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Heterogeneous selection on exploration behavior within and among West European populations of a passerine bird

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Abstract

Heterogeneous selection is often proposed as a key mechanism maintaining repeatable behavioral variation ("animal personality") in wild populations. Previous studies largely focused on temporal variation in selection within single populations. The relative importance of spatial versus temporal variation remains unexplored, despite these processes having distinct effects on local adaptation. Using data from >3500 great tits (*Parus major*) and 35 nest box plots situated within five West-European populations monitored over 4-18 years, we show that selection on exploration behavior varies primarily spatially, across populations, and study plots within populations. Exploration was, simultaneously, selectively neutral in the average population and year. These findings imply that spatial variation in selection may represent a primary mechanism maintaining animal personalities, likely promoting the evolution of local adaptation, phenotype-dependent dispersal, and nonrandom settlement. Selection also varied within populations among years, which may counteract local adaptation. Our study underlines the importance of combining multiple spatiotemporal scales in the study of behavioral adaptation.

Significance Statement

A key question in behavioral ecology is whether individual differences in behavior are adaptive rather than merely representing "noise around an adaptive mean". We show strong evidence for spatial and temporal variation in survival and recruitment selection, both within and among West European great tit (*Parus major*) populations, implying that spatiotemporal variation in environmental conditions contributes to the maintenance of animal personality variation. The majority of the variance in selection was attributable to large-scale geographical variation, selecting for local adaptation in behavior. Temporal variation was also important, counteracting spatially-driven local adaptation. Our study thereby demonstrates the importance of acknowledging both large- and small-scale geographical and temporal variation to understand the biological processes maintaining variation in animal behavior.

Main Text

Introduction

Repeatable and heritable variation in behavior ("animal personality") is ubiquitous among wild animal populations (1). Repeatable behavioral differences among individuals can be adaptive when the costs and benefits of alternative behavioral tactics vary with the environment (2, 3). This requires heterogeneous selection, either spatially, temporally, or spatiotemporally, e.g., within or among populations, habitats or years (3, 4). Social environments may also play a key role by inducing negative frequency-dependent selection (5, 6). Heterogeneous selection on repeatable individual variation in behavior has previously been demonstrated primarily within single populations sampled over limited numbers of years (7, 8), thus limiting our understanding of the relative importance of spatial and temporal variation in selection.

Spatial and temporal processes co-occur (8, 9) but have distinct effects on population dynamics and evolution. Strong spatial variation favors different behavioral phenotypes in different locations, which may induce selection for nonrandom dispersal, and rapid population divergence (10, 11). Temporal variation instead favors the coexistence of multiple behavioral phenotypes within populations, thereby counteracting population divergence. Estimates of selection from multiple study populations monitored over multiple years are required to estimate spatial and temporal variation simultaneously and determine their relative importance in maintaining individual behavioral variation.

To address this question, we assayed exploration behavior in a novel environment (12) among great tits (*Parus major*) breeding in 35 nest box plots across five populations in Western Europe, each sampled for multiple (4-18) years. For four of these populations, animal model-based quantitative genetics were conducted; in all cases exploration behavior was significantly repeatable and heritable (Boshoek, Belgium: R=0.42, h^2=0.30 (13, 14); Lauwersmeer, the Netherlands: R=0.40-0.44, h^2=0.10-0.11 (13, 15); Westerheide, the Netherlands: R=0.38, h^2=0.14 (13, 16); Wytham Woods, United Kingdom: R=0.34, h^2=0.26 (13, 16). We estimated the average pattern of selection (directional, stabilizing, disruptive) within the average population, plot, and year, and examined whether selection was heterogeneous as predicted by state-dependent personality models (3, 4). Finally, we estimated the relative proportion of variation in selection that was attributable to five distinct sources: a) macro-spatial variation (among populations), b) micro-spatial variation (among plots within populations), c) temporal variation (among years), d) population-specific (or macro-scale) temporal variation (unique combinations of population and year), and e) plot-specific (or micro-scale) temporal variation (unique combinations of plot and year) (Fig. 1).

Results

Exploration behavior was neither subject to linear nor to nonlinear viability (adult survival) selection within the average population, plot and year, though estimates of nonlinear selection suggested weak disruptive viability selection (γ, Table 1; SI Appendix Table S1). By contrast, exploration behavior was, on average, subject to stabilizing local offspring recruitment selection (γ, Table 1; SI Appendix Table S1). The effect of stabilizing local recruitment selection appeared to be cancelled out by the weak effect of disruptive viability selection. Indeed, selection measured using integrative fitness, which combines annual survival and local recruitment, was not different from zero (Table 1; SI Appendix Table S1). Previous research has shown that faster explorers disperse further (14, 17). Consistent with this idea, immigrants are often faster explorers than local recruits (14, 17, 18); this was also the case in our dataset (SI Appendix Table S2). We therefore examined whether our estimates of local recruitment selection were biased against faster explorers. To do so, we re-estimated fecundity (and integrative) fitness selection using annual fledgling production, a pre-dispersal reproductive success metric that should not suffer from dispersal-related bias. These analyses produced the same results as reported above, thus suggesting that nonrandom dispersal did not bias our estimates of selection (SI Appendix Table S3). We conclude, therefore, that exploration behavior was indeed selectively neutral overall.

Exploration behavior was, however, under heterogeneous selection. This conclusion was supported for all fitness metrics considered based on hierarchical random regression analyses and associated permutation tests (Table 2; SI Appendix Table S1). Combined with evidence for neutral selection overall, our finding of heterogeneous directional selection implies that selection varied not just in strength but also in direction (Table 2, Fig.2). The effect of exploration on integrative fitness varied spatially and temporally at both macro- and micro-scales (variance in random slopes; all permutation $P<0.01$, SI Appendix Table S1). Macro-spatial variation in selection explained the largest percentage of the total variance in selection (effect of population; 47%; Table 2). Micro-spatial (plot; 13%), temporal (year: 19%), population-specific (i.e., macro-scale) temporal (population × year; 11%) and plot-specific (i.e., micro-scale) temporal (plot × year; 9%) variation in selection existed but were of lesser importance (Table 2). Analyses of survival and local recruitment

led to the same conclusions: macro-spatial variation in selection explained the largest percentage of the variance in selection (viability selection: 35%; recruitment selection; 39%); variation in selection at other spatiotemporal levels explained similar relative amounts of variance as described for integrative fitness (Table 2, SI Appendix Table S1). This implies that overall patterns of variation in selection were similar for both fitness components.

Statistical support for heterogeneous selection can occur as an artefact when phenotypes vary among levels of random effects in situations where selection is nonlinear (SI Appendix Fig. S1). We addressed this concern by re-fitting our models to incorporate level-specific nonlinear patterns of selection, which were not detected (SI Appendix Table S4), thus suggesting that this concern was unfounded. Patterns of (variation in) selection also did not depend on whether trait values were standardized at the lowest hierarchical level (i.e. within unique combinations of plot and year) rather than over the entire dataset (SI Appendix Table S5).

Discussion

Strong spatial variation in selection can induce selection for individuals to settle in habitats best fitting their behavioral phenotype (19). Temporal variation would instead favor the coexistence of multiple behavioral phenotypes within populations. Our analyses showed that selection on exploration behavior varied macro-spatially, micro-spatially and temporally. We further detected evidence for population- and plot-specific differences in patterns of temporal variation in selection. Additionally, integrative fitness selection was neutral overall due to weak disruptive viability selection counterbalanced by stabilizing local recruitment selection. Our findings imply that heterogeneous selection on personality exists at many (if not all) major ecological levels, and, in combination with neutral selection overall, that environmental variation at multiple spatial and temporal scales contributes to the maintenance of behavioral variation.

Our discovery of a major role for macro-spatial variation in selection implies that large-scale geographical variation in ecological factors has the potential to select for population divergence, which, consequently, might promote nonrandom dispersal and settlement. Specifically, individuals should settle in habitats where they do best, which will differ between behavioral phenotypes (19, 20). Ecological factors that constrain dispersal of certain genotypes (e.g., winter temperature) may also facilitate genetic differentiation (21). Moreover, behavioral phenotypes may choose populations based on social rather than nonsocial environmental conditions. For example, positive frequency-dependent selection favors non-aggressive Western bluebirds (*Sialia mexicana*) when surrounded by non-aggressive conspecifics because those are more cooperative (22). Similarly, fast-exploring great tits are known to acquire relatively low dominance ranks as first-year birds, and are more likely to disperse away from their natal area (17, 23); this may result in fast-exploring birds consequently settling in less competitive (i.e., low density) areas where their behavioral phenotype may perform best (24), and supports the nonrandom-dispersal hypothesis. Regardless of the causal factors, nonrandom dispersal may thereby reinforce assortative mating (25), induce biased gene flow, accelerate (genetic) population divergence, and eventually, enhance population evolvability (26). The simultaneous occurrence of micro-spatial variation in selection (i.e., among plots within populations) implies that selection also favors local adaptation among habitats of the same population. Local adaptation within populations may, however, often be counteracted by substantial gene flow given the species' dispersal characteristics (21, 27). Studies characterizing selection on personality-dependent habitat choice (a form of phenotype-environment matching (19)) and dispersal are required to reveal the interplay of mechanisms shaping evolutionary trajectories of behavioral traits in natural populations.

Temporal fluctuations favors certain behavioral phenotypes in certain years and other phenotypes in other years (3). Fluctuating selection will thus inherently counteract the speed of population divergence and consequently, plays a key role in preventing genetic differentiation required in the process of local adaptation. The existence of behavioral variation in all five great tit

populations despite the large magnitude of macro-scale spatial variation in selection however suggests that local adaptation may be reduced by the combined action of temporal variation at small spatial scales and of gene flow at larger spatial scales. This may explain why the combined additive and interactive effects of plot, year, and population explained as little as 4% of the variance in exploration behavior among first-year birds (SI Appendix Table S2). A key question is therefore at what spatial scale which mechanism predominantly counteracts population divergence and whether genetic population divergence in behavior occurs at all. Forcefully addressing this question would require study plots at spatial scales intermediate to our within- and among-population levels, e.g., multiple populations within countries.

Temporal variation in selection can also result in the evolution of reversible plasticity but previous great tit studies suggest that limits to plasticity prevent this mechanism from evolving (28). Temporal variation in selection resulted from ecological factors varying over large spatial scales, but also from local fluctuations. Specifically, our finding of a main effect of year on selection reveals that selection on personality changes in concert across large geographical scales. These selection pressures likely result from ecological factors varying in conjunction across Western-Europe (29). Beech (*Fagus sylvatica*) masting, a phenomenon where beech trees produce high numbers of seeds in some years but few (or none) in other years, may represent such a key biotic factor. Beech masting strongly affects winter survival of great tits (30), and is often synchronized over the entire continent (31). Such temporal variation in food availability (and selection), however, will be evidently modulated by local habitat conditions, such as tree species composition. This may explain why we also found strong evidence for population-specific (i.e., macro-scale) temporal variation in selection (population × year effects). Other factors may also play a key role here, for example, predator- or parasite-induced selection varying more among years in populations with high versus low overall levels of these biological factors (32–35). Our finding of plot-specific (i.e., micro-scale) temporal variation in selection (plot × year effects) indicates that similar factors act among habitat patches within populations.

Previous studies revealed a key role of social environmental variation by demonstrating that selection on exploration behavior (18, 28) and aggression (22) varies with breeding density within populations. We investigated this explanation by expanding our models to include the interactive effect of breeding density (pair/ha) and exploration on fitness. Doing so did not result in a detectable change in random slope variance at any of the hierarchical levels (SI Appendix Table S6). This implies that heterogeneous selection largely resulted from ecological processes independent of density, yet to be determined. Here, social interactions inducing negative frequency-dependent selection may constitute a key mechanism contributing to the maintenance of variation (5). Forcefully investigating this idea requires large sample sizes for each social environment (here, each unique combination of plot and year) to accurately and precisely estimate phenotype frequencies. The many small plots characterizing our study do not fulfill this requirement.

A popular explanation for the persistence of personalities is that behavioral phenotypes differ in how they resolve life-history trade-offs (36). Personality-related pace-of-life theory predicts that fast explorers produce larger clutches but either live less long, or senesce at an earlier age, compared to slow explorers (36, 37). Though previous work on great tits supports some of these predictions (38–40), meta-analyses do not (41, 42). Our analyses, similarly, fail to find support for personality-related pace-of-life syndromes: annual adult survival was not lower for faster explorers, and nor did this type of bird produce more fledglings or local recruits annually compared to slower explorers. The detected pattern of stabilizing recruitment selection combined with weak disruptive viability selection implies that other ecological explanations are required to explain any personality-related differences in life-history in this system (43, 44).

Nonrandom natal dispersal may bias estimates of variance in recruitment selection, though this would require that, in different places or at different times, different behavioral phenotypes are most dispersive; this condition is unlikely met at all five spatiotemporal scales at which we detected heterogeneous recruitment selection. Moreover, variance estimates of fecundity

selection using annual fledgling number were similar to variance estimates of local recruitment selection, refuting the idea that our estimates of heterogeneous selection measured through local recruitment rates were biased (SI Appendix Table S3). Capture-mark-recapture analyses have demonstrated that capture rates do not vary with exploration behavior among adult breeders (45). As great tits show limited breeding dispersal (46, 47), sampling bias cannot easily affect the variance in adult viability selection. Altogether, these arguments suggest that sampling bias does not play a major role in explaining the spatiotemporal patterns of heterogeneous selection revealed by this study.

Our analyses of temporal and spatial patterns of variation in selection represent an important contribution to our understanding of population dynamics and the evolution of behavior. Macro-spatial variation in selection counteracted by temporal variation demonstrates the importance of estimating heterogeneous selection on individual behavior at multiple hierarchical scales. Microevolutionary responses to selection now require study to reveal whether the spatial patterns of variation in selection uncovered by this study reduce the genetic variation in behavior within populations and whether temporal variation combined with gene flow are indeed sufficient to prevent this erosion of genetic variation due to population-specific fitness optima. Our insights are likely not specific to selection on behavior or personality but may apply generally, and warrant analyses of spatiotemporal variation in selection for other key phenotypic traits, such as physiology, morphology or life-history traits. Our study exemplifies the need for long-term studies across multiple habitats, and international collaborations to reveal large-scale geographical patterns of selection and the key role of ecology in shaping selection and evolution (48).

Materials and Methods

Study populations and field data collection. Data were collected in five nest box populations of great tits between 2006-2017 (Boshoek near Antwerp, Belgium; 51°08'N, 043°2'E), 2006-2009 (Lauwersmeer, The Netherlands; 53°20'N, 06°12'E), 2010-2014 (Starnberg District, Bavaria; Germany; 47°58'N, 11°14'E), 1999-2016 (Westerheide; The Netherlands; 52°00'N, 05°50'E) and 2005-2016 (Wytham Woods, United Kingdom; 51°47'N, 1°20'W). In Boshoek, nine nest box plots were fitted in 0.6-9 ha woodland fragments at a density of six boxes per ha (49). In both Bavaria and Lauwersmeer, 12 nest box plots were fitted in 8-11 ha woodland fragments at a density of 4.5 to 6.2 boxes per ha (28). In Westerheide and Wytham Woods, a single nest box plot was fitted within continuous woodland habitat of, respectively, ca. 112 and 290 ha at a density of 3 and 3.5 boxes per ha.

We checked nest boxes at least once a week during the breeding season (April-July) to determine key life-history traits and breeding density. Breeders were caught in their nest box when their nestlings were 7-12 days old and ringed at first capture. We also ringed offspring before fledging to determine which offspring recruited into the population as breeders in subsequent years. Outside the breeding season, birds were captured in nest boxes when roosting (November-February; all populations except Wytham Woods) and/or with mist-nets (July-March, in Boshoek, Westerheide and Wytham Woods).

Exploration assays. We assayed exploration behavior under standardized laboratory conditions using a novel environment test (50) made suitable for wild birds (12). Prior to the test, birds were individually housed in a small cage overnight with *ad libitum* access to food and water. Each cage connected to the novel environment, a standard laboratory room fitted with five artificial trees, via a sliding door that allowed release without handling (12). Slight differences in setup and procedure existed across populations as detailed elsewhere (13, 51). An exploration score was calculated by summing up the total number of flights and hops between perches made within the first two minutes after entering the room (13). This score of movement behavior genetically correlated with the number of areas visited, thus it represents a good proxy of spatial exploration (18). Birds were tested between 8h00-13h00. The dataset consisted of 5459 records collected from 3551 individuals

typed for exploration behavior, distributed over 188 unique combinations of plot and year ("plot-years").

Data characterization and selection. To estimate selection on exploration behavior, we used an integrative measure of fitness that represents an individual's overall annual fitness. We calculated it as 1 × the focal adult's survival probability + 0.5 × the number of its locally recruited offspring for a given year. This integrative fitness measure acknowledges that each individual contributes fully its genes to the next year when returning as a breeder but that only half of its genes are present in any recruited offspring (52, 53). This inherently avoids biases attributable to individual differences in how tradeoffs between offspring quality and quantity, or between current and future reproduction are resolved (36, 37, 42). We defined adult survival as the binary probability that a focal bird breeding in a focal year was found breeding in the following year (binomial; not found [0] or found breeding [1]). In this species, capture probabilities of breeders are high (75-95%) (45) and breeding dispersal rates low (46, 47), implying that this metric appropriately measures local survival. We defined local offspring recruitment as the annual number of offspring recruiting as breeders in the focal population (regardless of plot identity). Because nonrandom dispersal can bias estimates of fecundity selection based on counting local recruits, we also estimated selection using the annual number of produced fledglings as alternative metric.

Our dataset included only individuals for which exploration behavior was scored prior to a focal breeding season; this avoids bias in estimates of adult survival and local offspring recruitment between subsequent breeding seasons (45). We used the first exploration score of each individual as a measure of exploration behavior. We assumed this reflected an individual's personality (54) because elsewhere we show that individual-mean values (proposed to best reflect an individual's average behavior (55)) are tightly positively correlated with an individual's first exploration score among repeatedly assayed birds (28). We did not use individual-mean values because (i) many individuals were not tested repeatedly (i.e., individual-mean values would be based on unequal replication between individuals), and (ii) individuals differ in how exploration behavior changes with repeated exposure to the testing procedure (13).

Statistical analyses. We estimated selection on exploration behavior using both our integrative fitness metric and its underlying components (adult survival and local offspring recruitment or fledgling production). Doing so enabled identifying whether selection acted via specific pathways (e.g., via survival rather than recruitment selection (28)) and whether selection varied in the same proportion at each hierarchical level for each fitness component.

We fitted generalized linear mixed-effects models (GLMMs) with Gaussian (integrative fitness analyses), binomial (logit link; survival analyses), and Poisson errors (recruitment and fledgling analyses). Each model simultaneously estimated the magnitude of variation in directional selection among populations (macro-spatial variation), plots (micro-spatial variation), years (micro-temporal variation), unique population-year combinations (population-specific or macro-scale temporal variation) and unique plot-year combinations (plot-specific or micro-scale temporal variation). This was achieved by fitting random intercepts and slopes (with respect to exploration score fitted as a fixed effect covariate (28)) at each of these hierarchical levels. Insights into variation in nonlinear selection (i.e., in shape of selection) would require fitting nonlinear random slopes, however, our data do not provide enough statistical power to forcefully address this question.

Exploration scores were corrected for seasonal plasticity (12, 13) following Ref. (12) to avoid biased estimates (56). They were then squared-root transformed and standardized (i.e., zero mean and unit standard deviation) to acquire (standardized) selection gradients. We performed this standardization over the entire dataset because this produces estimates that are comparable across all hierarchical levels (57). However, great tits experience strong density-dependent selection within plots among years ("plot-years') (58, 59), and previous studies implied that traits should be standardized at the level at which competition occurs (60). We therefore also ran our

analyses after standardizing traits within plot-years. We estimated linear and nonlinear (quadratic) selection on exploration behavior to test for directional and disruptive or stabilizing selection. Nonlinear selection was assessed by adding the squared term of the standardized exploration value (defined above) as a fixed effect covariate. Standardized linear and nonlinear selection gradients were estimated by re-running our models using relative fitness (i.e., the focal fitness metric divided by the grand mean of the dataset) as a response variable; quadratic selection gradients were calculated by doubling the estimated parameter for the square of exploration (61).

We ran all analyses in R v. 3.5.3. (62), using the Bayesian inference package R-INLA (63) and the "iid2d" model. We estimated posterior means and their 95% credible intervals (CIs) for all fixed and random effects. Fixed effect priors were normally distributed with zero mean and precision (inverse of variance) of 0.001. The iid2d-model fixes random effect priors to a two-dimensional Normal Wishart distribution. For recruitment selection analyses, we controlled for overdispersion by adding an observation-level random effect with log-gamma prior with shape ($\alpha = 0.5$) and mean value (β = variance (offspring recruitment) * α).

We interpreted estimates of fixed effects as statistically significant if their 95% CIs did not overlap zero. Statistical significance of average selection was inferred from models fitting absolute fitness as the response variable, as those fully fulfilled distributional assumptions (SI Appendix Table S1), while standardized selection gradients are instead provided in the main text (Table 1). Because variance estimates are always zero-positive, the statistical significance of random slope variance (indicative of variation in selection) was instead calculated by generating a null distribution for the amount of variance expected by chance. We calculated this null distribution for each hierarchical level separately (i.e., population, plot, year, population-year or plot-year) by permuting the focal levels (e.g., 188 plot-years) associated with a focal variance component (e.g., plot × year), and rerunning each analysis 1000 times (64). We subsequently calculated the proportion of 1000 null values that were greater than the observed variance as a value of *P*. Values of $P < 0.05$ were considered statistically significant.

Data availability. Data and code to reproduce statistical analyses and Fig. 2 are available on Dryad repository: https://doi.org/10.5061/dryad.mkkwh70z8 (65)

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Figures and Tables

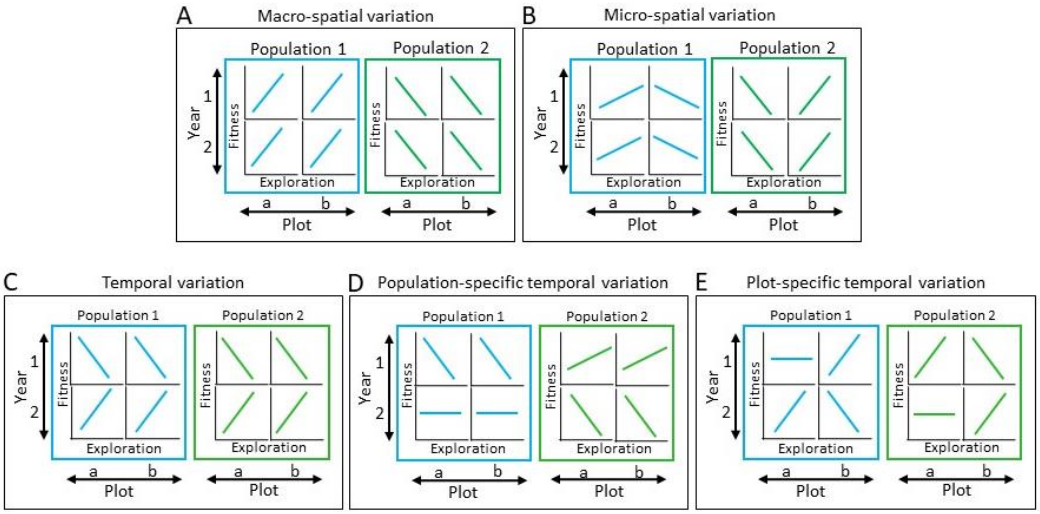


Figure 1. Distinct heterogeneous selection scenarios illustrated for two populations with two plots each sampled over the same two years. Selection can vary A) macro-spatially (among populations), B) micro-spatially (among plots), C) temporally (among years), D) macro-spatiotemporally (year-effects are population-specific) and E) micro-spatiotemporally (year-effects are plot-specific). Illustrated scenarios are mutually nonexclusive; our analyses of the sources of variation in selection on exploration behavior imply all mechanisms are important.

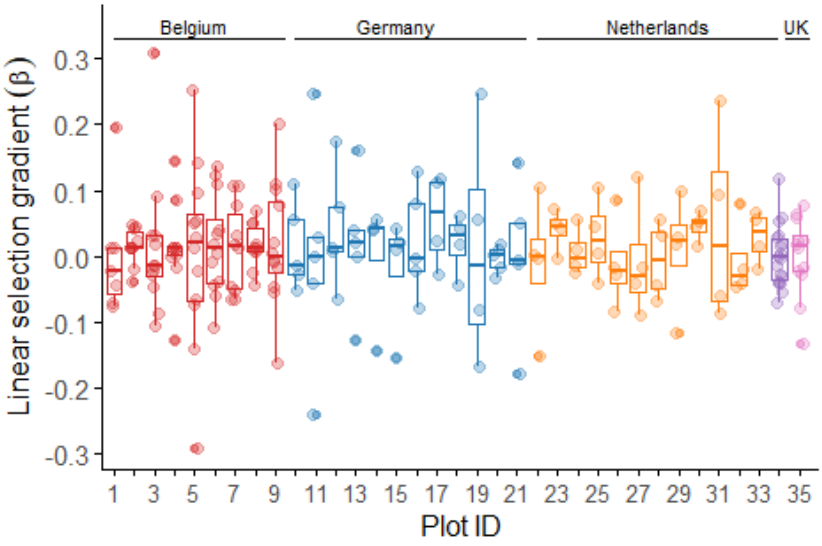


Figure 2. Patterns of heterogeneous selection on exploration behavior within and among five great tit populations sampled across Western Europe. Colors represent populations, which were located across four countries. Boxplots show the median, first and third quartile of the standardized selection gradient (with whiskers) for each study plot, and dots the standardized selection gradient for each sampled year within a focal plot. While some populations had multiple plots (red: Boshoek, Belgium; blue: Starnberg, Germany; orange: Lauwersmeer, the Netherlands), other populations consisted of a single plot (purple: Westerheide, the Netherlands; pink: Wytham Woods, UK). We used integrative fitness as our metric of annual fitness. Positive (vs. negative) selection gradients indicate selection favoring fast (vs. slow) explorers.

Table 1. Linear (β) and nonlinear (γ) standardized selection gradients estimated for exploration behavior, with integrative fitness, adult survival (viability) or local offspring recruitment as fitness metrics. Estimates, with 95% credible interval (CI), are derived from random regression models fitting exploration behavior standardized over the entire dataset.

	Integrative fitness	**Survival**	**Local recruitment**
Selection gradient	Estimate (95% CI)	Estimate (95% CI)	Estimate (95% CI)
β	0.02 (-0.45, 0.48)	0.02 (-0.49, 0.52)	0.06 (-0.56, 0.67)
γ	0.00 (-0.03, 0.02)	0.02 (-0.02, 0.05)	-0.10 (-0.11, 0.01)

Table 2. Proportion of variance in selection attributable to each ecological level with associated 95% credible intervals (CIs), for integrative fitness, adult survival (viability) or local offspring recruitment as focal fitness metric.

	Integrative fitness	**Survival**	**Local recruitment**
Ecological level	R (95% CI)	R (95% CI)	R (95% CI)
Population	0.47 (0.37, 0.60)	0.36 (0.28, 0.46)	0.39 (0.31, 0.50)
Plot	0.13 (0.10, 0.16)	0.16 (0.13, 0.17)	0.16 (0.13, 0.19)
Year	0.19 (0.16, 0.21)	0.17 (0.15, 0.18)	0.18 (0.16, 0.19)
Population x Year	0.11 (0.08, 0.14)	0.13 (0.11, 0.16)	0.13 (0.10, 0.16)
Plot x Year	0.09 (0.06, 0.12)	0.18 (0.15, 0.20)	0.13 (0.10, 0.16)