive adaptation when preference alleles differ among individuals and are coupled (though physical linkage or linkage disequilibrium) with other phenotypic differences that increase the ecological match with the preferred habitat. In this case, the chosen habitat can be seen as genetically determined and to evolve via natural selection acting on variation in habitat use that affects individual fitness (Jaenike & Holt, 1991). Plastic habitat choice refers to habitat choice driven by individual preference induced during its ontogeny by environmental cues (as habitat imprinting). This kind of habitat choice is adaptive when offspring resemble their parents phenotypically; in that case preferring the habitat that their parents used with success is likely successful for the offspring as well. Finally, matching habitat choice is a performance-dependent type of habitat choice where individuals assess their local performance in different habitats and based on that settle where it is highest (Edelaar et al., 2008), thereby increasing individual phenotype-environment match and local adaptation. Thus, besides estimating the heritability of the environment, identifying the inheritance mechanism would provide insight in how it can evolve.

We also investigated the mechanism involved in any habitat heritability. So far, there is no evidence for direct genetic habitat choice (variation in genetic preference for a specific vegetation composition) for this species. In contrast, it is well known that early experiences in the natal site have effects on habitat choice for pied flycatchers, causing individuals to select breeding sites similar to their natal sites. This seems to support that flycatchers have plastic habitat choice (i.e., based on imprinting), which leads to philopatry (Camacho et al., 2016; Chernetsov et al., 2006). Philopatry in itself could also be a mechanism causing parent-offspring similarity in habitat, when nearby habitat patches are more similar than distant habitat patches (i.e., when there is positive spatial autocorrelation). Hence, when dispersal distances are not long enough to break the pattern of spatial autocorrelation, then this will cause the environment to be heritable. To disentangle the effects of habitat choice versus limited dispersal as the cause for heritability of the environment, we separately estimated heritability for philopatric and non-philopatric individuals (i.e., dispersing within or between study plots). Additionally, to ensure that applying animal models to these relatively small population samples did not reduce statistical power and that interpretations were not biased, we ran simulations of different scenarios in which the nest box locations of different population subsamples (based on philopatry status) were randomized. By doing this, we were able to remove the effect of habitat selection in the different groups and test where any observed heritability at the level of the total population came from.

Methods

Study species

The pied flycatcher is an insectivorous passerine that migrates long distances, wintering in Sub-Saharan Western Africa and breeding in temperate and boreal forests across Europe. The species easily adopts nest boxes for breeding and is present in habitats ranging from deciduous to coniferous forests.

Study sites

Our study was carried out in Drenthe in the Netherlands (52^{o}49'N, 6^{o}35'N). The study population was established in 2007, comprising twelve distinct study plots. Each of these study plots was equipped with 50 or 100 nest boxes, totaling 1,050 boxes. The distance between adjacent plots varied between 2.6 to 7 km, with the most distant plots being 18 km apart in the north-south direction and 12 km apart in the east-west direction.

Data collection

Arrival Date. Since 2007, the arrival of individuals has been monitored at least once every other day starting from the beginning of April. This process has been described in detail in Both et al. (2016). During each observation session, the focal study plot was traversed on foot, and all evidence of pied flycatcher presence was recorded. The observations were carried out from shortly after sunrise until around noon. The arrival date of male individuals was determined as the first day of observation when the study plot was visited daily. The arrival of females was recorded as the date when they formed a pair since previous studies have demonstrated that females typically form pairs within a few hours of arrival (Dale et al. 1992).

Pedigree. On day 7 after nestlings had hatched (hatch date = 0), parents were caught using a spring trap and identified or ringed (if unringed) in each box. On the same day, nestlings were ringed. Thus, virtually all breeding birds and nestlings are formally identified with their individual ring number, which allows for the construction of a robust population pedigree. For unringed birds that were caught for the first time, the minimum age was estimated, making a distinction between first-year birds and older ones (Jenni and Winkler, 1994).

Breeding individual status. Individuals were initially classified as either "recruits", indicating they were born in our study area (in any of the 12 plots) and later found breeding within this area, or as "immigrants," indicating they were breeding in the study area but were not locally ringed (either originally unringed or ringed outside the study plots at >20 km). Then, for each year of observation, recruits were further classified as either "philopatric," indicating they were breeding in the same plot where they were born, or as "disperser," indicating they were breeding in a non-natal study plot. It is worth noting that the same individual could hence be classified as philopatric and disperser in different years.

Breeding site vegetation composition. In a subset of 7 plots, the vegetation composition was measured around all the boxes present in the study sites. The average distance between nest boxes and foraging sites in the study plots was 13 m (Oosting, unpublished data), (although longer flights are difficult to track so this average distance is probably somewhat underestimated). For this reason, the vegetation composition was scored in a 15 m radius around each focal nest box tree. All tree species were counted, and the proportion of deciduous trees was calculated. The vegetation composition was collected by 7 observers, and a subset of 10 boxes was scored by all observers to check for observer effects. The data showed high interobserver correlation coefficients, implying that the measurements are not biased (Nicolaus et al., 2019). Vegetation composition around the nest box was the focal local environment that was treated as a dependent variable (i.e., as an extended phenotype).

Statistical analysis

Study plots variance. We estimated the variance of breeding site vegetation composition for each plot and between plots. We did this to predict if philopatry could create enhanced parent-offspring similarity in breeding site vegetation composition.

Quantitative Genetics Analyses and Animal models. All mixed-effect model analyses were performed using ASReml-R version 4.1.0.130 (Butler, 2020) using a restricted maximum-likelihood approach. The social pedigree was constructed using all available information on individuals that were marked in the nest boxes between 2007 and 2022. The pedigree was built based on the assumptions that all immigrant birds are unrelated to any other individual, and that the observed parents in the nest are also the genetic parents. Since extrapair paternity is not common in this species (<5%, Brommer et al., 2010), this last assumption should have little effect on heritability estimates (Charmantier & Réale, 2005). Maximum pedigree depth was nine generations. For univariate models, we fitted year, individual identity and individual additive genetic merit (i.e., breeding value) as random effects to decompose the extended phenotypic variance (V_{EP}) into among-year variance (V_Y), additive genetic variance (V_A) and permanent environmental variance (V_{PE}), and residual variance (V_R). Thus, the variance of the extended phenotype was estimated as $V_{EP} = V_A + V_{PE} + V_Y + V_R$, and then we calculated the relative importance of each variance as (i) narrow sense heritability of the extended phenotype $h^2 = V_A/V_{EP}$, (ii) permanent environmental variance $pe^2 = V_{PE}/V_{EP}$, , (iii) year variance $y^2 = V_Y/V_{EP,}$ and (iv) residual variance $r^2 = V_R/V_{EP}$.

When applying the animal model to the different data subsets, if all the heritability for the total population is due to philopatric individuals (those that stay in the natal study patch), we should only observe heritability when applying the animal models to that subset. On the other hand, if there is some degree of other habitat choice, we should also observe heritability when applying the models to the non-philopatric individuals.

Finally, we ran a binomial animal model for philopatry (philopatric vs non-philopatric status). We classified both dispersers and immigrant individuals as non-philopatric. For this model we fitted year, individual identity and individual additive genetic merit (i.e., breeding value) as random effects to decompose the phenotypic variance (V_P) into among-year variance (V_Y), additive genetic variance (V_A) and permanent environmental variance (V_{PE}), and residual variance (V_R). V_R from the binomial model was fixed at $\pi^2/3 = 3.29$ (Falconer and Mackay, 1996). Thus, the variance of the phenotype was estimated as $V_P = V_A + V_{PE} + V_Y + 3.29$, and then we calculated the narrow sense heritability of the phenotype $h^2 = V_A/V_P$. We also estimated philopatry heritability for males and females separately.

Simulations

Simulations were based on randomization of individual breeding nest boxes together with the local environment associated with them (i.e., the vegetation composition). Randomization in principle removes the effect of habitat choice. In different simulations, we randomized nest boxes for different population subsets and combinations of them (philopatric, n = 621; disperser, n = 522; and immigrant individuals n = 2822) while maintaining the original data for the rest of the population. We varied the pool of potential nest boxes that were assigned to each individual (Supplementary material Methods). For half the simulations, breeding individuals were assigned a random nest box out of the ones that were occupied by any pied flycatcher (including itself) that specific year, but only out of the set of boxes in the same plot (within-plot randomization). This removes the effect of habitat choice. For the other half of the simulations, breeding individuals could get a nest box occupied in any of the 12 study plots that year. This removes the effect of philopatry, and habitat choice. By only including nest boxes that were occupied by pied flycatchers each specific year, we ensured that those nest boxes were truly acceptable for individuals to breed that year. Additionally, the pool of potential nest boxes for each individual was dependent on their arrival date (if their arrival date was unknown, individuals were assigned a random arrival date from the pool of arrival dates in that specific year). This is because if certain territories are preferred, these may become scarcer as more individuals have chosen a box. Therefore, individuals could only get a nest box that was unoccupied at their arrival date. In this way, individuals that arrived on day 1 of a specific year could get any of the nest boxes occupied that year, while those arriving on the last day could only get any of the nest boxes that were being occupied that same day. Finally, to increase the randomness of the assignments and because we do not investigate competitive interactions other than depletion by arrival date, nest boxes were assigned without replacement; the same nest box could be assigned several times to different individuals. Overall, following these criteria, we conducted eight different simulation designs (i.e., eight different scenarios) by changing which population subset was being randomized (philopatric, disperser or immigrant individuals) and whether the randomized nest boxes for each individual were restricted to the individual's breeding plot or not. Thus, we were able to remove habitat choice and philopatry effects for each group separately.

We simulated each different scenario 1000 times, and each resulting new dataset was analyzed using animal models to decompose the extended phenotypic variance (see below). For each scenario, we first calculated the h^2, pe^2, y^2 and r^2 ratios for each simulation and then extracted their mean from the 1000 simulations.

In these simulations, if heritability is only due to philopatry, heritability should only decrease when randomizing the nest box location of philopatric individuals between patches. If it decreases when only non-philopatric individuals are randomized, it would mean that another type of habitat choice is also acting.

Results

Study plot variance

We found that the variance of breeding site vegetation composition between plots was higher than the variance within plots (Table 1).

	Plot							
	2	5	6	7	8	10	12	Between
Variance	254.17	770.51	680.57	529.59	403.78	629.26	1.02	781.31

Table 1. Breeding site vegetation composition variance within each plot and between plots.

Observed heritability of breeding site vegetation composition in relation to philopatry

We found a highly significant heritability for breeding site vegetation composition (0.19 ± 0.04) (estimate ± SE). The heritability was similar for males and females (males: 0.34 ± 0.09; females: 0.23 ± 0.09) (Table S1).

Heritability depended on the dispersal status of individuals. For non-philopatric individuals (immigrants + dispersers), there was no heritability for breeding site vegetation composition (0.00 ± 0.00), and all individual repeatability was estimated to be due to permanent environment effects (0.44 ± 0.03) (Table S1)). In contrast, for philopatric individuals we found a high heritability (0.38 ± 0.10) and no permanent environment effects (0.00 ± 0.10) (This last model output did not fully converge properly, so the estimate is less reliable). The heritability was similar for male and female philopatric individuals (males: 0.40 ± 0.07; females: 0.39 ± 0.09; Table S1).

Heritability estimates in different randomization scenarios

We found negligible change in the estimated heritability of breeding site vegetation composition in simulated scenarios where individuals were randomly assigned a nest box from their natal breeding plot (Fig. 1a; Table S2). These results suggest that, for this population of pied flycatchers, breeding in a randomly assigned box from their natal breeding plot would not affect the inheritance of vegetation composition.

In contrast, we did observe large changes in heritability estimates in simulated scenarios where individuals were assigned a random nest box from any study plot (Fig. 1b; Table S2). Notably, we observed an almost complete elimination of heritability when the breeding nest boxes of philopatric individuals were randomized, indicating that philopatric individuals breeding in their natal plot are responsible for the observed vegetation composition heritability. We also found a considerable decrease in heritability when immigrant individuals (representing the majority of the population) were included in the randomizations. This is because when philopatric individuals have immigrant parents (or ancestors) whose breeding box is randomized, the parent-offspring similarity for the extended phenotype is also reduced (we don't randomize offspring but we do randomize parents) and heritability decreases. Finally, as expected, when all individuals were assigned a random nest box, almost all the observed variance of the extended phenotype was attributed to residual effects.

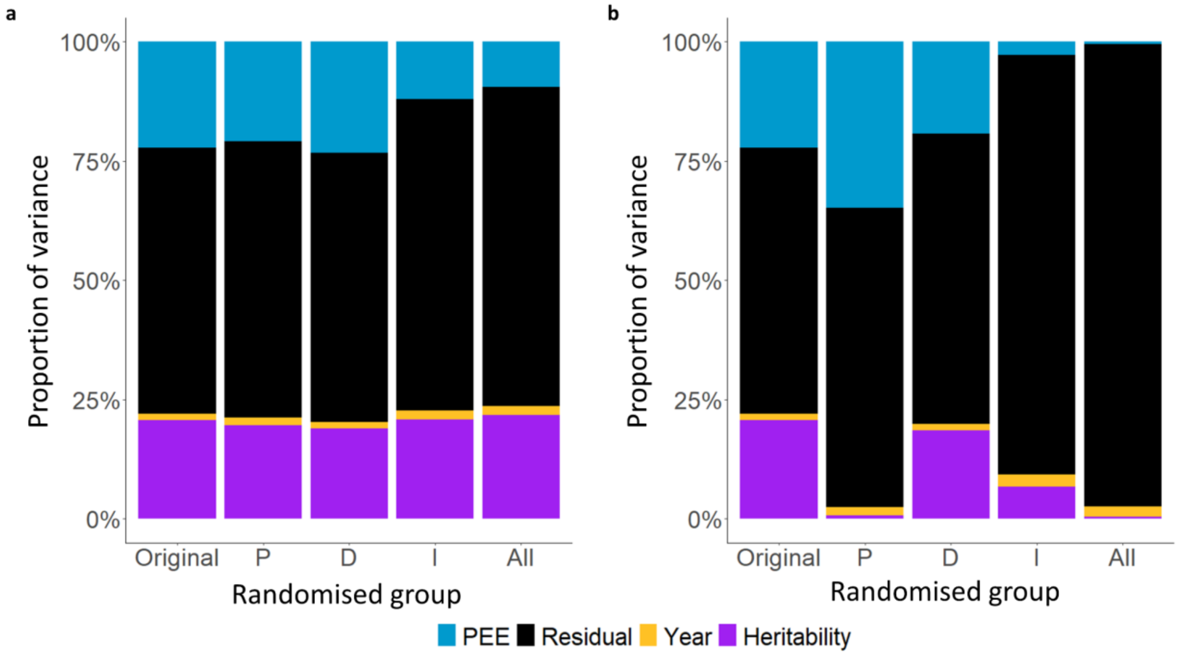

Figure 1. Breeding site vegetation composition (i.e., extended phenotype) variance partitioned into heritability, permanent environmental effects (PEE), among-year variance (Year) and residual variance for the different datasets: original dataset without randomization (Original), or randomizing philopatric (P), disperser (D), immigrant (I), or all individuals. For the simulated scenarios, plotted values are the means from the 1000 independent simulations. In **a**) randomized breeding individuals were assigned a random nest box from their original breeding plot while in **b**) they were assigned a random nest box from any of the study plots.

Philopatry heritability

Regarding philopatry itself (breeding in the natal plot or not), we found a significant heritability for natal philopatry (0.27 ± 0.04), with no significant differences in heritability between males and females (males: 0.27 ± 0.08; females: 0.38 ± 0.09).

Discussion

Heritability of the environment as an extended phenotype

This study aimed at evaluating the use of animal models to estimate the heritability in a wild population of an aspect of the environment, as an extended phenotype. As expected (Munar-Delgado et al., 2023), we were able to fit animal models with the focal local environment as a dependent variable and estimate its heritability. We found a heritability of the breeding site vegetation composition of 0.19 ± 0.04. This is lower than the mean heritability estimated for morphological, behavioral, physiological, and life-history traits using animal models (0.31 ± 0.03; Postma, 2014) but still statistically different from 0. The first direct consequence is that breeding site vegetation composition can evolve, if it affects fitness (i.e., if it affects the phenotype-environment match). The influence of breeding site vegetation composition on pied flycatchers' fitness is well established, as they rely on insect peaks in their breeding area to feed their offspring (Burger et al., 2012; Samplonius et al., 2016; Sanz et al., 2003), and different vegetation types (deciduous trees vs non-deciduous) can differ strongly in food availability throughout the breeding season (Both et al., 2009). The temperature increase due to climate change has caused an advance in insect peaks faster than pied flycatchers are able to adjust their laying date via phenotypic plasticity (Both, 2008; Both et al., 2006; Both & Visser, 2001). However, individuals breeding in sites with less deciduous vegetation have a minor need to adjust the timing of breeding because of the relative lack of seasonal insect peaks (Burger et al., 2012). Thus, inheriting breeding site vegetation composition can have direct effects on individuals' fitness in a changing world. Although it is thought that pied flycatchers usually prefer to breed in deciduous patches (Lundberg & Atalo, 1992; Siikamäki, 1995), there might be some fitness trade-offs that maintain this environmental variability and heritability. For example, it could be possible that in warmer years, when pied flycatchers are unable to accordingly adjust their laying date to match the caterpillar peak in deciduous habitats (Both et al., 2006), flycatchers inheriting non-deciduous habitats have a higher reproductive success and, thus, non-deciduous habitat would be positively selected (Both et al., 2006). Thus, an additional step in disentangling this could be estimating the selection differential for the habitat.

Pied flycatchers breeding in deciduous habitats mostly rely on caterpillars (Sanz, 1998) while individuals in more coniferous habitats rely more on flying insects (Lundberg et al., 1981). This difference in diet provisioning during growth as nestlings could affect individuals' phenotypic traits via phenotypic plasticity (Buchanan et al., 2022; Lindström, 1999; Monaghan, 2007), which can also affect their fitness. A direct consequence of the effects of the heritable extended phenotype on other phenotypic traits of the individuals via phenotypic plasticity is that it also increases the heritability of those phenotypic traits (Munar-Delgado et al., 2023; Saltz, 2019). For example, the heritability underpinning the expression (selection) of the breeding site vegetation composition could indirectly affect the heritability of fledgling body mass (that are fed with different insects while in the nest). In fact, this could occur with any of the phenotypic traits affected by breeding site vegetation composition. Researchers should be aware of this when trying to disentangle genetic and environmental effects shaping the evolution of pied flycatcher phenotypic traits. In quantitative genetics, when estimating the heritability of a phenotypic trait, is a common practice to add to the animal model all the environmental variables hypothesized to affect the phenotypic trait, because it is thought to avoid overestimation of the heritability (Wilson et al., 2010). However, when the environmental variable included as a covariate is heritable, its effects on the phenotypic trait heritability would be statistically removed and the estimated heritability would decrease (Munar-Delgado et al., 2023). Thus, it is necessary to take this into account when interpreting the estimates provided by animal models.

As a summary, all these environment-phenotype interactions suggest that breeding site vegetation composition influences individual fitness and thus it should evolve to improve the environment-phenotype match. In other words, that habitat choice could lead to adaptive evolution of habitat use (Edelaar et al., 2023).

Disentangling the mechanism behind the inheritance of the habitat

We also aimed at identifying the mechanism driving habitat heritability in our pied flycatcher study population. Applying animal models to different subsets of the population based on their dispersal status, we observed that the heritability as estimated for the whole population's extended phenotype could be attributed solely to philopatric individuals. Testing for heritability in non-philopatric individuals, including dispersers and immigrants, resulted in a heritability estimate of zero (0.00 ± 0.00). However, when we applied the animal model only to the subset of philopatric individuals, heritability was estimated to be higher than for the total population. This indicates that the heritability of breeding site vegetation composition was due to philopatric individuals, which represented only 16% of the observations in our dataset.

The impact of philopatric individuals on the observed heritability was supported by the simulation results. When dispersing individuals were included in the randomizations (representing 13% of the observations) and thereby any habitat choice by them was removed, the mean heritability estimate was similar to the heritability estimate from the original dataset. This suggests that dispersing individuals were not exerting any habitat choice that was promoting habitat inheritance. When philopatric individuals were assigned a random nest box from their original breeding plot, we did not observe any change in the extended phenotype heritability. However, when those individuals were assigned a random nest box from any of the study plots, heritability estimates dropped towards zero (0.01 ± 0.00). These results confirm that the observed overall habitat heritability was due to philopatric individuals breeding in their natal plot and, thus, to location heritability. The fact that heritability dropped when immigrants were randomized across the study plots reflects the elimination of the parent-offspring link for breeding site vegetation composition. When randomizing the breeding nest box for the majority of the population (71%), the natal box of the philopatric individuals was most likely in a different study plot with a different vegetation, and the vegetation composition of their own breeding box and their natal box was dissimilar. Overall, these results are in concordance with previous studies that have suggested that early experience in the natal site influences habitat choice in the pied flycatcher (Camacho et al., 2016; Chernetsov et al., 2006).

The subset data analysis and simulations provided no evidence for direct genetic habitat choice (i.e., genetic preference for a specific breeding site vegetation composition) or matching habitat choice. If either of these mechanisms had been present, we would have observed heritability in the subset of non-philopatric individuals too. In the first case, offspring would have inherited their parents' genetic preferences, which would have led them to choose a similar environment to that preferred by their parents. In the second case, because offspring generally inherit a phenotype similar to that of their parents, this would have led them to select a similar environment where they would have optimal local performance. There is no reason to think that only philopatric individuals exert either of these types of habitat choice. However, our study could be extended to test for matching habitat choice by using animal models with the habitat as a dependent variable and phenotypic traits as covariates (Munar-Delgado et al., 2023). In this way it could be possible to test if the phenotypic traits have any effect on habitat choice. For example, body size is thought to affect phenotype-dependent dispersal in pied flycatchers (Camacho et al., 2019) that could directly affect habitat choice.

In our study population, vegetation composition in each plot is relatively more homogeneous than vegetation composition between plots. This is likely why philopatric pied flycatchers inherit breeding site vegetation composition: philopatric individuals inherit the location, and thereby indirectly the vegetation. This is a form of non-genetic inheritance (of the extended phenotype), and results in non-genetic parent-offspring similarity (Bonduriansky et al., 2012). If so, this contradicts the common assumption in quantitative genetics that the estimated heritability reflects the genetic basis of the trait.

However, the philopatric behavior causing the extended phenotype inheritance was estimated to be heritable itself too. We found a heritability of natal philopatry of 0.27 ± 0.04, which is close to the mean value reported for behavioral traits (0.30 ± 0.03; Stirling et al., 2002) and also close to the observed range for heritability of this trait in the closely related collared flycatcher *Ficedula albicollis* (0.30 ± 0.07 and 0.47 ± 0.10; Doligez et al., 2009; although note that these values could be overestimated due to the parent-offspring regression methodology used, Postma, 2014). In this case, the animal model could in fact be reflecting the genetic basis of philopatry (Munar-Delgado et al., 2023), and thereby a genetic basis to the environment. Here, we did not take into account that dispersal in males pied flycatchers can be dependent on arrival date in the recruitment year (Hušek et al., 2014), on natal brood size (Pärt, 1990), on hatching date (Smith et al., 1989) or natal territory quality (Potti & Montalvo, 1991). These variables could be taken into account to expand the study on the heritability of the environment.

Although the observed heritability of breeding site vegetation composition may be influenced by these various factors, the observation that pied flycatchers (partially) inherit the habitat remains unchanged. Therefore, we repeat that it is possible that for this pied flycatcher population the habitat can evolve to improve the phenotype-environment match.

In conclusion, as a case study we have shown how animal models can be used to estimate the heritability of the environment. This confirms that applying this methodology to other existing datasets which contain information on relatedness and individual local environments can provide insight into the heritability of the environment, and its consequences for the evolution of extended phenotypes and regular phenotypes alike.

Bibliography

Akcali, C. K., & Porter, C. K. (2017). Comment on Van Belleghem et al. 2016: Habitat choice mechanisms in speciation and other forms of diversification. *Evolution*, *71*(11), 2754–2761. https://doi.org/10.1111/evo.13375

Bolnick, D. I., Yang, L. H., Fordyce, J. A., Davis, J. M., & Svanbäck, R. (2002). Measuring Individual-Level Resource Specialization. *Ecology*, *83*(10), 2936–2941. https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2

Bonduriansky, R., Crean, A. J., & Day, T. (2012). The implications of nongenetic inheritance for evolution in changing environments. *Evolutionary Applications*, *5*(2), 192–201. https://doi.org/10.1111/j.1752-4571.2011.00213.x

Both, C. (2008). Climate change and the advance of laying dates in Pied Flycatchers Ficedula hypoleuca: The Harz and the rest of Europe. *Vogelkdl. Ber. Niedersachs*, *26*, 91-97.

Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, *441*(7089), Article 7089. https://doi.org/10.1038/nature04539

Both, C., Bijlsma, R. G., & Ouwehand, J. (2016). Repeatability in spring arrival dates in pied flycatchers varies among years and sexes. *Ardea*, *104*(1), 3-21.

Both, C., Van Turnhout, C. A. M., Bijlsma, R. G., Siepel, H., Van Strien, A. J., & Foppen, R. P. B. (2009). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1685), 1259–1266. https://doi.org/10.1098/rspb.2009.1525

Both, C., & Visser, M. E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, *411*(6835), Article 6835. https://doi.org/10.1038/35077063

Brommer, J. E., Alho, J. S., Biard, C., Chapman, J. R., Charmantier, A., Dreiss, A., Hartley, I. R., Hjernquist, M. B., Kempenaers, B., Komdeur, J., Laaksonen, T., Lehtonen, P. K., Lubjuhn, T., Patrick, S. C., Rosivall, B., Tinbergen, J. M., van der Velde, M., van Oers, K., Wilk, T., & Winkel, W. (2010). Passerine Extrapair Mating Dynamics: A Bayesian Modeling Approach Comparing Four Species. *The American Naturalist*, *176*(2), 178‑187. https://doi.org/10.1086/653660

Buchanan, K. L., Meillère, A., & Jessop, T. S. (2022). Early Life Nutrition and the Programming of the Phenotype. In D. Costantini & V. Marasco (Eds.), *Development Strategies and Biodiversity: Darwinian Fitness and Evolution in the Anthropocene* (pp. 161–214). Springer International Publishing. https://doi.org/10.1007/978-3-030-90131-8_6

Burger, C., Belskii, E., Eeva, T., Laaksonen, T., Mägi, M., Mänd, R., Qvarnström, A., Slagsvold, T., Veen, T., Visser, M. E., Wiebe, K. L., Wiley, C., Wright, J., & Both, C. (2012). Climate change, breeding date and nestling diet: How temperature differentially affects seasonal changes in pied flycatcher diet depending on habitat variation. *Journal of Animal Ecology*, *81*(4), 926–936. https://doi.org/10.1111/j.1365-2656.2012.01968.x

Butler, D. (2020). asreml: Fits the Linear Mixed Model. R package version 4.1.0.130. www.vsni.co.uk

Callahan, B. J., Fukami, T., & Fisher, D. S. (2014). Rapid evolution of adaptive niche construction in experimental microbial populations. *Evolution*, *68*(11), 3307–3316. https://doi.org/10.1111/evo.12512

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*(1), 158. https://doi.org/10.1186/s12862-016-0724-y

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. https://doi.org/10.1093/beheco/ary195

Charmantier, A., & Réale, D. (2005). How do misassigned paternities affect the estimation of heritability in the wild? *Molecular Ecology*, *14*(9), 2839–2850. https://doi.org/10.1111/j.1365-294X.2005.02619.x

Chernetsov, N., Sokolov, L. V., Kosarev, V., Leoke, D., Markovets, M., Tsvey, A., & Shapoval, A. P. (2006). Sex-Related Natal Dispersal of Pied Flycatchers: How Far Away From Home? *The Condor*, *108*(3), 711–717. https://doi.org/10.1093/condor/108.3.711

Dale, S., Rinden, H., & Slagsvold, T. (1992). Competition for a mate restricts mate search of female pied flycatchers. *Behavioral Ecology and Sociobiology, 30*, 165-176.

Darwin, C. R. (1859). *On the Origin of Species by Means of Natural Selection.* John Murray, London.

Dawkins, R. (1982). *The extended phenotype*. Oxford: Oxford University Press

Davis, J. M., & Stamps, J. A. (2004). The effect of natal experience on habitat preferences. *Trends in Ecology & Evolution*, *19*(8), 411–416. https://doi.org/10.1016/j.tree.2004.04.006

Doligez, B., Daniel, G., Warin, P., Pärt, T., Gustafsson, L., & Réale, D. (2012). Estimation and comparison of heritability and parent–offspring resemblance in dispersal probability from capture–recapture data using different methods: the Collared Flycatcher as a case study. *Journal of Ornithology*, *152*, 539-554.

Edelaar, P., Baños-Villalba, A., Quevedo, D. P., Escudero, G., Bolnick, D. I., & Jordán-Andrade, A. (2019). Biased movement drives local cryptic coloration on distinct urban pavements. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1912), 20191343. https://doi.org/10.1098/rspb.2019.1343

Edelaar, P., Otsuka, J., & Luque, V. J. (2023). A generalised approach to the study and understanding of adaptive evolution. *Biological Reviews*, *98*(1), 352–375. https://doi.org/10.1111/brv.12910

Edelaar, P., Siepielski, A. M., & Clobert, J. (2008). Matching Habitat Choice Causes Directed Gene Flow: A Neglected Dimension in Evolution and Ecology. *Evolution*, *62*(10), 2462–2472. https://doi.org/10.1111/j.1558-5646.2008.00459.x

Falconer, D.S. (1960). *Introduction to Quantitative Genetics*. Oliver and Boyd, Edinburgh

Gervais, L., Hewison, A. J. M., Morellet, N., Bernard, M., Merlet, J., Cargnelutti, B., Chaval, Y., Pujol, B., & Quéméré, E. (2020). Pedigree-free quantitative genetic approach provides evidence for heritability of movement tactics in wild roe deer. *Journal of Evolutionary Biology*, *33*(5), 595–607. https://doi.org/10.1111/jeb.13594

Gervais, L., Morellet, N., David, I., Hewison, M., Réale, D., Goulard, M., Chaval, Y., Lourtet, B., Cargnelutti, B., Merlet, J., Quéméré, E., & Pujol, B. (2022). Quantifying heritability and estimating evolutionary potential in the wild when individuals that share genes also share environments. *Journal of Animal Ecology*, *91*(6), 1239–1250. https://doi.org/10.1111/1365-2656.13677

Hušek, J., Lampe, H. M., & Slagsvold, T. (2014). Natal dispersal based on past and present environmental phenology in the pied flycatcher (Ficedula hypoleuca). *Oecologia*, *174*(4), 1139–1149. https://doi.org/10.1007/s00442-013-2842-1

Jaenike, J., & Holt, R. D. (1991). Genetic Variation for Habitat Preference: Evidence and Explanations. *The American Naturalist*, *137*, S67–S90. https://doi.org/10.1086/285140

Järvinen, P., Kluen, E., & Brommer, J. E. (2017). Low heritability of nest construction in a wild bird. *Biology Letters*, *13*(10), 20170246. https://doi.org/10.1098/rsbl.2017.0246

Jenni, L., & Winkler, R. (2020). *Moult and ageing of European passerines*. Bloomsbury Publishing.

Kruuk, L. E. B. (2004). Estimating genetic parameters in natural populations using the 'animal model.' *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *359*(1446), 873–890. https://doi.org/10.1098/rstb.2003.1437

Laland, K., Matthews, B., & Feldman, M. W. (2016). An introduction to niche construction theory. *Evolutionary Ecology*, *30*(2), 191–202. https://doi.org/10.1007/s10682-016-9821-z

Laland, K. N., & Sterelny, K. (2006). PERSPECTIVE: SEVEN REASONS (NOT) TO NEGLECT NICHE CONSTRUCTION. *Evolution*, *60*(9), 1751–1762. https://doi.org/10.1111/j.0014-3820.2006.tb00520.x

Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, *14*(9), 343–348. https://doi.org/10.1016/S0169-5347(99)01639-0

Lundberg, A., Alatalo, R. V., Carlson, A., & Ulfstrand, S. (1981). Biometry, Habitat Distribution and Breeding Success in the Pied Flycatcher Ficedula hypoleuca. *Ornis Scandinavica (Scandinavian Journal of Ornithology)*, *12*(1), 68–79. https://doi.org/10.2307/3675907

Lundberg, A. & Atalo, R.V. 1992 *The pied flycatcher*. *London*: T & AD Poyser.

Lynch M, Walsh B, (1998). *Genetics and Analysis of Quantitative Traits*. Sinauer Associates.

Monaghan, P. (2007). Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1497), 1635–1645. https://doi.org/10.1098/rstb.2007.0011

Munar-Delgado, G., Araya-Ajoy, Y. G., & Edelaar, P. (2023). Estimation of additive genetic variance when there are gene–environment correlations: Pitfalls, solutions and unexplored questions. *Methods in Ecology and Evolution*, *14*(5), 1245–1258. https://doi.org/10.1111/2041-210X.14098

Nicolaus, M., Barrault, S. C. Y., & Both, C. (2019). Diet and provisioning rate differ predictably between dispersing and philopatric pied flycatchers. *Behavioral Ecology*, *30*(1), 114–124. https://doi.org/10.1093/beheco/ary152

Pärt, T. (1990). Natal Dispersal in the Collared Flycatcher: Possible Causes and Reproductive Consequences. *Ornis Scandinavica (Scandinavian Journal of Ornithology)*, *21*(2), 83–88. https://doi.org/10.2307/3676802

Postma, E. (2014). Four decades of estimating heritabilities in wild vertebrate populations: improved methods, more data, better estimates. *Quantitative genetics in the wild*, 16, 33.

Potti, J., & Montalvo, S. (1991). Male Arrival and Female Mate Choice in Pied Flycatchers Ficedula hypoleuca in Central Spain. *Ornis Scandinavica (Scandinavian Journal of Ornithology)*, *22*(1), 45–54. https://doi.org/10.2307/3676620

Ravigne, V., Olivieri, I., & Dieckmann, U. (2004, January). *Implications of Habitat Choice for Protected Polymorphysms* [Monograph]. IR-04-005. https://iiasa.dev.local/

Saltz, J. B. (2019). Gene–Environment Correlation in Humans: Lessons from Psychology for Quantitative Genetics. *Journal of Heredity*, *110*(4), 455–466. https://doi.org/10.1093/jhered/esz027

Samplonius, J. M., Kappers, E. F., Brands, S., & Both, C. (2016). Phenological mismatch and ontogenetic diet shifts interactively affect offspring condition in a passerine. *Journal of Animal Ecology*, *85*(5), 1255–1264. https://doi.org/10.1111/1365-2656.12554

Sanz, J. J. (1998). Effect of habitat and latitude on nestling diet of Pied Flycatchers *Ficedula hypoleuca*. *Ardea*, 86(1), 81.

Sanz, J. J., Potti, J., Moreno, J., Merino, S., & FRÍAs, O. (2003). Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Global Change Biology*, *9*(3), 461–472. https://doi.org/10.1046/j.1365-2486.2003.00575.x

Schluter, D. (2001). Ecology and the origin of species. *Trends in Ecology & Evolution*, *16*(7), 372–380. https://doi.org/10.1016/s0169-5347(01)02198-x

Siikamäki, P. (1995). Habitat Quality and Reproductive Traits in the Pied Flycatcher: An Experiment. *Ecology*, *76*(1), 308–312. https://doi.org/10.2307/1940652

Smith, H. G., Kallander, H., & Nilsson, J. A. (1989). The trade-off between offspring number and quality in the great tit Parus major. *The Journal of Animal Ecology*, 383-401.

Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., Kruuk, L. E. B., & Nussey, D. H. (2010). An ecologist's guide to the animal model. *Journal of Animal Ecology*, *79*(1), 13–26. https://doi.org/10.1111/j.1365-2656.2009.01639.x

Supplementary information

	V_A (se)	**V_{PE} (se)**	**V_Y (se)**	**V_R (se)**	**h^2 (se)**	**pe^2 (se)**	**y^2 (se)**	**r^2 (se)**	**Df**
All individuals	155.51 (35.65)	196.53 (38.49)	12.35 (5.80)	467.66 (18.67)	0.19 (0.04)	0.24 (0.05)	0.01 (0.01)	0.56 (0.02)	3964
Males	281.62 (74.61)	98.85 (72.04)	6.99 (5.00)	440.72 (23.53)	0.34 (0.09)	0.12 (0.08)	0.01 (0.01)	0.53 (0.03)	1911
Females	199.29 (76.00)	125.28 (78.06)	8.74 (5.63)	505.41 (30.49)	0.24 (0.09)	0.15 (0.09)	0.01 (0.01)	0.60 (0.04)	2052
Philopatric individuals	287.49 (84.98)	0.80 (76.87)	10.80 (9.90)	450.24 (42.56)	0.38 (0.10)	0.001 (0.10)	0.01 (0.01)	0.60 (0.06)	620
Philopatric males	296.94 (67.74)	0.0009 (NA)	12.24 (14.14)	440.98 (53.76)	0.40 (0.07)	$1.2*10^{-6}$ ($9.7*10^{-8}$)	0.02 (0.02)	0.59 (0.07)	361
Philopatric females	294.58 (80.38)	0.0008 (NA)	18.72 (20.65)	432.53 (62.66)	0.39 (0.09)	$1.1*10^{-6}$ ($1.1*10^{-7}$)	0.03 (0.03)	0.58 (0.09)	258
Non-philopatric individuals	$2.6*10^{-4}$ (NA)	377.03 (26.37)	11.80 (5.86)	460.99 (20.43)	$3.1*10^{-7}$ ($8.1*10^{-9}$)	0.44 (0.03)	0.01 (0.01)	0.54 (0.03)	3343

Table S1. Results of univariate animal models of female different subset of individuals. Estimates of variance components are given with their standard error: additive genetic variance (V_A), permanent environmental variance (V_{PE}), among-study year variance (V_Y), and residual within-individual variance (V_R). Estimates of heritability (h^2), permanent environmental effects (pe^2), year variance (y^2), and residual variance (r^2). And model degrees of freedom (Df)

	V_A mean (se)	**V_{PE} mean (se)**	**V_Y mean (se)**	**V_R mean (se)**	**h^2 mean**	**pe^2 mean**	**y^2 mean**	**r^2 mean**	**Df**
Philopatric simulated	163.40 (0.60)	173.32 (0.63)	13.11 (0.05)	481.43 (0.29)	0.20	0.21	0.02	0.58	3964
Dispersers simulated	157.90 (0.47)	195.03 (0.55)	11.66 (0.03)	471.26 (0.23)	0.19	0.23	0.01	0.56	3964
Immigrants simulated	176.51 (0.57)	102.41 (0.74)	16.06 (0.12)	554.13 (0.61)	0.21	0.12	0.02	0.65	3964
All	185.35 (0.94)	81.30 (1.12)	16.16 (0.13)	568.52 (0.78)	0.22	0.10	0.02	0.68	3964
Philopatric simulated (A)	6.67 (0.40)	294.97 (0.52)	12,72 (0.05)	531.58 (0.40)	0.01	0.35	0.02	0.63	3964
Dispersers simulated (A)	154.73 (0.71)	161.34 (0.77)	11.41 (0.05)	506.35 (0.32)	0.19	0.19	0.01	0.61	3964
Immigrants simulated (A)	55.97 (0.55)	23.86 (0.68)	21.53 (0.16)	730.96 (0.66)	0.07	0.03	0.03	0.87	3964
All (A)	3.91 (0.24)	4.81 (0.30)	18.48 (0.17)	821.43 (0.62)	0.005	0.01	0.02	0.97	3964

Table S2. Mean value of estimates of variance components additive genetic variance (V_A), permanent environmental variance (V_{PE}), among-study year variance (V_Y), and residual within-individual variance (V_R) and mean value of estimates of heritability (h^2), permanent environmental effects (pe^2), year variance (y^2), and residual variance (r^2). Standard error represents the standard error of that mean value not for each estimate of each model as in Table S1. For all mean estimates of h, pe^2, y^2 and r^2 se was < 0.0001. And model degrees of freedom (Df).