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

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1 **Main Manuscript for**

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

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29 local adaptation

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31 **This PDF file includes:**

32 Main Text
33 Figures 1 to 2
34 Tables 1 to 2

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37 Abstract

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

51 Significance Statement

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

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63 Main Text

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65 Introduction

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

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

83 To address this question, we assayed exploration behavior in a novel environment (12) among
84 great tits (*Parus major*) breeding in 35 nest box plots across five populations in Western Europe,
85 each sampled for multiple (4-18) years. For four of these populations, animal model-based
86 quantitative genetics were conducted; in all cases exploration behavior was significantly
87 repeatable and heritable (Boshoek, Belgium: $R=0.42$, $h^2=0.30$ (13, 14); Lauwersmeer, the
88 Netherlands: $R=0.40-0.44$, $h^2=0.10-0.11$ (13, 15); Westerheide, the Netherlands: $R=0.38$, $h^2=0.14$
89 (13, 16); Wytham Woods, United Kingdom: $R=0.34$, $h^2=0.26$ (13, 16). We estimated the average
90 pattern of selection (directional, stabilizing, disruptive) within the average population, plot, and
91 year, and examined whether selection was heterogeneous as predicted by state-dependent
92 personality models (3, 4). Finally, we estimated the relative proportion of variation in selection that
93 was attributable to five distinct sources: a) macro-spatial variation (among populations), b) micro-
94 spatial variation (among plots within populations), c) temporal variation (among years), d)
95 population-specific (or macro-scale) temporal variation (unique combinations of population and
96 year), and e) plot-specific (or micro-scale) temporal variation (unique combinations of plot and
97 year) (Fig. 1).

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100 Results

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

117 Exploration behavior was, however, under heterogeneous selection. This conclusion was
118 supported for all fitness metrics considered based on hierarchical random regression analyses
119 and associated permutation tests (Table 2; SI Appendix Table S1). Combined with evidence for
120 neutral selection overall, our finding of heterogeneous directional selection implies that selection
121 varied not just in strength but also in direction (Table 2, Fig.2). The effect of exploration on
122 integrative fitness varied spatially and temporally at both macro- and micro-scales (variance in
123 random slopes; all permutation $P<0.01$, SI Appendix Table S1). Macro-spatial variation in
124 selection explained the largest percentage of the total variance in selection (effect of population;
125 47%; Table 2). Micro-spatial (plot; 13%), temporal (year: 19%), population-specific (i.e., macro-
126 scale) temporal (population \times year; 11%) and plot-specific (i.e., micro-scale) temporal (plot \times
127 year; 9%) variation in selection existed but were of lesser importance (Table 2). Analyses of
128 survival and local recruitment led to the same conclusions: macro-spatial variation in selection
129 explained the largest percentage of the variance in selection (viability selection: 35%; recruitment
130 selection; 39%); variation in selection at other spatiotemporal levels explained similar relative
131 amounts of variance as described for integrative fitness (Table 2, SI Appendix Table S1). This
132 implies that overall patterns of variation in selection were similar for both fitness components.

133 Statistical support for heterogeneous selection can occur as an artefact when phenotypes
134 vary among levels of random effects in situations where selection is nonlinear (SI Appendix Fig.

135 S1). We addressed this concern by re-fitting our models to incorporate level-specific nonlinear
136 patterns of selection, which were not detected (SI Appendix Table S4), thus suggesting that this
137 concern was unfounded. Patterns of (variation in) selection also did not depend on whether trait
138 values were standardized at the lowest hierarchical level (i.e. within unique combinations of plot
139 and year) rather than over the entire dataset (SI Appendix Table S5).

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142 Discussion

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

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154 Our discovery of a major role for macro-spatial variation in selection implies that large-
155 scale geographical variation in ecological factors has the potential to select for population
156 divergence, which, consequently, might promote nonrandom dispersal and settlement.
157 Specifically, individuals should settle in habitats where they do best, which will differ between
158 behavioral phenotypes (19, 20). Ecological factors that constrain dispersal of certain genotypes
159 (e.g., winter temperature) may also facilitate genetic differentiation (21). Moreover, behavioral
160 phenotypes may choose populations based on social rather than nonsocial environmental
161 conditions. For example, positive frequency-dependent selection favors non-aggressive Western
162 bluebirds (*Sialia mexicana*) when surrounded by non-aggressive conspecifics because those are
163 more cooperative (22). Similarly, fast-exploring great tits are known to acquire relatively low
164 dominance ranks as first-year birds, and are more likely to disperse away from their natal area
165 (17, 23); this may result in fast-exploring birds consequently settling in less competitive (i.e., low
166 density) areas where their behavioral phenotype may perform best (24), and supports the
167 nonrandom-dispersal hypothesis. Regardless of the causal factors, nonrandom dispersal may
168 thereby reinforce assortative mating (25), induce biased gene flow, accelerate (genetic)
169 population divergence, and eventually, enhance population evolvability (26). The simultaneous
170 occurrence of micro-spatial variation in selection (i.e., among plots within populations) implies that
171 selection also favors local adaptation among habitats of the same population. Local adaptation
172 within populations may, however, often be counteracted by substantial gene flow given the
173 species' dispersal characteristics (21, 27). Studies characterizing selection on personality-
174 dependent habitat choice (a form of phenotype-environment matching (19)) and dispersal are
175 required to reveal the interplay of mechanisms shaping evolutionary trajectories of behavioral
176 traits in natural populations.

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177 Temporal fluctuations favors certain behavioral phenotypes in certain years and other
178 phenotypes in other years (3). Fluctuating selection will thus inherently counteract the speed of
179 population divergence and consequently, plays a key role in preventing genetic differentiation
180 required in the process of local adaptation. The existence of behavioral variation in all five great tit
181 populations despite the large magnitude of macro-scale spatial variation in selection however
182 suggests that local adaptation may be reduced by the combined action of temporal variation at
183 small spatial scales and of gene flow at larger spatial scales. This may explain why the combined
184 additive and interactive effects of plot, year, and population explained as little as 4% of the
185 variance in exploration behavior among first-year birds (SI Appendix Table S2). A key question is
186 therefore at what spatial scale which mechanism predominantly counteracts population
187 divergence and whether genetic population divergence in behavior occurs at all. Forcefully

187 addressing this question would require study plots at spatial scales intermediate to our within-
188 and among-population levels, e.g., multiple populations within countries.

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

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

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

228 Nonrandom natal dispersal may bias estimates of variance in recruitment selection,
229 though this would require that, in different places or at different times, different behavioral
230 phenotypes are most dispersive; this condition is unlikely met at all five spatiotemporal scales at
231 which we detected heterogeneous recruitment selection. Moreover, variance estimates of
232 fecundity selection using annual fledgling number were similar to variance estimates of local
233 recruitment selection, refuting the idea that our estimates of heterogeneous selection measured
234 through local recruitment rates were biased (SI Appendix Table S3). Capture-mark-recapture
235 analyses have demonstrated that capture rates do not vary with exploration behavior among adult
236 breeders (45). As great tits show limited breeding dispersal (46, 47), sampling bias cannot easily
237 affect the variance in adult viability selection. Altogether, these arguments suggest that sampling

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238 bias does not play a major role in explaining the spatiotemporal patterns of heterogeneous
239 selection revealed by this study.

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

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Materials and Methods

256 **Study populations and field data collection.** Data were collected in five nest box populations of
257 great tits between 2006-2017 (Boshoek near Antwerp, Belgium; 51°08'N, 043°2'E), 2006-2009
258 (Lauwersmeer, The Netherlands; 53°20'N, 06°12'E), 2010-2014 (Starnberg District, Bavaria;
259 Germany; 47°58'N, 11°14'E), 1999-2016 (Westerheide; The Netherlands; 52°00'N, 05°50'E) and
260 2005-2016 (Wytham Woods, United Kingdom; 51°47'N, 1°20'W). In Boshoek, nine nest box plots
261 were fitted in 0.6-9 ha woodland fragments at a density of six boxes per ha (49). In both Bavaria
262 and Lauwersmeer, 12 nest box plots were fitted in 8-11 ha woodland fragments at a density of 4.5
263 to 6.2 boxes per ha (28). In Westerheide and Wytham Woods, a single nest box plot was fitted
264 within continuous woodland habitat of, respectively, ca. 112 and 290 ha at a density of 3 and 3.5
265 boxes per ha.

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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).

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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").

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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 $1 \times$ the focal adult's survival probability + $0.5 \times$ the number of its locally recruited offspring for

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288 a given year. This integrative fitness measure acknowledges that each individual contributes fully
289 its genes to the next year when returning as a breeder but that only half of its genes are present
290 in any recruited offspring (52, 53). This inherently avoids biases attributable to individual
291 differences in how tradeoffs between offspring quality and quantity, or between current and future
292 reproduction are resolved (36, 37, 42). We defined adult survival as the binary probability that a
293 focal bird breeding in a focal year was found breeding in the following year (binomial; not found
294 [0] or found breeding [1]). In this species, capture probabilities of breeders are high (75-95%) (45)
295 and breeding dispersal rates low (46, 47), implying that this metric appropriately measures local
296 survival. We defined local offspring recruitment as the annual number of offspring recruiting as
297 breeders in the focal population (regardless of plot identity). Because nonrandom dispersal can
298 bias estimates of fecundity selection based on counting local recruits, we also estimated selection
299 using the annual number of produced fledglings as alternative metric.

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

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

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

326 Exploration scores were corrected for seasonal plasticity (12, 13) following Ref. (12) to
327 avoid biased estimates (56). They were then squared-root transformed and standardized (i.e.,
328 zero mean and unit standard deviation) to acquire (standardized) selection gradients. We
329 performed this standardization over the entire dataset because this produces estimates that are
330 comparable across all hierarchical levels (57). However, great tits experience strong density-
331 dependent selection within plots among years ("plot-years") (58, 59), and previous studies implied
332 that traits should be standardized at the level at which competition occurs (60). We therefore also
333 ran our analyses after standardizing traits within plot-years. We estimated linear and nonlinear
334 (quadratic) selection on exploration behavior to test for directional and disruptive or stabilizing
335 selection. Nonlinear selection was assessed by adding the squared term of the standardized
336 exploration value (defined above) as a fixed effect covariate. Standardized linear and nonlinear
337 selection gradients were estimated by re-running our models using relative fitness (i.e., the focal
338 fitness metric divided by the grand mean of the dataset) as a response variable; quadratic

339 selection gradients were calculated by doubling the estimated parameter for the square of
340 exploration (61).

341 We ran all analyses in R v. 3.5.3. (62), using the Bayesian inference package R-INLA
342 (63) and the “iid2d” model. We estimated posterior means and their 95% credible intervals (CIs)
343 for all fixed and random effects. Fixed effect priors were normally distributed with zero mean and
344 precision (inverse of variance) of 0.001. The iid2d-model fixes random effect priors to a two-
345 dimensional Normal Wishart distribution. For recruitment selection analyses, we controlled for
346 overdispersion by adding an observation-level random effect with log-gamma prior with shape (α
347 = 0.5) and mean value (β = variance (offspring recruitment) * α).

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

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

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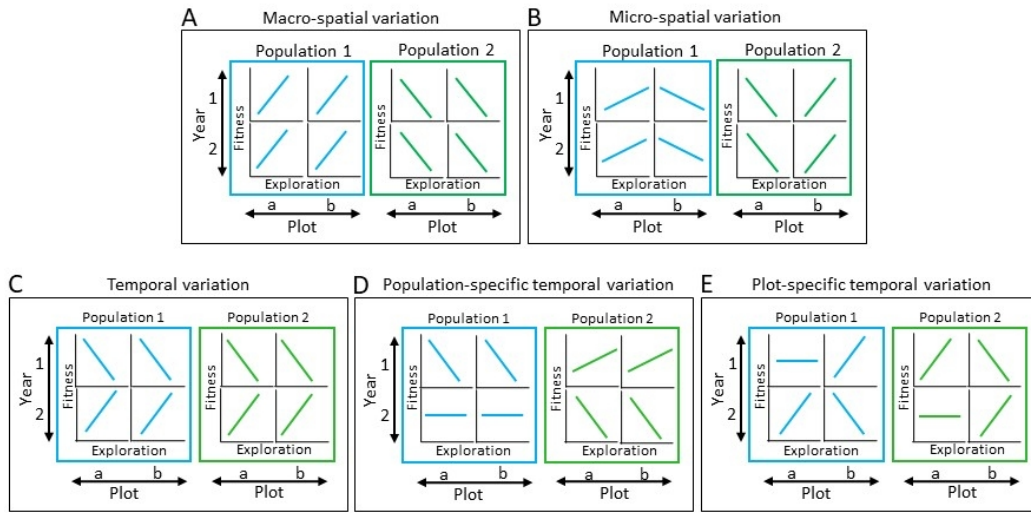
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538 **Figures and Tables**
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Figure 1. Distinct heterogeneous selection scenarios illustrated for two populations with two plots each sampled over the same two years. Selection can vary A) macro-spatially (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.

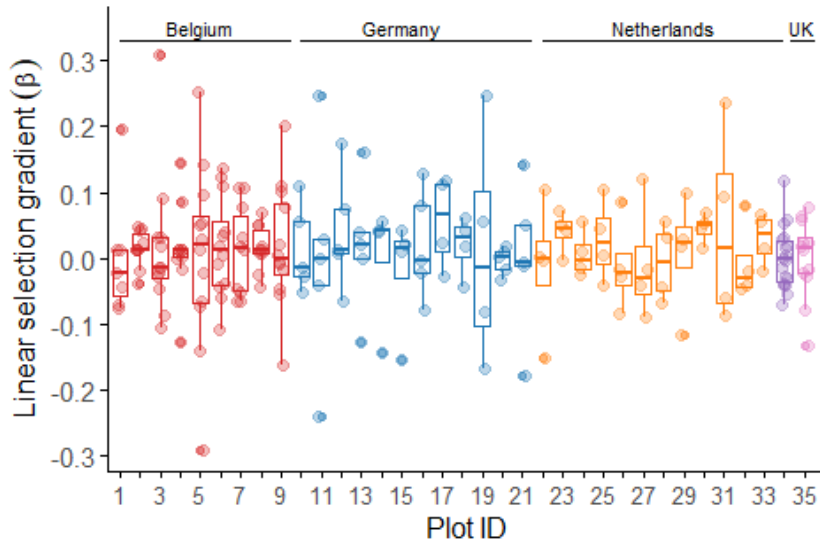
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Figure 2. Patterns of heterogeneous selection on exploration behavior within and among five great tit populations sampled across Western Europe. Colors represent populations, which were located across four countries. Boxplots show the median, first 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: Boshhoek, 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.

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

Selection gradient	Integrative fitness	Survival	Local recruitment
	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)

562 exploration behavior standardized over the entire dataset.

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570 **Table 2.** Proportion of variance in selection attributable to each ecological level with associated
571 95% credible intervals (CIs), for integrative fitness, adult survival (viability) or local offspring
572 recruitment as focal fitness metric.

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Ecological level	Integrative fitness	Survival	Local recruitment
	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)

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