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Quantifying heritability and estimating evolutionary potential in the wild when individuals that share genes also share environments

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Abstract (343words):

1. Accurate heritability estimates for fitness-related traits are required to predict an organism's ability to respond to global change. Heritability estimates are theoretically expected to be inflated if, due to limited dispersal, individuals that share genes are also likely to share similar environments. However, if relatives occupy similar environments due, at least partly, to genetic variation for habitat selection, then accounting for environmental similarity in quantitative genetic models may result in diminished heritability estimates in wild populations. This potential issue has been pointed out in the literature, but has not been evaluated by empirical studies.
2. Here, we investigate whether environmental similarity among individuals can be partly explained by genetic variation for habitat selection, and how this link potentially blurs estimates for heritability in fitness-related traits.
3. Using intensive GPS-monitoring, we quantified home-range habitat composition for 293 roe deer inhabiting a heterogeneous landscape to assess environmental similarity. To investigate if environmental similarity might harbour genetic variation, we combined genome-wide data in a quantitative genetic framework to evaluate genetic variation for home-range habitat composition, which is partly the result of habitat selection at settlement. Finally, we explored how environmental similarity affects heritability estimates for behaviours related to the risk avoidance-resource acquisition trade-off (i.e. being in open habitat, distance to roads) and proxies of individual performance (i.e. body mass, hind foot length). We found substantial heritability for home-range habitat composition, with estimates ranging from 0.40 (proportion of meadows) to 0.85 (proportion of refuge habitat). Accounting for similarity in habitat composition between relatives decreased the heritability estimates for both behavioural and morphological traits (reduction ranging from 55% to 100% and from 22% to 41%, respectively). As a consequence, only half of these heritability estimates remained significantly different from zero.
4. Our results show that similar genotypes occupy similar environments, which could lead to heritable variation being incorrectly attributed to environmental effects. To accurately distinguish the sources of phenotypic variation and predict the ability of organisms to respond to global change, it is necessary to develop quantitative genetic studies investigating the mechanisms underpinning environmental similarity among relatives.

Keywords: environmental similarity, genotype-environment correlation, Genomic Relatedness Matrix, habitat selection, heritability

Introduction

Environmental heterogeneity is a natural and dominant landscape feature that has been modified through global change (e.g. acceleration of landscape fragmentation, habitat uniformisation in human-dominated land use systems, Brook et al., 2008; Caillon et al., 2014). Rapid change in the degree of environmental heterogeneity likely constitutes a novel selection pressure on the performance of organisms (Cheptou et al., 2017). In this context, understanding how organisms respond to the heterogeneity of their environment is of crucial importance. Environment-organism interactions are partly driven by the behavioural decision of where to settle (i.e. habitat selection; Edelaar & Bolnick, 2019; Morris, 2003). The environmental characteristics of the selected home-range, in turn, may influence the individual’s phenotype and performance in terms of growth, reproduction and survival (Gaillard et al., 2010). As a result, behavioural decisions that determine the environment that an individual is exposed to will also influence the direction and strength of natural selection (Brown, 1990; Laland et al., 1999). For example, birds living in arid habitats minimise the effects of extreme heat events by temporarily modifying their habitat use (Martin et al., 2015). Habitat selection can, therefore, improve the match between an individual’s phenotype and local conditions, improving individual performance and, thus, shape the evolution of phenotypic traits (Edelaar & Bolnick, 2019; Porter & Akcali, 2020). Identifying the mechanisms behind these behavioural decisions has important implications for understanding their evolutionary consequences and forecasting whether organisms will adapt adequately to global change.

A growing number of studies have demonstrated among-individual variation in habitat selection (Leclerc et al., 2016) or its outcome (e.g. home-range composition, Bonnot et al., 2015; Schirmer et al., 2019). This among-individual variation is known to be driven by a variety of mechanisms (Akcali & Porter, 2017). For example, exposure to environmental stimuli during ontogeny can influence the selection of a given habitat as an adult (Davis & Stamps, 2004; Immelmann, 1975). Alternatively, but not exclusively, individuals may choose to settle in a specific environment in relation to their expected performance in that habitat given their intrinsic phenotypic characteristics (Matching habitat choice (MHC); Edelaar et al., 2008). Genes might indirectly influence habitat selection if, for example, the phenotypic characteristics that govern MHC have a genetic basis. Genes might also directly influence habitat preference (Jaenike & Holt, 1991; Wecker, 1964). For example, a few genes determine selection for swimming depth in deep-sea fish (Gaither et al., 2018), or for host type in insects (Matsubayashi et al., 2010). Certain outcomes of habitat selection, such as the habitat composition of the home-range (Van Moorter et al., 2016), can therefore also be influenced by genetic variation underpinning habitat selection. As a result, they are expected to evolve in response to selection. However, few studies have been able to quantify genetic variation for habitat selection or its outcomes in the wild (but see Gaither et al., 2018; Hoey & Pinsky, 2018).

If habitat selection harbours some genetic variation, genotypes should be spatially sorted between contrasting environments. As a result, genetically related individuals are expected to share a similar habitat (environmental similarity), which will generate genotype-environment correlations (Saltz & Nuzhdin, 2014). Consequently, it may become challenging to distinguish genetic and environmental sources of phenotypic resemblance and obtain reliable estimates of heritability (i.e. the proportion of phenotypic variation due to genetic variation). To date, this challenge has been addressed by considering that environmental similarity among relatives solely results from limited dispersal in heterogeneous environments (Kruuk & Hadfield, 2007). Some studies in the literature have shown that environmental similarity between relatives could lead to particularly high estimates of heritability, presumably due to an overestimation of genuine genetic variance (Germain et al., 2016; Jeugd & McCleery, 2002; Regan et al., 2017; Stopher et al., 2012). However, the conclusions are not uniform across phenotypic traits (e.g. life history, morphology) and studies (Rutschmann et al., 2020). Furthermore, most studies quantified environmental similarity as spatial proximity (e.g. spatial autocorrelation (hereafter '*SAC*'); home range overlap), although spatially close individuals may experience very different environments and vice versa (Thomson et al., 2018). Therefore, it is difficult to draw general conclusions about the propensity of environmental similarity approaches to overestimate genuine genetic variance, producing inflated estimates of heritability. More importantly, despite repeated warnings that, in the presence of genetic variation for habitat selection, controlling for environmental similarity may underestimate genuine genetic variance (Stopher et al., 2012; Thomson et al., 2018), no study has yet explicitly investigated this bias. Understanding the mechanisms underpinning environmental similarity between relatives (e.g. the genetic basis of habitat selection) is essential if we are to distinguish among the various sources of phenotypic variation for accurately predicting the ability of organisms to respond to global change.

We used a quantitative genetic framework combining genome-wide data, intensive GPS-monitoring and fine-scale habitat description (i) to investigate whether environmental similarity is partially explained by genetic variation for habitat selection, (ii) to estimate how environmental similarity affects estimates of heritability for behavioural and morphological traits. We assessed environmental similarity using home-range habitat composition and compared heritability estimates to those using traditional measures of environmental similarity (i.e. SAC). We focused on roe deer (*Capreolus capreolus*) inhabiting a spatially heterogeneous landscape, where individuals are likely to share similar environments due to limited-dispersal (i.e. ca. 50% philopatry; Ducros et al., 2020) and select their habitat at multiple spatial scales (Martin et al., 2018; Morellet et al., 2011; Padié et al., 2015). On the basis of the available knowledge on this biological system, we predict (i) that, due to limited dispersal, individuals that share genes will share similar environments and that (ii) taking into account environmental similarity will strongly affect estimates of heritability. In addition, as home-range habitat composition results, at least partly, from habitat selection at settlement, we predict (iii) that similarity in habitat composition could be partly shaped by genetic variation if habitat selection itself has a genetic basis.

Materials & Methods

See extended material & methods in the supporting information (SI) for more details

Study population and data collection

This study was based on the long-term monitoring of a free-ranging roe deer population in southwest France inhabiting a highly heterogeneous landscape composed of a mosaic of refuge habitat (woodland, hedgerows) and agricultural land (meadows and crops). Agricultural land provides high-quality foraging resources for roe deer (Abbas et al., 2011; Hewison et al., 2009), but exposes them to higher risk of predation (dogs, hunting and road traffic accidents) or disturbance by human activities (perceived risk of predation, Bonnot et al., 2015; Coulon et al., 2008; Padié et al., 2015).

Roe deer were caught between 2002 and 2018 during annual winter capture operations where each animal was sexed, aged as an adult (>1-year-old) or juvenile (< 1-year-old) based on tooth eruption (Ratcliffe & Mayle, 1992). Each animal was weighed (hereafter *body mass*), and *hind foot length* was measured, from the top of the calcaneum to the tip of the hoof, providing reliable indicators of body condition and demographic performance (Hewison et al., 2009; Toïgo et al., 2006). A sample of ear skin tissue was taken for genotyping. All capture and marking procedures was permitted by the land manager (hunting groups and farmers) and the prefecture of the Haute Garonne (prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer). All procedures were approved with respect to French and European law on animal welfare by the Ethical Committee 115 of Toulouse and were authorised by the French government (APAFIS#7880-2016120209523619_v5 and agreement nb. A31113001 approved by the Departmental Authority of Population Protection).

Genomic relatedness

We genotyped 334 individuals using a double-digest RAD sequencing approach (Peterson et al., 2012) following the procedure detailed in Gervais et al. (2019). We obtained 14,887 polymorphic loci that were used to compute the Genomic Relatedness Matrix (GRM) of the population, using identity by state SNP relationships and the Unified Additive Relationship estimator, as implemented in the GCTA software tool (Yang et al., 2011).

Spatial data

Based on aerial photographs of the study site, we manually digitised homogeneous habitat polygons (in ArcView GIS 3.3, Esri, Redlands, CA, USA). Each polygon was assigned to a habitat type (*e.g.* woodland, hedgerow, meadow or crop) determined annually by field observations.

Most of the genotyped deer (n=304/334) were equipped with GPS collars to monitor individual movement-related behaviours. Baseline and intensive monitoring were programmed to record a GPS fix every six hours (see SI for exceptions) and every 10 minutes over a 24h period once per month, respectively, for approximately one year. We removed aberrant GPS fixes and all locations prior to dispersal according to the procedure detailed in the supporting information.

a) Movement-related behaviour

We analysed four movement-related behaviours shown to be heritable (Gervais et al., 2020) and to vary in relation to environmental heterogeneity (Bonnot et al., 2015; Coulon et al., 2008; Padié et al., 2015). Risk taking was indexed by calculating (i) the probability of being in open habitat during daytime (P_{OH}), ranging between 0 for an individual that was always located in closed habitat (woodland, hedgerows or scrubland) and 1 for an individual that was always located in open habitat during daytime, and (ii) the distance (km) to the nearest road during daytime (*distance to roads*). We indexed routine movement behaviour by calculating (iii) *daily average speed* (km.h^{-1}) and (iv) home-range size (ha, *home-range size*) (Börger et al., 2008) using the fixed Kernel Density Estimation (package adehabitatHR; Calenge, 2006) at the 90% density isopleths (Börger et al., 2006). All movement-related behaviours were averaged per month for each individual.

b) Habitat composition of the home-range

We evaluated monthly habitat composition based on the principal habitat characteristics related to resource acquisition (occurrence of meadows, habitat heterogeneity) and risk perception (occurrence of refuge habitat and human infrastructure). First, to index the degree of habitat diversity within the home-range, we calculated the Simpson diversity index as:

$Habitat\ diversity = 1 - \sum_{i=1}^{m} P_i^{\,2}$, where$P_i$ is the proportion of habitat type i, and m is the number of habitat types (29 different habitat types). This represents the probability that two randomly selected habitat types are of the same type. Second, for further analysis, habitat types were grouped in broad habitat categories: we calculated the proportion of refuge habitat (wood, hedgerow, and scrubland) which is perceived as secure, the proportion of meadows (natural and artificial meadows), which provides high-quality resources, and the proportion of human infrastructure (house, road, garden, etc.), which is perceived as risky. These metrics were calculated as the ratio between the surface area of the given habitat type and the total home-range size (hereafter $P_{refuge,}$ P_{meadow}, $P_{HI,}$ respectively). We restricted the data set to those individuals for which we obtained information on habitat composition, based on the GPS-collar, over at least 80% of the home-range (276/334 genotyped roe deer).

c) Similarity in home-range habitat composition

To evaluate the proportion of phenotypic variation that could be attributed to environmental similarity, we assessed the degree of similarity in habitat composition among individuals as recommended in Thomson et al. (2018). First, we estimated habitat composition within the home-range (P_{refuge}, P_{meadow}, $P_{HI,}$ *Habitat diversity)* during the spring season only, when roe deer habitat use is not influenced by hunting or rutting behaviour (n=266 GPS-monitored roe deer). If individuals were monitored across multiple years, habitat composition was averaged over years. Then, for each pair of individuals, we calculated the Euclidean distance between scaled and centred measurements of habitat composition in multivariate space, assuming that each habitat composition metric has the same weight. Lastly, Euclidean distances were scaled so that environmental similarity took the value of 1 when an individual was compared with itself and the value of 0 between individuals that had the most dissimilar habitat composition in the population (hereafter *'Smatrix'*; Thomson et al., 2018; Stopher et al., 2012). To ensure similar dimensions between the GRM (n=334) and the *Smatrix* (n=266) (Thomson et al., 2018), a prerequisite for quantitative genetic models, we minimised the number of missing data by also including data on individuals whose spatial tracking was less intense (i.e. located opportunistically using the VHF system only, due to a dysfunctional GPS, n=27). Specifically, we constructed a buffer zone around the barycentre of their locations in order to assess the habitat composition of their home range. To reflect natural variation in home-range size, buffer zone sizes were determined according to the population mean for a given age and sex (see SI for more information). Finally, we removed individuals for which we had no information on habitat composition (n=41) from the GRM (Table S1 for more information about sample size per phenotypic trait and statistical model). Consequently, for all the statistical analyses, the final dimension of the GRM and *Smatrix* was 293 roe deer.

Statistical analyses

We used univariate quantitative genetic linear mixed models with a REML method (Lynch & Walsh, 1998) to partition the phenotypic variance for home-range habitat composition (P_{refuge}, P_{meadow}, P_{HI}, *Habitat diversity*), movement-related behaviours (P_{OH}, *distance to roads*, *daily average speed, home-range size*), and morphological traits (*body mass* and *hind foot length*). We included age class (juvenile vs. adult) as a fixed effect in all models. For models investigating variation in movement-related behavioural traits, we additionally included month (1-12), sex and their two-way interaction as fixed effects to account for sex differences in seasonal behavioural patterns (Malagnino et al., 2021). For models investigating variation in *body mass and hind foot length*, to account for sexual dimorphism and the sex-specific growth trajectories of roe deer (Hewison et al., 2011), we included sex, age class and their interaction. In addition, because juveniles continue to grow during winter in southern latitudes (Hewison et al., 2002), we standardised *body mass* and *hind foot length* for juveniles to the 1st of February by estimating the daily change in these traits over the winter catching season using a linear model. After inspection, we transformed the response variables so that the residuals had a closer approximation to normality: P_{refuge} and P_{HI} were square-root transformed, *Habitat diversity* was box-cox transformed (lambda=5.5), while *distance to roads* (+1 km), *daily average speed, home-range size*, P_{meadow}, *body mass* and *hind foot length* were log-transformed.

a) Assessing heritability of habitat composition, movement behaviour and morphological traits without accounting for environmental similarity (*basic* model)

First, we decomposed the phenotypic variance into among-individual variance (V_I), residual variance (V_R), including individual identity as a random effect, and fixed-effect variance (V_F) following the procedure detailed in de Villemereuil et al. (2018). Then, we added a random effect for individual identity linked to the GRM to distinguish among-individual variation associated with genetic differences (V_A) from variation associated with non-genetic differences (V_{PE}). From this 'genetic model', we estimated the phenotypic variance of traits as $V_P=V_A+V_{PE}+V_R+V_F$ and we calculated the relative importance of each variance as (i) narrow-sense heritability of the trait as $h^2=V_A/V_P$, (ii) the relative importance of permanent environmental variance as $pe^2=V_{PE}/V_P$, (iii) the relative importance of residual variance as $r^2=V_R/V_P$ (Wilson et al., 2010) (iv) the relative importance of fixed-effects $f^2=V_F/V_P$. Non-adjusted repeatability (Nakagawa & Schielzeth, 2010) was estimated as $ind^2=(V_A+V_{PE})/V_P$.

b) Investigating the effect of environmental similarity on heritability estimates (*SAC* and *Smatrix* models)

For each behavioural and morphological trait, the *basic* model was extended to estimate the phenotypic trait variance attributed to environmental similarity variance using two methods: by fitting the matrix of habitat similarity among individuals as an additional random effect (*Smatrix* model, Thomson et al., 2018), or by accounting for spatial proximity among individuals (i.e. *SAC*). The *SAC* model requires fitting a two-dimensional isotropic exponential covariation of the average XY coordinates on the residual structure with a *nugget effect* (see SI for details on XY coordinates). From *SAC* models, we calculated the relative importance of spatial proximity as $s^2=V_S/(V_A+V_{PE}+V_S+V_R+V_F)$, where V_s is the variance associated with spatial proximity. From *Smatrix* models, we calculated the relative importance of habitat similarity as $sm^2=V_S/(V_A+V_{PE}+V_{Sm}+V_R+V_F)$, where V_{sm} is the variance associated with habitat similarity. In addition, we recalculated h^2, pe^2, r^2 and f^2 by accounting for V_S (*SAC* model) or V_{Sm} (*Smatrix* model) in the denominator. *Smatrix* and *SAC* provide different information because spatially close individuals may use either similar or dissimilar habitats, while *Smatrix* provides information on similarity in habitat composition that may or may not be spatially autocorrelated (Fig. S2). One limitation of this approach, in our specific case, is that both environmental similarity effects depend on each other and cannot be estimated simultaneously, because the *Smatrix* model is highly spatially autocorrelated (Fig. S2). In addition, when decomposing variation in home-range habitat composition, we did not fit the *Smatrix* model as it is highly correlated with the dependent variable.

All mixed model analyses were conducted with ASReml-R v4.00 (Butler et al., 2018) and all model estimates are provided on the latent scale (i.e. the scale of the transformed variable). The standard error of fixed-effect variance was approximated according to Lynch & Walsh (1998). The statistical significance for variance components for each model (V_A, V_{PE}, V_S, V_{Sm}) was assessed using Likelihood Ratio Tests (LRT) (Wilson et al., 2010), assuming that twice the difference in log-likelihood between nested models follows a chi-squared distribution with one degree of freedom. Approximate standard errors for the relative importance of variance components were calculated according to Fischer et al. (2004). All model performances were checked according to methods detailed in the Supplementary Information. It is important to note that we could not always estimate the exact amount of variance, as some models had identifiability problems (Figs. S5-7, Table S3-4, Text S1). In particular, the models accounting for habitat similarity did not produce credible variance estimates for *distance to roads* because the total V_P increased by more than 100% between the *basic* and *Smatrix* models. As a consequence, results for this trait will be presented, but not interpreted.

Correlation between genomic relatedness and environmental similarity

To ensure model feasibility, we visually inspected the relationship between genomic relatedness and habitat similarity to check that some genetically-related individuals occupied different environments (Fig. S1). We also verified the spatial autocorrelation between genomic relatedness and habitat similarity to ensure they were not wholly confounded. By building spline correlograms of habitat similarity (*Smatrix*) and genomic relatedness (GRM), both separately and together (cross-correlograms*, ncf* package), we found that individuals that were close in space were also more related and had home ranges that were more similar in habitat composition than expected by chance (up to 2500 and 4000 meters, respectively i.e. 21% and 37% of pairs of individuals, Figs S2, S3). In addition, genomic relatedness and environmental similarity were correlated (at 11%) at a distance of a few meters, but this correlation progressively weakened to a value of zero at a distance above 4000 meters, i.e. 63% of pairs of individuals (Fig. S4), therefore ensuring model feasibility.

Results

Apparently strong estimates of heritability for habitat composition are diminished when accounting for spatial proximity

Individuals consistently differed in the habitat composition of their home-range, with repeatability ranging from 0.75 for *Habitat diversity* to 0.87 for P_{refuge} (Table S2). These among-individual variations were underpinned by high heritability (h^2), ranging from 0.40 (P_{meadow}) to 0.85 (P_{refuge}), and moderate relative importance of the permanent environment (pe^2), ranging from <0.01 (P_{refuge}) to 0.38 (P_{meadow}). Accounting for spatial proximity (s^2) explained almost all among- and within-individual variance in home-range habitat composition (s^2 ranging from 0.75 for *Habitat diversity* to 0.95 for P_{refuge}). Its inclusion in the model led to an average decrease of 67% in the relative importance of the residual variance (r^2) (decrease ranging from 60% for *Habitat diversity* to 79% for P_{refuge}) and 41 % in pe^2 (ranging from 33% for *Habitat diversity* to 82% for P_{meadow}). pe^2 remained significantly different from zero for P_{meadow}, P_{HI} and *Habitat diversity* (decreasing from pe^2=0.38, 0.12, 0.18 to pe^2=0.07, 0.06, 0.12, respectively). The greatest change concerned the heritability estimates that decreased, on average, by 98% when accounting for spatial proximity (decrease ranging from 90% for P_{meadow} to 98% for P_{refuge} and P_{HI}). However, heritability estimates for P_{refuge} and P_{meadow} remained significantly different from zero when accounting for spatial proximity (h^2=0.02 and 0.04 respectively, Table S2, Fig. 1).

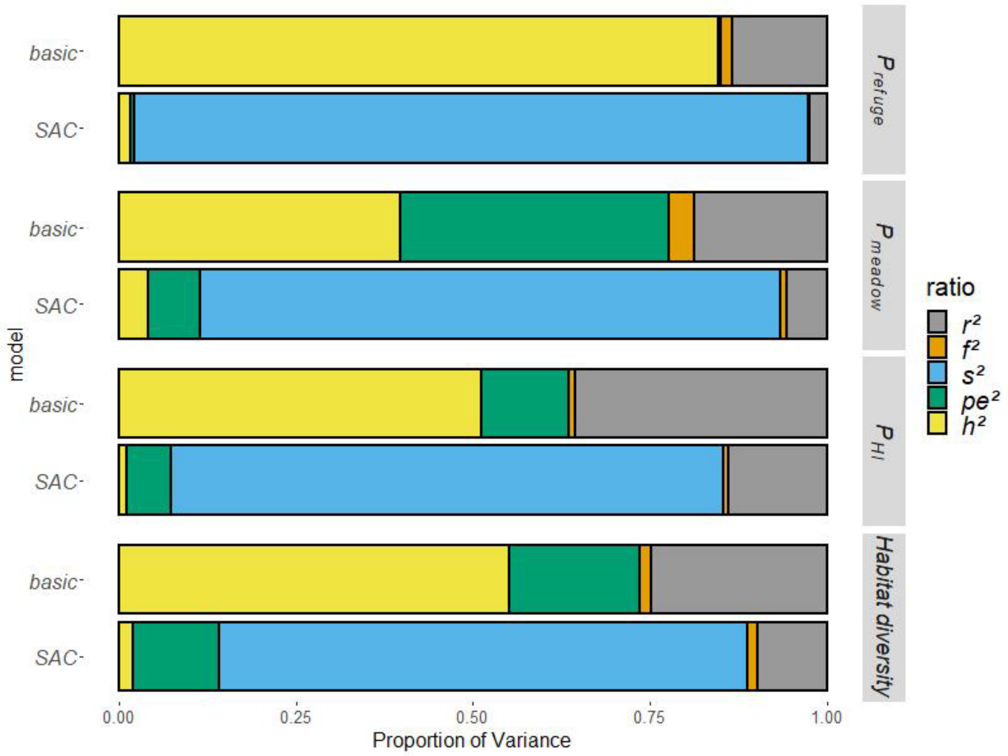

Figure 1. Decomposition of phenotypic variation into genetic and non-genetic variation for habitat composition traits. For each trait, results are reported either with (*SAC* model) or without (*basic* model) accounting for spatial proximity. The narrow-sense heritability (h^2) refers to the relative importance of additive genetic variance, while r^2, f^2, s^2, pe^2 refer respectively to the relative importance of residual, fixed-effect, spatial proximity and permanent environmental variances.

SAC and Smatrix approaches reveal that relatives share similar environments

Environmental similarity variance (s^2 or sm^2 for *SAC* or *Smatrix* models, respectively) explained moderate to substantial variation in both movement-related behaviour and morphological traits (Tables S3, 4 and Figs 2, 3). s^2 ranged from 0.07 for *body mass* to 0.67 for the probability of being in open habitat during daytime (P_{OH}), while sm^2 ranged from 0.09 for *hind foot length* to 0.53 for P_{OH}. For all traits except *body mass*, *SAC* models had consistently lower V_{PE} and V_R than the equivalent *Smatrix* models (table S3, S4). There was no methods-related trend in the decrease of V_A. In line with prediction (1), accounting for environmental similarity either with *SAC* or *Smatrix* models decreased V_A, on average, by 57% (ranging from 33% for *body mass* to

99.99% for *daily average speed*), indicating that relatives shared a similar environment. The only exception was for *hind foot length* where V_A was unchanged when using the *SAC* model compared to the *basic* model.

The influence of environmental similarity on estimates of heritability differs between behavioural and morphological traits

Consistent with our prediction (2), we found that accounting for environmental similarity lead to a reduction in h^2 and pe^2 for both behavioural and morphological traits. We found a greater impact of environmental similarity on the variance components for behavioural traits than for morphological traits. For morphological traits, the *SAC* model resulted in an average relative decrease of 15%, 26%, and 54% in h^2, pe^2, and r^2, respectively, whereas for behavioural traits, it resulted in an average decrease of 84%, 54%, and 44% for h^2, pe^2, and r^2, respectively. Similarly, the *Smatrix* model resulted in an average relative decrease of 31.5%, 5%, and 5.5% in h^2, pe^2, and r^2, respectively, for morphological traits, whereas for behavioural traits, it resulted in an average relative decrease of 74%, 25%, and 15%, in h^2, pe^2, and r^2, respectively. Both models caused heritability estimates to be weak and non-significant for three out of six traits (Table S3, S4, Figs 2, 3). In particular, heritability for P_{OH}, *distance to roads* and *daily average speed* was weak and non-significant after a sharp relative decrease of respectively 94%, 100% and 72% when using the *Smatrix* model and 97%, 99% and 100% when using the *SAC* model. In contrast, heritability estimates for *home-range size, body mass* and *hind foot length* (h^2=0.31, 0.27, and 0.32, respectively for *basic* model) decreased moderately (55%, 41%, and 22%, respectively), but remained significant (h^2= 0.14,0.16, and 0.25 respectively when using the *Smatrix* model, Table S4).

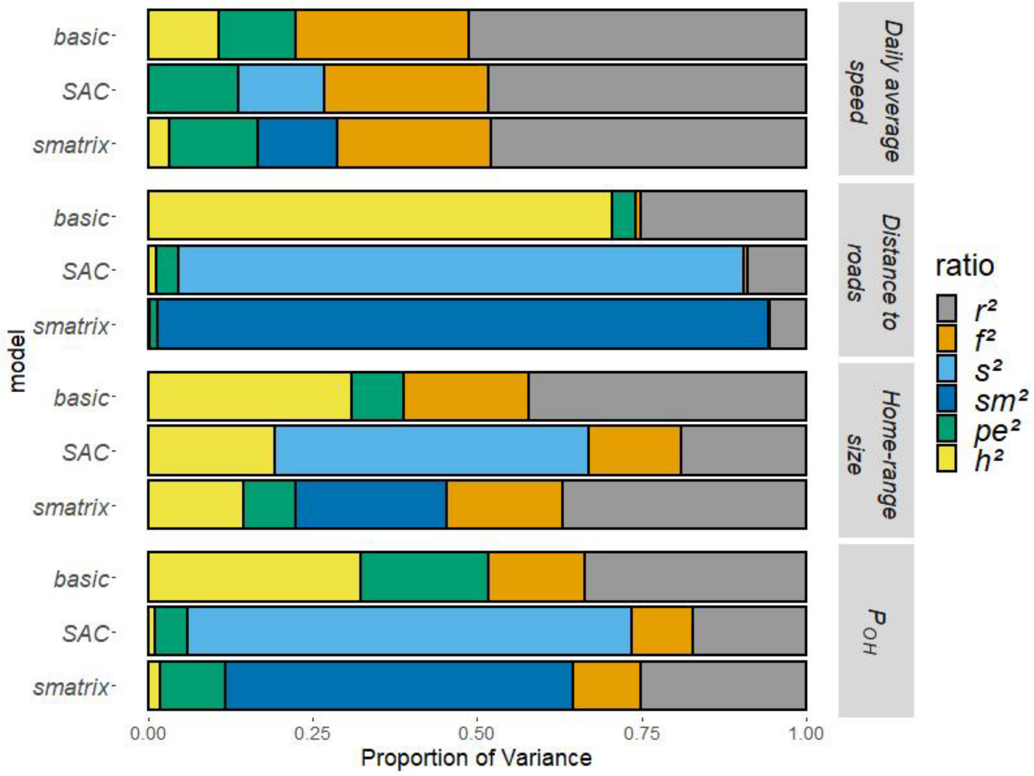

Figure 2. Decomposition of phenotypic variation into genetic and non-genetic variations for behavioural traits. For each trait the results of three models are presented: the *basic* model does not account for environmental similarity, the *SAC* model accounts for spatial proximity, while the *Smatrix* model accounts for habitat similarity. The narrow-sense heritability (h^2) refers to the relative importance of additive genetic variance, while r^2, f^2, s^2, sm^2, and pe^2 refer respectively to the relative importance of residual, fixed-effect, spatial proximity, habitat similarity and permanent environmental variances.

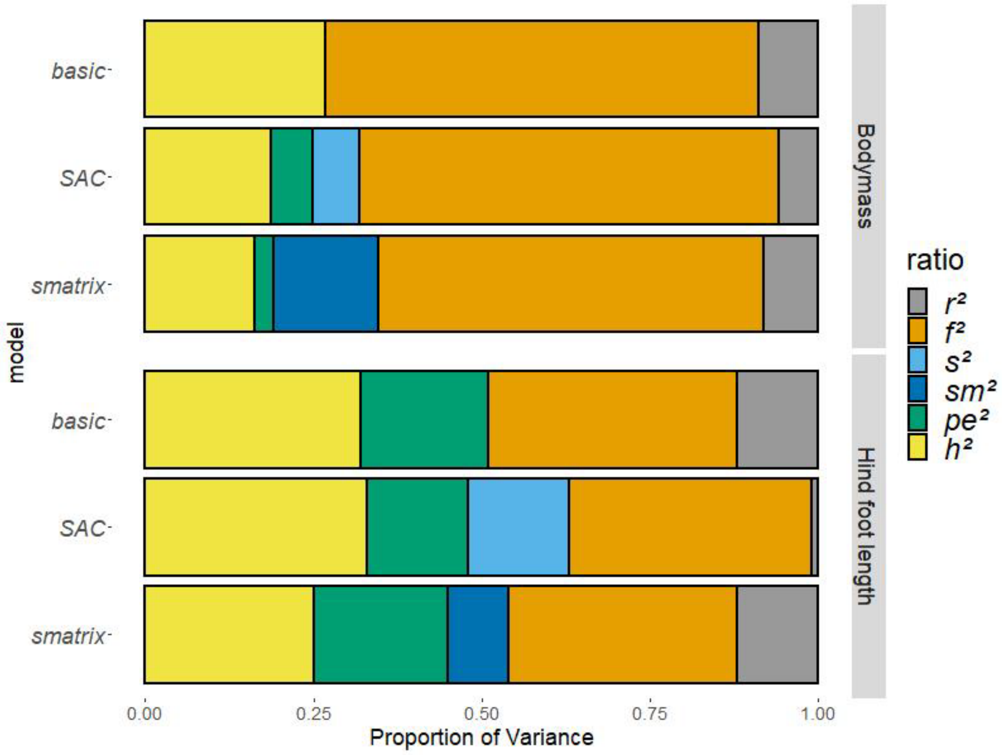

Figure 3. Decomposition of phenotypic variation into genetic and non-genetic variations for morphological traits. For each trait, the results of three models are presented: the *basic* model does not account for environmental similarity. The *SAC* model accounts for spatial proximity while the *Smatrix* model accounts for habitat similarity. The narrow-sense heritability (h^2) refers to the relative importance of additive genetic variance, while r^2, f^2, s^2, sm^2, and pe^2 refer respectively to the relative importance of residual, fixed-effect, spatial proximity, habitat similarity and permanent environmental variances.

Discussion

In the context of increasing habitat loss and fragmentation driven by ongoing global change, our findings highlight the need to consider the impact of environmental heterogeneity on our ability to assess the heritability of fitness-related traits in the wild. There is a growing awareness of the need to account for environmental similarity in quantitative genetic models to avoid overestimating heritability (Germain et al., 2016; Jeugd & McCleery, 2002; Regan et al., 2017; Rutschmann et al., 2020; Stopher et al., 2012; Thomson et al., 2018). On the flip side, below, we discuss why accounting for environmental similarity in quantitative genetic models of wild populations may instead drive heritability estimates downwards by removing genuine genetic variance for a given trait.

Different methods yield similar general conclusions about the impact of environmental similarity on heritability estimates

Our results showed that both *SAC* and *Smatrix* models resulted in greatly reduced estimates of heritability for both movement behaviours and proxies of individual performance (body mass, hind foot length, Toïgo et al., 2006). Both methods led to a reduction in the additive genetic variance (V_A), indicating that relatives that share genes also share similar environments. While the *Smatrix* approach theoretically accounts for the degree of similarity in environment between relatives better than the *SAC* approach (Thomson et al., 2018), we did not identify clear differences in the estimated V_A between *Smatrix* and *SAC* models, given the associated standard errors and the change in estimated phenotypic variance (Text S1). The relative performance of the *Smatrix* and *SAC* models should depend on the grain and stochasticity of environmental heterogeneity. For example, the *SAC* model may not be suitable if spatially close individuals do not necessarily share similar environments, or if long-distance dispersers are common and susceptible to choose an environment that is similar to their natal range (Stamps & Davis, 2004). Our study described environments at the scale of the home-range using a coarse grain. As a result, spatially close individuals had a high probability of sharing a similar environment because habitat composition was strongly spatially autocorrelated. While the *Smatrix* approach should be prioritised if it is possible to identify ecologically relevant environmental drivers, the *SAC* approach should be preferred if environmental information is not available or not biologically relevant for describing similarity in environment and/or (ii) environmental variables are susceptible to be highly spatially autocorrelated.

Contrasting impact of shared environments on heritability estimates between morphological and behavioural traits

Consistent with our first two predictions, our analyses revealed that roe deer that shared genes also shared similar environments. As a result, when we took environmental similarity into account, this strongly reduced our estimates of heritability. This reduction in heritability estimates was more pronounced for behavioural traits than for morphological traits, where it was moderate. This is consistent with previous studies: Stopher et al.(2012) found a strong effect of environmental similarity on the heritability of spatial behaviour (home-range size) in red deer (*Cervus elaphus*), whereas the effects were weak or negligible on heritability estimates for morphological and life-history traits obtained by Germain et al. (2016), Regan et al.(2017), Rustchmann et al. (2020) and Stopher et al. (2012) (for song sparrows *Melospizamelodia*, soay sheep *Ovis aries*, the hihi *Notiomystiscincta*, and red deer *Cervus elaphus*, respectively). This discrepancy among trait types may be partly explained by contrasting degrees of dependence on environmental characteristics. Unlike morphological or life-history traits, spatial behaviours may be intrinsically spatially autocorrelated (Valcu & Kempenaers, 2010). For example, home range size is strongly dependent on habitat composition (van Beest et al., 2011; Tufto et al., 1996) which often demonstrates strong spatial autocorrelation. In our case, environmental similarity (*SAC* accounting for spatial proximity or *Smatrix* accounting for similarity in habitat composition) explained, on average, 49 % of the variation in all spatial behaviours. This strong effect is likely because adult roe deer are highly sedentary, so that routine movement behaviour is highly dependent on habitat characteristics that are stable elements of the home-range (Hewison et al., 1998). To decipher the contrasting effects of environmental similarity on heritability estimates for behaviour versus morphology, we will require a more in-depth understanding of the mechanisms that link these traits to the environment.

Heritability for home-range habitat composition suggests genetic variation in habitat selection

While numerous studies have documented substantial among-individual variation in habitat use (Schirmer et al., 2019; Spiegel et al., 2015), few have highlighted its underlying genetic variation in wild populations (Gaither et al., 2018 for a recent example). In line with our third prediction, our results demonstrated that the habitat composition of the home-range, which results partly from habitat selection at settlement, is heritable (average h^2=0.58). Similarly, broad-sense environmental characteristics (e.g. family environment) are heritable in humans, but to a lesser degree (h^2=0.27 on average; Kendler & Baker, 2007). This evidence of genetic variation for habitat composition of the home-range in roe deer should be interpreted with caution. First, we did not account for maternal effects that are known to be of widespread importance (Moore et al., 2019) for both habitat selection (e.g. in multiple species, Stamps & Davis, 2004) and morphological traits in roe deer (Quéméré et al., 2018). Furthermore, when using the *SAC* model*,* our heritability estimates fell drastically, such that most became non-significant. However, it should be noted that using the *SAC* model reduced all variance components, without exception, suggesting that habitat composition of the home-range is intrinsically spatially autocorrelated. Consequently, it may be difficult to decompose phenotypic variation adequately, so that some genuine genetic variance for habitat composition may have been eliminated. Only P_{refuge} and P_{meadow} remained weakly heritable with the *SAC* models (h^2=0.02 and 0.04, respectively). Interestingly, these two traits for habitat composition are intimately involved in the key behavioural trade-off between resource acquisition and risk avoidance that partly drives among-individual behavioural (Bonnot et al., 2017) and morphological (Hewison et al., 2009) trait variation in roe deer. Therefore, morphological and behavioural traits might be linked to habitat selection by complex ecological interactions. As a consequence, accounting for environmental similarity may also downwardly bias genetic variance estimates of correlated traits if these correlations are susceptible to have a genetic basis and environmental similarity is susceptible to mask genetic variation for habitat selection.

Disentangling genetic effects from environmental effects, how to move forward?

The heritability of habitat composition and the correlation between genomic relatedness (GRM) and habitat similarity (*Smatrix*) indicates the presence of gene-environment correlations (rGE, Saltz, 2019). This rGE impedes our assessment of genetic inheritance because genetic and environmental sources of phenotypic variation cannot be properly teased apart. Simply ignoring the effects of environmental similarity could be an option, as both genetic and non-genetic inheritance may contribute to adaptation to global change (Bonduriansky et al., 2012). However, this might not be optimal if these sources of variation do not respond at the same rate or in the same direction to a given selection pressure (Helanterä & Uller, 2020; Townley & Ezard, 2013). Hence, to properly predict the ability of organisms to respond to global change, there is a need to understand the different mechanisms leading to rGE. While in wild quantitative genetics, rGE is generally considered as statistical noise generated by limited dispersal in a heterogeneous landscape, other non-exclusive mechanisms might be of evolutionary interest. For example, rGE might be generated if certain genotypes determine ecological performance in a particular habitat (e.g. feeding rate on a particular resource) and therefore preference for a particular habitat (e.g. Matching habitat choice; Akcali & Porter, 2017; Camacho & Hendry, 2020), resulting in divergent selection.

In the presence of rGE, additional experimental designs to disentangle genetic and non-genetic sources of phenotypic variation should be employed (Edelaar et al., 2019, for a comparable example on phenotypic sources of variation). However, this is not always possible because of study system limitations, as is the case with wild roe deer and many other systems. To move forward in the presence of rGE in wild populations: (1) if rGE is due to philopatry, the sampling design should be optimised by targeting the sampling effort on individuals who move away from their relatives (dispersers). An alternative strategy would be to estimate SNP-heritability based only on apparently unrelated individuals (e.g. $r<0.05$) (Yang et al., 2010, 2011). However, this would require many more individuals to have sufficient statistical power to offset the low variance in relatedness. (2) The sampling scheme should be guided by simulation studies testing the effect of different dispersal patterns (distance and rate) and different grains of environmental heterogeneity on rGE. Finally, (3) quantitative genetic multivariate linear-mixed models are powerful tools that could help address this challenge by investigating whether habitat selection, behaviours, and morphological traits might respond as a single trait complex to novel selection pressure (Morrissey, 2014).

Data availability:

Data and scripts are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.6wwpzgn1j (Gervais et al., 2022).

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Conflict of interest:

The authors declare that there is no conflict of interest.

Author contributions:

N.M., M.H., Y.C. and E.Q. collected the data. Y.C. and N.M. generated fine-grained description of habitat. J.M. and E.Q. carried out the DNA extraction and quality control. L.G., I.D. and M.G analysed the data. L.G., E.Q., B.P led the writing of the manuscript. L.G., N.M., M.H., E.Q., B.P. D.R. and I.D. interpreted the data. All authors contributed critically to the draft and gave final approval for publication.

References

Abbas, F., Morellet, N., Hewison, A. J. M., Merlet, J., Cargnelutti, B., Lourtet, B., Angibault, J.-M., Daufresne, T., Aulagnier, S., & Verheyden, H. (2011). Landscape fragmentation generates spatial variation of diet composition and quality in a generalist herbivore. *Oecologia*, *167*(2), 401–411. https://doi.org/10.1007/s00442-011-1994-0

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

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

Bonnot, N., Hewison, A. M., Morellet, N., Gaillard, J.-M., Debeffe, L., Couriot, O., Cargnelutti, B., Chaval, Y., Lourtet, B., & Kjellander, P. (2017). Stick or twist: Roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. *Animal Behaviour*, *124*, 35–46.

Bonnot, N., Verheyden, H., Blanchard, P., Cote, J., Debeffe, L., Cargnelutti, B., Klein, F., Hewison, A. J. M., & Morellet, N. (2015). Interindividual variability in habitat use: Evidence for a risk management syndrome in roe deer? *Behavioral Ecology*, *26*(1), 105–114. https://doi.org/10.1093/beheco/aru169

Börger, L., Dalziel, B. D., & Fryxell, J. M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, *11*(6), 637–650. https://doi.org/10.1111/j.1461-0248.2008.01182.x

Börger, L., Franconi, N., Ferretti, F., Meschi, F., Michele, G. D., Gantz, A., & Coulson, T. (2006). An Integrated Approach to Identify Spatiotemporal and Individual‐Level Determinants of Animal Home Range Size. *The American Naturalist*, *168*(4), 471–485. https://doi.org/10.1086/507883

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, *23*(8), 453–460. https://doi.org/10.1016/j.tree.2008.03.011

Brown, J. S. (1990). Habitat Selection as an Evolutionary Game. *Evolution*, *44*(3), 732–746. https://doi.org/10.1111/j.1558-5646.1990.tb05951.x

Butler, D. G., Cullis, B. R., & Gilmour, A. R. (2018). *ASReml-R Reference Manual Version 4 ASReml estimates variance components under a general linear mixed model by residual maximum likelihood (REML)*.

Caillon, R., Suppo, C., Casas, J., Woods, H. A., & Pincebourde, S. (2014). Warming decreases thermal heterogeneity of leaf surfaces: Implications for behavioural thermoregulation by arthropods. *Functional Ecology*, *28*(6), 1449–1458. https://doi.org/10.1111/1365-2435.12288

Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*(3), 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Camacho, C., & Hendry, A. P. (2020). Matching habitat choice: It’s not for everyone. *Oikos*, *n/a*(n/a). https://doi.org/10.1111/oik.06932

Cheptou, P.-O., Hargreaves, A. L., Bonte, D., & Jacquemyn, H. (2017). Adaptation to fragmentation: Evolutionary dynamics driven by human influences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712), 20160037. https://doi.org/10.1098/rstb.2016.0037

Coulon, A., Morellet, N., Goulard, M., Cargnelutti, B., Angibault, J.-M., & Hewison, A. J. M. (2008). Inferring the effects of landscape structure on roe deer (Capreolus capreolus) movements using a step selection function. *Landscape Ecology*, *23*(5), 603–614. https://doi.org/10.1007/s10980-008-9220-0

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

de Villemereuil, P., Morrissey, M. B., Nakagawa, S., & Schielzeth, H. (2018). Fixed-effect variance and the estimation of repeatabilities and heritabilities: Issues and solutions. *Journal of Evolutionary Biology*, *31*(4), 621–632. https://doi.org/10.1111/jeb.13232

Ducros, D., Morellet, N., Patin, R., Atmeh, K., Debeffe, L., Cargnelutti, B., Chaval, Y., Lourtet, B., Coulon, A., & Hewison, A. J. M. (2020). Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape. *Oikos*, *129*(1), 81–92. https://doi.org/10.1111/oik.06793

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., & Bolnick, D. I. (2019). Appreciating the Multiple Processes Increasing Individual or Population Fitness. *Trends in Ecology & Evolution*, *34*(5), 435–446. https://doi.org/10.1016/j.tree.2019.02.001

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

Fischer, T. M., Gilmour, A. R., & Werf, J. (2004). Computing approximate standard errors for genetic parameters derived from random regression models fitted by average information REML. *Genetics Selection Evolution*, *36*(3), 363. https://doi.org/10.1186/1297-9686-36-3-363

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., & Van Moorter, B. (2010). Habitat–performance relationships: Finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2255–2265. https://doi.org/10.1098/rstb.2010.0085

Gaither, M. R., Gkafas, G. A., de Jong, M., Sarigol, F., Neat, F., Regnier, T., Moore, D., Gröcke, D. R., Hall, N., Liu, X., Kenny, J., Lucaci, A., Hughes, M., Haldenby, S., & Hoelzel, A. R. (2018). Genomics of habitat choice and adaptive evolution in a deep-sea fish. *Nature Ecology & Evolution*, *2*(4), 680–687. https://doi.org/10.1038/s41559-018-0482-x

Germain, R. R., Wolak, M. E., Arcese, P., Losdat, S., & Reid, J. M. (2016). Direct and indirect genetic and fine-scale location effects on breeding date in song sparrows. *Journal of Animal Ecology*, *85*(6), 1613–1624. https://doi.org/10.1111/1365-2656.12575

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*, jeb.13594. https://doi.org/10.1111/jeb.13594

Gervais, L., Perrier, C., Bernard, M., Merlet, J., Pemberton, J. M., Pujol, B., & Quéméré, E. (2019). RAD-sequencing for estimating genomic relatedness matrix-based heritability in the wild: A case study in roe deer. Molecular Ecology Resources, 19(5), 1205–1217. https://doi.org/10.1111/1755-0998.13031

Gervais L., Morellet N, David I., Hewison A.J.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, Dryad, Dataset, https://doi.org/10.5061/dryad.6wwpzgn1j

Helanterä, H., & Uller, T. (2020). Different perspectives on non-genetic inheritance illustrate the versatile utility of the Price equation in evolutionary biology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1797), 20190366. https://doi.org/10.1098/rstb.2019.0366

Hewison, A. J. M., Gaillard, J. M., Angibault, J. M., Laere, G. V., & Vincent, J. P. (2002). The influence of density on post-weaning growth in roe deer Capreolus capreolus fawns. *Journal of Zoology*, *257*(3), 303–309. https://doi.org/10.1017/S0952836902000900

Hewison, A. J. M., Gaillard, J.-M., Delorme, D., Laere, G. V., Amblard, T., & Klein, F. (2011). Reproductive constraints, not environmental conditions, shape the ontogeny of sex-specific mass–size allometry in roe deer. *Oikos*, *120*(8), 1217–1226. https://doi.org/10.1111/j.1600-0706.2011.19316.x

Hewison, A. J. M., Morellet, N., Verheyden, H., Daufresne, T., Angibault, J.-M., Cargnelutti, B., Merlet, J., Picot, D., Rames, J.-L., Joachim, J., Lourtet, B., Serrano, E., Bideau, E., & Cebe, N. (2009).

Landscape fragmentation influences winter body mass of roe deer. *Ecography*, *32*(6), 1062–1070. https://doi.org/10.1111/j.1600-0587.2009.05888.x

Hewison, A. J. M., Vincent, J. P., & Reby, D. (1998). Social organisation of European roe deer. *The European Roe Deer: The Biology of Success. Scandinavian University Press, Oslo*, 189–219.

Hoey, J. A., & Pinsky, M. L. (2018). Genomic signatures of environmental selection despite near-panmixia in summer flounder. *Evolutionary Applications*, *11*(9), 1732–1747. https://doi.org/10.1111/eva.12676

Immelmann, K. (1975). Ecological significance of imprinting and early learning. *Annual Review of Ecology and Systematics*, *6*(1), 15–37.

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

Jeugd, H. P. V. D., & McCleery, R. (2002). Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. *Journal of Evolutionary Biology*, *15*(3), 380–387. https://doi.org/10.1046/j.1420-9101.2002.00411.x

Kendler, K. S., & Baker, J. H. (2007). Genetic influences on measures of the environment: A systematic review. *Psychological Medicine*, *37*(5), 615–626. https://doi.org/10.1017/S0033291706009524

Kruuk, L. E. B., & Hadfield, J. D. (2007). How to separate genetic and environmental causes of similarity between relatives: Separating genetic and environmental effects. *Journal of Evolutionary Biology*, *20*(5), 1890–1903. https://doi.org/10.1111/j.1420-9101.2007.01377.x

Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (1999). Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences*, *96*(18), 10242–10247. https://doi.org/10.1073/pnas.96.18.10242

Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J. E., Kindberg, J., & Pelletier, F. (2016). Quantifying consistent individual differences in habitat selection. *Oecologia*, *180*(3), 697–705. https://doi.org/10.1007/s00442-015-3500-6

Lynch, M., & Walsh, B. (1998). *Genetics and analysis of quantitative traits* (Vol. 1). Sinauer Sunderland, MA.

Malagnino, A., Marchand, P., Garel, M., Cargnelutti, B., Itty, C., Chaval, Y., Hewison, A. J. M., Loison, A., & Morellet, N. (2021). Do reproductive constraints or experience drive age-dependent space use in two large herbivores? *Animal Behaviour*, *172*, 121–133. https://doi.org/10.1016/j.anbehav.2020.12.004

Martin, J., Vourc'h, G., Bonnot, N., Cargnelutti, B., Chaval, Y., Lourtet, B., Goulard, M., Hoch, T., Plantard, O., Hewison, A. J. M., & Morellet, N. (2018). Temporal shifts in landscape connectivity for an ecosystem engineer, the roe deer, across a multiple-use landscape. *Landscape Ecology*, *33*(6), 937–954. https://doi.org/10.1007/s10980-018-0641-0

Martin, R. O., Cunningham, S. J., & Hockey, P. A. (2015). Elevated temperatures drive fine-scale patterns of habitat use in a savanna bird community. *Ostrich*, *86*(1–2), 127–135.

Matsubayashi, K. W., Ohshima, I., & Nosil, P. (2010). Ecological speciation in phytophagous insects. *Entomologia Experimentalis et Applicata*, *134*(1), 1–27. https://doi.org/10.1111/j.1570-7458.2009.00916.x

Moore, M. P., Whiteman, H. H., & Martin, R. A. (2019). A mother's legacy: The strength of maternal effects in animal populations. *Ecology Letters*, *22*(10), 1620–1628.

Morellet, N., Van Moorter, B., Cargnelutti, B., Angibault, J.-M., Lourtet, B., Merlet, J., Ladet, S., & Hewison, A. J. M. (2011). Landscape composition influences roe deer habitat selection at both home range and landscape scales. *Landscape Ecology*, *26*(7), 999–1010. https://doi.org/10.1007/s10980-011-9624-0

Morris, D. W. (2003). Toward an ecological synthesis: A case for habitat selection. *Oecologia*, *136*(1), 1–13. https://doi.org/10.1007/s00442-003-1241-4

Morrissey, M. B. (2014). Selection and Evolution of Causally Covarying Traits. *Evolution*, *68*(6), 1748–1761. https://doi.org/10.1111/evo.12385

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, *85*(4), 935–956. https://doi.org/10.1111/j.1469-185X.2010.00141.x

Padié, S., Morellet, N., Hewison, A. J. M., Martin, J.-L., Bonnot, N., Cargnelutti, B., & Chamaillé-Jammes, S. (2015). Roe deer at risk: Teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. *Oikos*, *124*(11), 1536–1546. https://doi.org/10.1111/oik.02115

Peterson, B. K., Weber, J. N., Kay, E. H., Fisher, H. S., & Hoekstra, H. E. (2012). Double Digest RADseq: An Inexpensive Method for De Novo SNP Discovery and Genotyping in Model and Non-Model Species. *PLoS ONE*, *7*(5), e37135. https://doi.org/10.1371/journal.pone.0037135

Porter, C. K., & Akcali, C. K. (2020). Evolutionary Implications of Habitat Choice. *ELS*, *1*, 85–93.

Quéméré, E., Gaillard, J. M., Galan, M., Vanpé, C., David, I., Pellerin, M., Kjellander, P., Hewison, A. J. M., & Pemberton, J. M. (2018). Between-population differences in the genetic and maternal components of body mass in roe deer. *BMC Evolutionary Biology*, *18*(1), 39. https://doi.org/10.1186/s12862-018-1154-9

Ratcliffe, P. R., & Mayle, B. A. (1992). Age determination of roe deer. *Forestry Commission Bulletin*, *105*, 26–28.

Regan, C. E., Pilkington, J. G., Berenos, C., Pemberton, J. M., Smiseth, P. T., & Wilson, A. J. (2017). Accounting for female space sharing in St. Kilda Soay sheep (Ovis aries) results in little change in heritability estimates. *Journal of Evolutionary Biology*, *30*(1), 96–111.

Rutschmann, A., de Villemereuil, P., Brekke, P., Ewen, J. G., Anderson, N., & Santure, A. W. (2020). Consequences of space sharing on individual phenotypes in the New Zealand hihi. *Evolutionary Ecology*, *34*(5), 821–839. https://doi.org/10.1007/s10682-020-10063-z

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

Saltz, J. B., & Nuzhdin, S. V. (2014). Genetic variation in niche construction: Implications for development and evolutionary genetics. *Trends in Ecology & Evolution*, *29*(1), 8–14. https://doi.org/10.1016/j.tree.2013.09.011

Schirmer, A., Herde, A., Eccard, J. A., & Dammhahn, M. (2019). Individuals in space: Personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialisation. *Oecologia*, *189*(3), 647–660. https://doi.org/10.1007/s00442-019-04365-5

Spiegel, O., Leu, S. T., Sih, A., Godfrey, S. S., & Bull, C. M. (2015). When the going gets tough: Behavioural type-dependent space use in the sleepy lizard changes as the season dries. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1819), 20151768.

Stopher, K. V., Walling, C. A., Morris, A., Guinness, F. E., Clutton-Brock, T. H., Pemberton, J. M., & Nussey, D. H. (2012). Shared Spatial Effects on Quantitative Genetic Parameters: Accounting for Spatial Autocorrelation and Home Range Overlap Reduces Estimates of Heritability in Wild Red Deer. *Evolution*, *66*(8), 2411–2426. https://doi.org/10.1111/j.1558-5646.2012.01620.x

Thomson, C. E., Winney, I. S., Salles, O. C., & Pujol, B. (2018). A guide to using a multiple-matrix animal model to disentangle genetic and non-genetic causes of phenotypic variance. *PLOS ONE*, *13*(10), e0197720. https://doi.org/10.1371/journal.pone.0197720

Toïgo, C., Gaillard, J.-M., Van Laere, G., Hewison, A. J. M., & Morellet, N. (2006). How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography*, *29*(3), 301–308.

Townley, S., & Ezard, T. H. G. (2013). A G matrix analogue to capture the cumulative effects of non-genetic inheritance. *Journal of Evolutionary Biology*, *26*(6), 1234–1243. https://doi.org/10.1111/jeb.12089

Tufto, J., Andersen, R., & Linnell, J. (1996). Habitat Use and Ecological Correlates of Home Range Size in a Small Cervid: The Roe Deer. *Journal of Animal Ecology*, *65*(6), 715–724. JSTOR. https://doi.org/10.2307/5670

Valcu, M., & Kempenaers, B. (2010). Is spatial autocorrelation an intrinsic property of territory size? *Oecologia*, *162*(3), 609–615. https://doi.org/10.1007/s00442-009-1509-4

van Beest, F. M. van, Rivrud, I. M., Loe, L. E., Milner, J. M., & Mysterud, A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology*, *80*(4), 771–785. https://doi.org/10.1111/j.1365-2656.2011.01829.x

Van Moorter, B. V., Rolandsen, C. M., Basille, M., & Gaillard, J.-M. (2016). Movement is the glue connecting home ranges and habitat selection. *Journal of Animal Ecology*, *85*(1), 21–31. https://doi.org/10.1111/1365-2656.12394

Wecker, S. C. (1964). Habitat selection. *Scientific American*, *211*(4), 109–117.

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

Yang, J., Benyamin, B., McEvoy, B. P., Gordon, S., Henders, A. K., Nyholt, D. R., Madden, P. A., Heath, A. C., Martin, N. G., Montgomery, G. W., Goddard, M. E., & Visscher, P. M. (2010). Common SNPs explain a large proportion of the heritability for human height. *Nature Genetics*, *42*(7), 565–569. https://doi.org/10.1038/ng.608

Yang, J., Lee, S. H., Goddard, M. E., & Visscher, P. M. (2011). GCTA: A Tool for Genome-wide Complex Trait Analysis. *The American Journal of Human Genetics*, *88*(1), 76–82. https://doi.org/10.1016/j.ajhg.2010.11.011

Graphical Abstract text: Environmental similarity among individuals can, in part, be explained by genetic variation for habitat selection. Consequently, accounting for environmental similarity in quantitative genetics may blur the heritability estimates of fitness-related traits by removing genuine genetic variance for a given trait