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Authors	Mouchet, Alexia; Cole, Ella F.; Matthysen, Erik; Nicolaus, Marion; Quinn, John L.; Roth, Allison M.; Tinbergen, Joost M.; van Oers, Kees; van Overveld, Thijs; Dingemans, Niels J.
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## Main Manuscript for

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

Alexia Mouchet<sup>1\*</sup>, Ella F. Cole<sup>2</sup>, Erik Matthysen<sup>3</sup>, Marion Nicolaus<sup>4</sup>, John L. Quinn<sup>5</sup>, Allison M. Roth<sup>2, 6</sup>, Joost M. Tinbergen<sup>4</sup>, Kees van Oers<sup>7</sup>, Thijs van Overveld<sup>8</sup>, Niels J. Dingemanse<sup>1</sup>

<sup>1</sup> Behavioural Ecology, Department of Biology, Ludwig-Maximilians-University Munich, 82152 Planegg-Martinsried, Germany

<sup>2</sup> Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, United Kingdom

<sup>3</sup> Evolutionary Ecology Group, Department of Biology, University of Antwerp, B-2610 Antwerp, Belgium

<sup>4</sup> Conservation Ecology Group, Groningen Institute for Evolutionary Life Science (GELIFES), University of Groningen, Groningen, The Netherlands

<sup>5</sup> School of Biological, Earth and Environmental Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland

<sup>6</sup> Department of Biology, University of Florida, Gainesville, FL 32611, USA

<sup>7</sup> Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, the Netherlands

<sup>8</sup> Department of Conservation Biology, Estación Biológica de Doñana (CSIC), Américo Vespucio s/n E-41092 Sevilla, Spain

\* Alexia Mouchet

**Email:** mouchet@bio.lmu.de

**Author Contributions:** A.M. and N.D. designed the study. E.M., M.N., J.Q., A.R. and K.O. provided the data and all authors collected the data. A.M. compiled the dataset and conducted the statistical analyses. A.M. and N.D. wrote the manuscript, with input from all authors.

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**Keywords:** animal personality, macro-spatial variation, fluctuating selection, integrative fitness, local adaptation

**This PDF file includes:**

Main Text  
Figures 1 to 2  
Tables 1 to 2

1 **Abstract**

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

15 **Significance Statement**

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

26  
27 **Main Text**

28  
29 **Introduction**

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

39 Spatial and temporal processes co-occur (8, 9) but have distinct effects on population  
40 dynamics and evolution. Strong spatial variation favors different behavioral phenotypes in different  
41 locations, which may induce selection for nonrandom dispersal, and rapid population divergence  
42 (10, 11). Temporal variation instead favors the coexistence of multiple behavioral phenotypes within  
43 populations, thereby counteracting population divergence. Estimates of selection from multiple  
44 study populations monitored over multiple years are required to estimate spatial and temporal  
45 variation simultaneously and determine their relative importance in maintaining individual  
46 behavioral variation.

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

61  
62

## 63 Results

64 Exploration behavior was neither subject to linear nor to nonlinear viability (adult survival) selection  
65 within the average population, plot and year, though estimates of nonlinear selection suggested  
66 weak disruptive viability selection ( $\gamma$ , Table 1; SI Appendix Table S1). By contrast, exploration  
67 behavior was, on average, subject to stabilizing local offspring recruitment selection ( $\gamma$ , Table 1; SI  
68 Appendix Table S1). The effect of stabilizing local recruitment selection appeared to be cancelled  
69 out by the weak effect of disruptive viability selection. Indeed, selection measured using integrative  
70 fitness, which combines annual survival and local recruitment, was not different from zero (Table  
71 1; SI Appendix Table S1). Previous research has shown that faster explorers disperse further (14,  
72 17). Consistent with this idea, immigrants are often faster explorers than local recruits (14, 17, 18);  
73 this was also the case in our dataset (SI Appendix Table S2). We therefore examined whether our  
74 estimates of local recruitment selection were biased against faster explorers. To do so, we re-  
75 estimated fecundity (and integrative) fitness selection using annual fledgling production, a pre-  
76 dispersal reproductive success metric that should not suffer from dispersal-related bias. These  
77 analyses produced the same results as reported above, thus suggesting that nonrandom dispersal  
78 did not bias our estimates of selection (SI Appendix Table S3). We conclude, therefore, that  
79 exploration behavior was indeed selectively neutral overall.

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

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

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

103  
104

## 105 Discussion

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

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

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

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

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

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

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

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

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

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

214

215

## 216 **Materials and Methods**

217 **Study populations and field data collection.** Data were collected in five nest box populations of  
218 great tits between 2006-2017 (Boshoek near Antwerp, Belgium; 51°08'N, 043°2'E), 2006-2009  
219 (Lauwersmeer, The Netherlands; 53°20'N, 06°12'E), 2010-2014 (Starnberg District, Bavaria;  
220 Germany; 47°58'N, 11°14'E), 1999-2016 (Westerheide; The Netherlands; 52°00'N, 05°50'E) and  
221 2005-2016 (Wytham Woods, United Kingdom; 51°47'N, 1°20'W). In Boshoek, nine nest box plots  
222 were fitted in 0.6-9 ha woodland fragments at a density of six boxes per ha (49). In both Bavaria  
223 and Lauwersmeer, 12 nest box plots were fitted in 8-11 ha woodland fragments at a density of 4.5  
224 to 6.2 boxes per ha (28). In Westerheide and Wytham Woods, a single nest box plot was fitted  
225 within continuous woodland habitat of, respectively, ca. 112 and 290 ha at a density of 3 and 3.5  
226 boxes per ha.

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

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

244 typed for exploration behavior, distributed over 188 unique combinations of plot and year (“plot-  
245 years”).

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

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

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

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

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



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

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

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

320 **Data availability.** Data and code to reproduce statistical analyses and Fig. 2 are available on Dryad  
321 repository: <https://doi.org/10.5061/dryad.mkkwh70z8> (65)  
322

323

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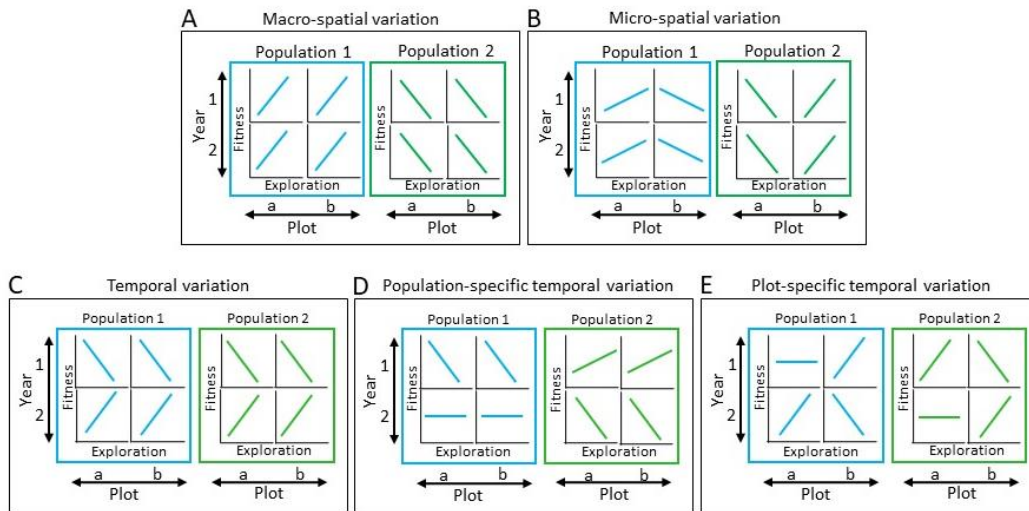
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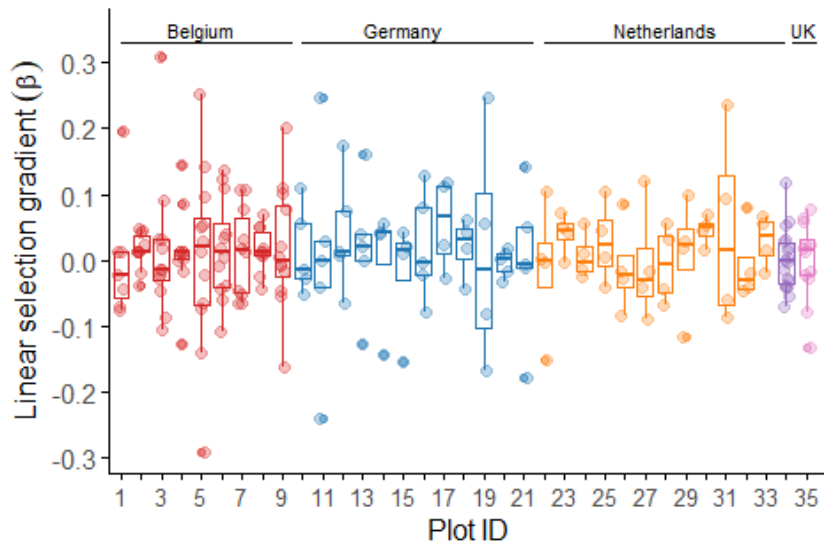
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501 **Figure 1.** Distinct heterogeneous selection scenarios illustrated for two populations with two plots  
502 each sampled over the same two years. Selection can vary A) macro-spatially (among populations),  
503 B) micro-spatially (among plots), C) temporally (among years), D) macro-spatiotemporally (year-  
504 effects are population-specific) and E) micro-spatiotemporally (year-effects are plot-specific).  
505 Illustrated scenarios are mutually nonexclusive; our analyses of the sources of variation in selection  
506 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.

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

	521		
	<b>Integrative fitness</b>	<b>Survival</b>	<b>Local recruitment</b>
<b>Selection gradient</b>	Estimate (95% CI)	Estimate (95% CI)	Estimate (95% CI)
$\beta$	0.02 (-0.45, 0.48)	0.02 (-0.49, 0.52)	0.06 (-0.56, 0.67)
$\gamma$	0.00 (-0.03, 0.02)	0.02 (-0.02, 0.05)	-0.10 (-0.11, 0.01)

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528 **Table 2.** Proportion of variance in selection attributable to each ecological level with associated  
 529 95% credible intervals (CIs), for integrative fitness, adult survival (viability) or local offspring  
 530 recruitment as focal fitness metric.

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<b>Ecological level</b>	<b>Integrative fitness</b>	<b>Survival</b>	<b>Local recruitment</b>
	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)