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1 **Boldness and exploration vary between shell morphs but not environmental**  
2 **contexts in the snail *Cepaea nemoralis***

3 **Running title:** Personality and shell morph in snails

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9

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12 thermal tolerance, as well as two anonymous referees and the editor for their comments on previous  
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14 **Conflicts of interest**

15 The authors have no conflict of interest to declare.

16 **Data accessibility**

17 Data and code to reproduce all analyses are available on GitHub  
18 (<https://github.com/mdahirel/cepaea-personality-2017>) and archived in Zenodo (DOI:  
19 10.5281/zenodo.3899042; version 1.1).

20

21

22 **Abstract**

23 Understanding the maintenance of among-individual behavioral variation in populations, and  
24 predicting its consequences, are key challenges in behavioral ecology. Studying the association  
25 between repeatable behaviors and other traits under selection may shed light on the underlying  
26 selective pressures. We used the model snail *Cepaea nemoralis* to examine whether individual  
27 behavior is associated with shell morph, a key trait that has been extensively studied in the context  
28 of thermal tolerance and predator avoidance, and which is known to be under strict genetic control  
29 in this species. We quantified proxies of boldness and exploration in snails of three morphs coming  
30 from two habitats with different thermal contexts. We show that both behaviors were repeatable at  
31 the among-individual level (within-state  $R_{boldness} = 0.22$  [95% credible interval: 0.15, 0.29];  $R_{exploration} =$   
32  $0.20$  [0.15, 0.25]). Behavior was associated with shell morph, with the darker morph (five-banded)  
33 being consistently shyer and slower to explore. There was no evidence that thermal environment of  
34 origin influenced behavior. Snails became faster when test temperature increased; we found no  
35 evidence morphs differed in their thermal response. Boldness and exploration were correlated  
36 among individuals, forming a syndrome ( $r = 0.28$  [0.10, 0.46]). We discuss what these results may tell  
37 us about the type of selection exerted by predators. We also detail how our results hint to a genetic  
38 link between shell morph and behavior, and the evolutionary implications of such a link. Finally, we  
39 discuss how our findings combined with decades of evolutionary research make *C. nemoralis* a very  
40 valuable model to study the evolution of behavior in response to environmental changes.

41 **Keywords** animal personality; behavioral syndromes; Gastropoda; multivariate multilevel model;  
42 shell color; temperature

## 43 Introduction

44 A key question in behavioral ecology, and more broadly in evolutionary ecology, is how to explain the  
45 persistence of variation in phenotypic traits. Although behavior is often seen as highly labile and  
46 dynamically adjustable to experienced conditions, individuals of many animal species exhibit  
47 “personalities”, i.e. behave consistently across time and contexts, and differ consistently from each  
48 other (Kralj-Fišer & Schuett, 2014; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell,  
49 Johnson, & Ziemba, 2004). This among-individual variation persists even when better adjustments of  
50 behaviors to environmental conditions would be adaptive, and the ability to tune behavior to  
51 conditions may itself vary among individuals (variation in “behavioral reaction norms”; Dingemanse,  
52 Kazem, Réale, & Wright, 2010). Moreover, behaviors are often correlated with each other and with  
53 other traits, forming multivariate syndromes (Réale et al., 2007; Royauté, Berdal, Garrison, &  
54 Dochtermann, 2018; Santostefano, Wilson, Niemelä, & Dingemanse, 2017), further constraining the  
55 range of behavioral phenotypes that are on display in populations (Dochtermann & Dingemanse,  
56 2013).

57 State-dependent behavior is often invoked as one of the key mechanisms/frameworks potentially  
58 explaining both adaptive correlations/feedbacks between behaviors and other traits, and the  
59 maintenance of among-individual variation (Sih et al., 2015; Wolf & McNamara, 2012; Wolf &  
60 Weissing, 2010). Individuals can differ in morphology, size, past experienced environment, or any  
61 other so-called “state variables”, typically less labile than behavior or even fixed at the individual  
62 level. If the costs and benefits of behaviors vary depending on these state variables, then we should  
63 expect individuals differing in state to adaptively differ in behaviors as well (Wolf & Weissing, 2010).  
64 The pace-of-life hypothesis, which ties several axes of behavioral variation to underlying differences  
65 in life history and metabolism along a fast-slow axis (Réale et al., 2010; Wolf & McNamara, 2012;  
66 Wright, Bolstad, Araya-Ajoy, & Dingemanse, 2019), can be seen under this lens. Other examples  
67 include cases of phenotypic compensation, where predation risk can either be mitigated by

68 behavioral changes or morphological defenses, leading to a positive association between risk-taking  
69 behavior and defenses (e.g. Ahlgren, Chapman, Nilsson, & Brönmark, 2015; but see De Winter,  
70 Ramalho Martins, Trovo, & Chapman, 2016 for a contradictory example). In some cases, quantitative  
71 genetics and/or experimental evolution approaches may provide evidence of the evolution of state-  
72 behavior associations (e.g. Kern, Robinson, Gass, Godwin, & Langerhans, 2016). In other cases in  
73 which this may be difficult, we believe that studying the association between personality and state  
74 traits can still provide valuable insights, especially if (i) the state trait is known to be fully genetically  
75 determined with little to no plasticity, (ii) we are able to study behavioral variation across a range of  
76 environments known to select on the state variable.

77 The grove snail *Cepaea nemoralis* (Linnaeus 1758) (family Helicidae) is a simultaneous  
78 hermaphrodite, medium-sized land gastropod common in western Europe (adult shell diameter 18-  
79 25mm; Welter-Schultes, 2012). It has a long history as a model in evolutionary biology, due to its  
80 conspicuous shell polymorphism (reviewed by Jones, Leith, & Rawlings, 1977; Özgo, 2009)(Fig. 1A-B).  
81 Genetic variation in shell background color (from pale yellow to brown, but usually divided in yellow,  
82 pink, and brown; Davison, Jackson, Murphy, & Reader, 2019) and in the number or width of dark  
83 bands has been well described (Jones et al., 1977). Shell polymorphism is governed by a limited  
84 number of loci with a limited number of alleles (Richards et al., 2013), and by all evidence shows no  
85 phenotypic plasticity. Modern genomics studies now aim to pinpoint the actual  
86 molecular/physiological underpinnings of shell color (Kerkvliet, Boer, Schilthuizen, & Kraaijeveld,  
87 2017; Richards et al., 2013).

88 In *C. nemoralis*, lighter-colored shells absorb less heat and allow snails to maintain a lower body  
89 temperature (Heath, 1975) and higher water content (Chang, 1991). Many studies have shown that  
90 lighter (vs. darker) snails have a selective advantage in hotter/sunnier (vs. colder/shaded)  
91 environments, whether one looks at continental-scale latitudinal clines (Jones et al., 1977; Silvertown  
92 et al., 2011), local-scale habitat comparisons (Kerstes, Breeschoten, Kalkman, & Schilthuizen, 2019;

93 Ozgo & Kinnison, 2008; Schilthuizen, 2013), or historical comparisons in the context of climate  
94 change (Ozgo, Liew, Webster, & Schilthuizen, 2017; Ozgo & Schilthuizen, 2012). Local variations in  
95 morph frequencies have also been linked to predation pressure, generally in the context of visual  
96 selection (frequency-dependent selection and/or crypsis; Jones et al., 1977; Surmacki, Ożarowska-  
97 Nowicka, & Rosin, 2013, and references therein; but see Cook, 2008), but morph differences in shell  
98 resistance to crushing have also been described (Rosin, Kobak, Lesicki, & Tryjanowski, 2013).

99 Although this has been much less studied, shell morphs also vary in their behavior (Chang, 1991;  
100 Jones, 1982; Ozgo & Kubea, 2005; Rosin et al., 2018). Part of this variation is likely the direct  
101 consequence of differences in shell thermal properties and thus effective body temperature, as  
102 demonstrated by experiments that created “artificial” morphs by painting shells (Tilling, 1983).  
103 However, they probably also reflect, at least partly, intrinsic physiological differences: preferred  
104 temperatures can be altered using opioid agonists or antagonists, but banded snails are less  
105 responsive to this pharmaceutical manipulation (Kavaliers, 1992). Existing studies, however, have  
106 several major shortfalls for our understanding of the association between *Cepaea* morphology and  
107 behavioral syndromes. In particular, individuals are generally assayed once, which means separating  
108 within- from among-individual variation is impossible (Dingemanse & Wright, 2020; Niemelä &  
109 Dingemanse, 2018). This also means the level of total among-individual variation, and how it  
110 compares with among-morph variation, has remained to our knowledge unstudied. Additionally, all  
111 snails are often sampled from the same habitat, or habitat information is not used in behavioral  
112 analyses, meaning there is often no way to determine how behavior responds to selection pressures  
113 on shell color.

114 In this context, we investigated the existence and magnitude of personality variation and behavioral  
115 syndromes in *C. nemoralis*, how behavior is linked to shell variation, and how it is influenced by the  
116 environment of origin (sun-exposed or shaded) and currently experienced conditions. More  
117 specifically, we make the following hypotheses:

118 (i) Exploration and boldness (risk-taking behavior) are both repeatable in this species, and positively  
119 correlated in a behavioral syndrome (Réale et al., 2010).

120 (ii) As boldness may increase predation risk (e.g. Hulthén et al., 2017), we may expect phenotypic  
121 compensation through shell characteristics to be present in bolder individuals. This would lead to  
122 correlations between morph and behavior, the direction of which providing insights into the  
123 dominant selection pressures.

124 (iii) As snails are ectotherms, exploration should increase with temperature due to increased  
125 metabolism (over the range of temperatures suitable to movement; Abram, Boivin, Moiroux, &  
126 Brodeur, 2017; Cloyed, Dell, Hayes, Kordas, & O’Gorman, 2019). We expect this temperature-  
127 exploration reaction norm should vary both in its slope and average value according to shell morph  
128 and habitat of origin. Populations having evolved in sun-exposed habitats, and lighter (unbanded)  
129 snails should be better adapted to maintain activity in the face of high temperatures (e.g. Cloyed et  
130 al., 2019), at the possible costs of lower activity at lower temperatures (Tilling, 1983).

## 131 **Methods**

### 132 *Sampled sites and snail maintenance under laboratory conditions*

133 Snails were sampled in fall 2016 in and close to the village of Arçais, France (Fig. 1C), roughly in the  
134 middle of the recorded latitudinal range of *Cepaea nemoralis* (GBIF Secretariat, 2020). We studied  
135 two sites located about 2 km apart and differing in terms of vegetation cover. One was a garden with  
136 few isolated trees, and thus under relatively direct sun exposure all year long (hereafter the “open  
137 habitat”; approximate location: 46° 17' 50"N, 0° 41' 30" W, Fig. 1D). The other was a 200 by 150 m  
138 deciduous forested lot, and thus fully shaded a large part of the year, especially the hottest spring  
139 and summer months (“shaded habitat”; approximately 46° 18' 01" N, 0° 42' 56" W, Fig. 1E). Only  
140 adult snails were selected (recognizable by a reflected “lip” on their shell opening), as a way to partly  
141 control for age. We only sampled snails with the three most abundant shell banding patterns: shells

142 with no bands, three bands on the lower side of the shell, and five bands (Fig. 1B). Following previous  
143 authors (e.g. Kavaliers, 1992), we here focused for simplicity solely on band presence, and thus  
144 sampled only snails with yellow background shells, which are the most common in the study region  
145 (Silvertown et al., 2011; personal observations) and on which the contrast between shell background  
146 and dark bands is the strongest. We acknowledge that this may prevent us from fully generalizing, for  
147 now, to natural populations, as the effect of darker background color is not always the same as the  
148 effect of increased shell banding (e.g. Kerstes et al., 2019). Snails were hand-collected during the day,  
149 their period of inactivity, both by simplicity and to avoid skewing our sample towards more active  
150 individuals. If there were nonetheless a bias towards catching more conspicuous/ less likely to hide  
151 snails, we believe it would have artificially reduced, rather than increased, our effect sizes: we would  
152 have sampled the most active morph and the most active individuals from the least active morph,  
153 reducing mean morph differences.

154 Sampling for the present study was targeted and adjusted in the field to obtain roughly equal  
155 numbers of each banding pattern from both landscapes; it therefore did not allow us to make  
156 inferences on their relative abundances. The same sites were however sampled again in 2018 for a  
157 separate experiment, this time with random sampling relative to banding pattern. As in previous  
158 studies (e.g. Schilthuizen, 2013) and reflecting potential thermal selection, the darker five-banded  
159 snails were more frequent in the shaded habitat than in the open habitat (22.3 vs. 13.5 %; see  
160 Supplementary Material S1).

161 We transferred snails to the lab and kept them under dormancy conditions ( $6 \pm 1^\circ\text{C}$ , no light, food or  
162 water sources) until March 2017, about 3 weeks before the start of the experiment. We then divided  
163 them into groups of 15 individuals from the same landscape, five (randomly chosen) of each shell  
164 phenotype. Comparing group size to natural densities is difficult, due to the way natural densities are  
165 often reported in the literature (averages over entire habitats, including empty areas). However,  
166 groups of 10-20 individuals are commonly seen in the wild (personal observations) and are also often



167 used in experiments (Oosterhoff, 1977; Rosin et al., 2018; Wolda, 1967). Groups were kept under  
168 controlled conditions ( $20 \pm 1^\circ\text{C}$ , L:D 16:8) in  $8.5 \times 15 \times 12$  cm polyethylene boxes lined with 1-2 cm of  
169 soil kept humid at the bottom. Snails had *ad libitum* access to prepared snail food (cereal flour  
170 supplemented with calcium, Hélinove, Saint Paul en Pareds, France) in a Petri dish. We gave each  
171 snail a unique ID written on the side of their shell with a paint marker (uni Posca, Mitsubishi Pencil  
172 Co., Ltd, Tokyo, Japan; Henry & Jarne, 2007). A total of 360 snails (60 for each habitat  $\times$  shell  
173 phenotype combination) were used in the experiments described below. By necessity, the observer  
174 (see below) was not blind to individual habitat of origin/phenotype; note that the analyst (MD) did  
175 not contribute to the actual observations.

#### 176 *Behavioral tests: boldness*

177 We studied boldness using simulated predator attacks as in Dähirel et al. (2017). All tests were done  
178 by the same operator (VG) to avoid effects of inter-experimenter variability. Snails were assayed  
179 individually during the last four hours of the photophase, i.e. the early part of the daily activity  
180 period. Like other helicids, *Cepaea nemoralis* is nocturnal but tends to start activity sometime before  
181 dark (Cameron, 1970). To stimulate activity, we first placed them in a Petri dish with water for 5  
182 minutes, before putting them on individual clean glass plates. After snails had moved at least one  
183 shell length ( $\approx 20$  mm) from their starting position, the operator used a pipette tip to pinch them for 5  
184 seconds on the right side of the foot. Preliminary tests confirmed that this was the shortest time  
185 needed to ensure all snails retracted fully in their shell. We then recorded the time snails took to exit  
186 the shell and resume activity after the attack (from retraction to the full extension of all tentacles out  
187 of the shell), as our measure of boldness (snails with shorter latencies being considered bolder). We  
188 stopped observations after 20 min if snails did not exit the shell. Snails from the same test box were  
189 tested on the same day, and placed back in their box after testing. To estimate the repeatability of  
190 boldness, snails were tested a second time after seven days, using the same protocol. The initial

191 order in which groups were tested within a sequence was random; this order was conserved for all  
192 subsequent tests.

193 *Behavioral tests: exploration/speed*

194 We studied snail movement at four temperatures within the activity range of *C. nemoralis* (Cameron,  
195 1970): 15, 18, 22, and 25 °C. All tests were again performed by the same operator (VG), and again  
196 during the last four hours of the photophase each day. Movement tests started 7 days after the last  
197 boldness test for a given individual, successive movement tests were separated by 24h. Half of the  
198 boxes, equally distributed between landscapes of origin, were tested in increasing temperature order  
199 (from 15 to 25 °C), the other half in decreasing order (25°C to 15°). Twenty-four hours before a given  
200 test, we placed snails and their rearing box at the testing temperature for habituation, using  
201 temperature-controlled cabinets (ET 619-4, Lovibond, Dortmund, Germany). For testing, each snail  
202 was placed individually at the center of a clean 25 × 25 cm polyethylene box (height: 9 cm) and left  
203 free to move. Snails were deemed active once they had moved more than 2 cm away from their  
204 starting point. We used the time snails took to move more than 10 cm from their starting point,  
205 minus the time taken to start activity, as our exploration metric (with lower values for snails that  
206 moved away faster). We stopped observations after 20 min post-activity initiation. This metric was  
207 chosen for its ease of implementation; we acknowledge that it conflates exploration of the  
208 environment with movement speed (as both slow-moving individuals and thorough explorers would  
209 have higher first-passage times).

210 *Ethical note and compatibility with reporting guidelines*

211 This study complies with all relevant national and international laws, and the ASAB/ABS Guidelines  
212 for the use of animals (2020) were adhered to as closely as possible. Potentially stressful  
213 experimental treatments (boldness experiment) were limited to the shortest possible time to elicit  
214 the behaviors of interest. No ethical board recommendation or administrative authorization was  
215 needed to work on or sample *Cepaea nemoralis*. The marking method used is non-invasive and has

216 minimal to no documented effects on life-history traits (Henry & Jarne, 2007). We do not believe  
217 there is any potential for bias due to social background, self-selection, experience or other factors  
218 indicated in the STRANGE framework (Webster & Rutz, 2020). To the best of our knowledge, the  
219 studied individuals are representative of the local populations studied, except for the two constraints  
220 explicitly imposed on collection by our experimental design (only adults, equal numbers of a few  
221 morphs of interest). All individuals were subjected to the same experimental conditions once  
222 collected.

### 223 *Statistical analyses*

224 We analyzed snail behavioral data in a Bayesian multilevel/mixed model framework, using the Stan  
225 language (Carpenter et al., 2017), with R (version 4.0; R Core Team, 2020) and the *brms* R package  
226 (Bürkner, 2017) as frontends. Scripting, analysis, and plotting relied on the *tidybayes*, *bayesplot*, and  
227 *patchwork* packages, as well as the *tidyverse* family of packages (Gabry, Simpson, Vehtari,  
228 Betancourt, & Gelman, 2019; Kay, 2019; Pedersen, 2019; Wickham et al., 2019).

229 We used a bivariate generalized linear multilevel model to estimate the effect of shell phenotype,  
230 habitat and temperature on behavior, quantify behavioral (co)variances and partition them across  
231 hierarchical levels (among-box, among-individual and within-individual variation) (Dingemanse &  
232 Dochtermann, 2013; Houslay & Wilson, 2017). We did not estimate within-individual trait  
233 correlations, as exploration and boldness were tested independently at the within-individual level  
234 (that is, boldness measure 1 had no stronger “link” to exploration measure 1 than boldness measure  
235 2; scenario 4 of table 2 in Dingemanse & Dochtermann, 2013). We present a full write-up of the  
236 model as Supplementary Material S2; a general description follows below.

237 Boldness and exploration were analyzed assuming a lognormal distribution to account for the  
238 skewed distribution of time to event data. We accounted for the fact that monitoring was stopped  
239 before some individuals could express the behavior of interest by including a censored data indicator  
240 in the model. Fixed effects for both behaviors included shell banding (three-level categorical

241 variable), landscape of origin (binary variable), and their interaction, as well as test order (1 or 2 for  
242 boldness, 1 to 4 for exploration). The model for exploration additionally included a test temperature  
243 effect as well as its interactions with shell banding and landscape. Categorical variables (shell  
244 banding, landscape of origin) were converted to centered dummy variables, and numeric variables  
245 (test order, temperature) were centered, following Schielzeth (2010)(temperature was additionally  
246 scaled to unit 1SD). This has two benefits. First, it makes main effect coefficients directly  
247 interpretable even in the presence of interactions (Schielzeth, 2010). Second, for categorical  
248 variables, having the intercept on an “average” rather than on one arbitrary default category avoids  
249 the problem of putting a more precise prior on an arbitrary reference category (which would be  
250 defined by the intercept only) than on the others (which would be defined by the intercept and one  
251 or several other coefficients)(McElreath, 2020). Morph-specific coefficients (intercepts, slopes)  
252 remain easy to obtain post-fitting, by simply adding the relevant posterior coefficients. Random  
253 effects included box-level and individual-level intercepts as well as, in the case of exploration, the  
254 associated slopes for temperature. This allowed us to estimate among-box and among-individual  
255 variation in mean behavior and thermal behavioral reaction norms as well as the box- and individual-  
256 level covariances among them (Dingemanse & Dochtermann, 2013).

257 We used a Normal( $\mu = \ln(400)$ ,  $\sigma = 0.5$ ) prior for the fixed effects intercepts (mean log- latencies), so  
258 that ~99% of the probability mass was within the range of latencies that was observable during the  
259 experiment (i.e. 0 to 1200 sec, see above), but not excluding larger values, because of censoring. We  
260 set the other priors to be weakly informative and follow some suggestions by McElreath (2020): a  
261 Normal(0,1) prior for the other fixed effects, a half-Normal(0, 1) prior for both random effect and  
262 distributional standard deviations. For the random effects correlation matrices, we use an LKJ( $\eta = 3$ )  
263 prior, as it helps reach convergence faster than McElreath (2020)’s  $\eta = 2$  default. Note that our choice  
264 here is more skeptical of high correlations and thus penalizes against our hypotheses of interest  
265 (there are detectable correlations).

266 We partitioned total phenotypic variation  $V_P$  for each behavior into the following components:  $V_P =$   
267  $V_F + V_I + V_B + V_D$ , where  $V_F$  is the fixed effect variation, including  $V_{F(state)}$  the portion of fixed-effect  
268 variance attributable to known individual state (banding pattern, environment of origin), i.e.  
269 excluding experimental effects (test order, temperature) (estimated following de Villemereuil,  
270 Morrissey, Nakagawa, & Schielzeth, 2018);  $V_I$  the average among-individual variation (including the  
271 effect of random temperature slope, estimated following Johnson, 2014), with  $V_{I(intercept)}$  the among-  
272 individual variation at the average test temperature ( $V_I = V_{I(intercept)}$  for boldness);  $V_B$  and  $V_{B(intercept)}$  are  
273 the equivalent box-level variances; and  $V_D$  is the distributional, or residual, variation. As pointed by  
274 Wilson (2018) and de Villemereuil et al. (2018), there is in most cases no one “true” repeatability  
275 estimate just as there is no one “true” way of partitioning the phenotypic variance pie; several  
276 estimates with differing interpretations can be presented. Therefore, both absolute variance  
277 components and analytical choices regarding repeatabilities should be made explicit. We estimated  
278 the following two unadjusted repeatabilities (i.e. including the entirety of  $V_P$  in the denominator;  
279 Nakagawa & Schielzeth, 2010): within-state repeatability  $R_{(within-state)} = V_{I(intercept)} / V_P$ , and what we  
280 term total repeatability,  $R_{(total)} = ( V_{I(intercept)} + V_{F(state)} ) / V_P$ . The proportion of persistent among-  
281 individual variation that is attributable to individual state (banding and landscape of origin) is then  
282 denoted by  $V_{F(state)} / ( V_{I(intercept)} + V_{F(state)} )$ . Variance components and repeatabilities are presented on  
283 the observed data scale (sensu de Villemereuil, Schielzeth, Nakagawa, & Morrissey, 2016). Variance  
284 components on the latent log scale (i.e. directly using model coefficients) led to qualitatively and  
285 quantitatively similar results.

286 We ran four chains for 12000 iterations, with the first 2000 iterations of each chain used for warmup.  
287 We checked mixing graphically and confirmed chain convergence using the improved  $\hat{R}$  statistic by  
288 Vehtari et al. (2020). The chains were run longer than the default number of iterations to ensure the  
289 effective sample size was satisfactory for all parameters (both bulk- and tail-effective sample sizes  
290 sensu Vehtari et al., 2020 at least  $> 400$ , here  $> 1000$ ). All posterior summaries are given as mean  
291 [95% highest posterior density interval].

## 292 Results

293 Exploration was related to shell morph (Table 1, Fig. 2), with morph-specific intercepts, i.e. mean log-  
294 latencies, for 0, 3 and 5-banded snails of 6.65 [6.59, 6.69], 6.64 [6.59, 6.69] and 6.71 [6.66, 6.76],  
295 respectively. Five-banded snails were on average slower to explore their surroundings than either  
296 three-banded or unbanded snails (in both cases, mean difference: 0.07 [0.01, 0.13])(Fig.2) Snails also  
297 became slower as tests went on (Table 1). We found no clear evidence of an effect of the landscape  
298 of origin on exploration. Snails explored faster with increasing temperature (Table 1, Fig. 2;  
299 temperature slopes for 0, 3, and 5-banded snails: -0.12 [-0.16,-0.07], -0.11 [-0.16, -0.07], -0.10 [-  
300 0.15,-0.06]). There was however no clear evidence that the slope of the temperature reaction norm  
301 varied between the three morphs, or between snails coming from different landscapes (Table 1;  
302 credible intervals for all interactions largely overlap 0).

303 Morphs also varied in average boldness (Table 1, Fig. 2), with morph-specific intercepts for 0, 3 and  
304 5-banded snails of 2.84 [2.65, 3.04], 2.99 [2.79, 3.18] and 3.10 [2.90, 3.30], respectively. Unbanded  
305 snails were bolder than five-banded snails (mean difference: -0.26 [-0.47, -0.05]); three-banded snails  
306 presenting intermediate values, with no clear difference with either extreme morph. Again, there  
307 was no evidence for landscape or landscape  $\times$  morph effects.

308 Both exploration and boldness were repeatable at the individual level, with average repeatabilities in  
309 the same range for both behaviors (Table 2). Including fixed effect variation due to individual state  
310 (morph and landscape of origin) in the calculation only slightly increased repeatabilities. Indeed, the  
311 proportion of persistent among-individual variation attributable to fixed effects was different from  
312 zero but small, with over 90% of individual-level variation attributable to other, unmeasured sources  
313 (Fig. 3, Table 2). Among-individual variation in temperature slopes was minimal, with variation in  
314 intercepts explaining 98% [89%, 100%] of the average exploration  $V_i$  (Fig. 3, Table 2). Accordingly, we  
315 find no clear evidence that the level of among-individual variation changes across the temperature  
316 gradient; following equations in Brommer (2013), the ratio between latent-scale  $V_i$  at the lowest and

317 highest tested temperatures is not different from 1 (0.76 [0.39, 1.13]). We also found no evidence of  
318 widespread rank switching across the temperature gradient (faster than average individuals in one  
319 environment remained overall faster across contexts): indeed, the cross-environmental correlation,  
320 which is higher the more predicted individual rankings stay consistent across environmental  
321 gradients (Brommer, 2013), was close to 1 when comparing the two extremes of the thermal  
322 gradient (0.85 [0.62, 1.00] on the latent scale).

323 Variation among boxes was small but non-negligible, in the same range as the proportion of variation  
324 explained by fixed effects for both behaviors. Average exploration and boldness were positively  
325 correlated at the individual level (Table 3, Fig. 4). There was no evidence that among-individual  
326 variation in responses to temperature was correlated with either mean exploration times or mean  
327 boldness (Table 3). There was no evidence for box-level correlations among traits (Table 3).

## 328 **Discussion**

329 By showing that behaviors linked to boldness and exploration are repeatable in *Cepaea nemoralis*,  
330 we add to a growing list of personality studies in gastropods, highlighting the usefulness of this taxon  
331 to address key questions in behavioral ecology (see e.g. Ahlgren et al., 2015; Cornwell, McCarthy, &  
332 Biro, 2020; Cornwell, McCarthy, Snyder, & Biro, 2019; Dähirel et al., 2017; Goodchild, Schmidt, &  
333 DuRant, 2020; Seaman & Briffa, 2015). We note however that this list is biased towards freshwater  
334 and marine gastropods; more studies are needed to understand among-individual variation in  
335 behavior in land mollusks. Additionally, we demonstrated that boldness and exploration are  
336 positively correlated in a common syndrome and that their expression varies depending on shell  
337 banding, a trait under strictly genetic determinism (little to no plasticity) that has been the focus of a  
338 lot of research in this species (Ozgo, 2009; Richards et al., 2013). Given how behavior can shape  
339 effective thermal tolerance (Abram et al., 2017) or vulnerability to predation (e.g. Hulthén et al.,  
340 2017), we believe these behavioral differences must be taken into account when discussing the  
341 evolution of shell color in this model species.

342 Unbanded snails were both bolder and explored faster than five-banded snails (Table 1, Fig. 2).  
343 Three-banded snails behaved similarly to unbanded snails for exploration (but were intermediate  
344 between unbanded and five-banded snails for boldness). This shows the “effectively unbanded”  
345 category sometimes used in *Cepaea* studies (Cain & Sheppard, 1954; Ožgo & Schilthuizen, 2012) has  
346 at least some behavioral relevance (that category groups together snails with little to no banding on  
347 the side of their shell exposed to the sun). Exploration and boldness were positively correlated both  
348 at the among-individual (Table 2) and among-morph levels (the shyest morph was also the slowest,  
349 Fig. 2). At the individual level, while some clutches were laid during the experiments, we were not  
350 able to test if this behavioral syndrome was integrated into a broader pace of life syndrome *sensu*  
351 Réale et al. (2010) by linking behavioral and life-history variation. Indeed, we were unable to  
352 ascertain the maternal and especially paternal origin of most clutches, and were not able to follow  
353 snail fecundity or longevity over their entire life. There are however some indications in the literature  
354 that more active/mobile snails are faster-growing (Oosterhoff, 1977), as the pace-of-life syndrome  
355 hypothesis would predict.

356 Five-banded snails were on average shyer than unbanded snails (Fig. 2). Birds, thrushes in particular  
357 (genus *Turdus*), are key predators of *Cepaea nemoralis* (Rosin, Lesicki, Kwieciński, Skórka, &  
358 Tryjanowski, 2017; Rosin, Olborska, Surmacki, & Tryjanowski, 2011). Historically, both frequency-  
359 dependent predation and direct visual selection due to crypsis have been invoked as explanations for  
360 predator-dependent morph variation in *Cepaea* (Jones et al., 1977; Ožgo, 2009), but discussions  
361 often used human vision as a baseline. More recently, crypsis explanations have received increased  
362 support from an experiment using models of avian vision to more rigorously test how thrushes see  
363 different shell morphs (Surmacki et al., 2013). In both our test sites, the boldest morph (unbanded  
364 shell) is the least conspicuous (based on Surmacki et al., 2013), not the rarest. Building on the  
365 phenotypic compensation hypothesis (i.e. that risk-taking individuals should be better defended;  
366 Ahlgren et al., 2015; Kuo, Irschick, & Lailvaux, 2015), this result then adds support to crypsis-based  
367 explanations of *Cepaea* morph variation. However, phenotypic compensation is not a hard rule, and



368 risk-taking individuals are sometimes less defended than risk-avoiding ones (De Winter et al., 2016;  
369 Goodchild et al., 2020). Besides, snails are also predated by rodents (Rosin et al., 2011), and shell  
370 morphs differ in shell strength in ways that go counter to the phenotypic compensation hypothesis  
371 (5-banded shells being stronger; Rosin et al., 2013). The combined effect of color and shell  
372 thickness/strength on predation risk remains to be studied. Finally, we must remember that (i) our  
373 knowledge of how avian predators perceive snails is very limited (Surmacki et al., 2013), (ii) we only  
374 tested a small set of the available morphs, which do not include the rarest background colors (pink  
375 and brown), and (iii) shell banding is a trait under multiple selection pressures, including thermal  
376 selection (see below).

377 Exploration speed was temperature-dependent: as expected from an ectothermic species, snails  
378 were on average faster at higher temperatures (Fig. 2). The temperature reaction norm of  
379 exploration was remarkably conserved among individuals (the near-totality of the among-individual  
380 variance  $V_i$  was due to differences in average behavior, rather than in temperature slopes; Table 2,  
381 Fig. 3). In addition, there was surprisingly no evidence that behavioral differences among morphs are  
382 influenced by the thermal environment, whether we consider the environment of origin (no habitat  $\times$   
383 morph interaction) or the current environment (no effect of morph identity on thermal reaction  
384 norms) (Table 1). This is despite abundant evidence in the literature for thermal selection on shell  
385 morphs, based on both field comparisons (e.g. Richardson, 1974; Schilthuizen, 2013; Kerstes et al.,  
386 2019; for this study, see Methods), and experiments (Lamotte, 1959; Tilling, 1983; Wolda, 1967).  
387 Studies giving snails a choice between multiple temperatures show snail morphs do have different  
388 thermal preferences that align with expectations based on thermal selection (Kavaliers, 1992). Some  
389 studies suggest that snails use shade and humidity just as much (and potentially more) as  
390 temperature as cues to adjust their behavior to microclimate (Ozgo & Kubea, 2005; Rosin et al.,  
391 2018). Our exploration tests were short, under standardized lighting conditions and with no water,  
392 and snails were brought back to favorable humidity soon after. It is possible longer experiments, or  
393 experiments comparing the responses of snails from different habitats to realistic climate variation

394 (including shade and/or humidity) would yield different responses. Maybe more importantly, we only  
395 tested temperatures favorable for activity, i.e. the limited part of the thermal niche closer to the  
396 optimum. Morph differences in behavior might be stronger closer to critical minimal or maximal  
397 temperature thresholds (Tilling, 1983). This can be investigated by using a wider range of  
398 temperatures and expanding the reaction norm approach used here to either a character state  
399 approach (e.g. Houslay, Earley, Young, & Wilson, 2019) or a non-linear reaction norm approach  
400 (Arnold, Kruuk, & Nicotra, 2019); both would account for the typical non-linearity of complete  
401 thermal performance curves (Arnold et al., 2019). It is very important to note, however, that these  
402 results do not mean populations from landscapes differing in sun exposure are identical in behavior,  
403 even for the range of situations we tested. Indeed, because morphs differ in their behavior, and  
404 because morph frequencies differ among landscapes (see Supplementary Material S1), the average  
405 snail from a sun-exposed population may well be bolder and more active than its counterpart from a  
406 shaded population.

407 In any case, the links between behaviors and morphs we observed are conserved across contexts,  
408 despite (apparent) selection on shell morph. While this is not a definite proof by itself, we consider  
409 this a first hint in favor of a genetic association between morphs and behaviors that cannot be easily  
410 broken by environmental changes. In addition to studies aiming to confirm these behavioral traits are  
411 heritable, further research into the physiological underpinnings of behavioral differences between  
412 morphs (building on e.g. Kavaliers, 1992) and of shell color and pattern determination (Kerkvliet et  
413 al., 2017) should help confirm (or infirm) this putative genetic correlation and elucidate its proximate  
414 basis.

415 Assuming this genetic link is confirmed, any discussion about how selection on morph may influence  
416 the evolution of behavior (or vice versa) must be tempered by one fact: the greater part of the  
417 repeatable among-individual variation in behavior was not explained by shell morph (see Fig. 3, Table  
418 1, and the fact that morph differences are hard to see from raw data in Fig. 2). It is in a way

419 unsurprising, as we did not expect a single discrete trait to entirely constrain individual behavioral  
420 variation. Indeed, the expression of animal personalities can be influenced by many unobserved  
421 drivers and state variables which should have a priori limited links to shell morph and its drivers  
422 (Burns et al., 2012; Petelle, Martin, & Blumstein, 2019; Sih et al., 2015; Wright et al., 2019). This  
423 includes for instance sex or reproductive history (DiRienzo & Aonuma, 2017; Kralj-Fišer, Hebets, &  
424 Kuntner, 2017), predation risk (Goodchild et al., 2020), age or life stage (Dahirel et al., 2017), or body  
425 size (Santostefano et al., 2017). Snail behavior is particularly sensitive to population density including  
426 during development (Cameron & Carter, 1979; Oosterhoff, 1977), an environmental axis we ignored  
427 in the present study. Also, our study focused on relatively short-term repeatability; it is possible that  
428 over larger time scales, the variance component related to morph differences plays a more  
429 important role. In a fish community, for instance, some differences among species are detectable  
430 over long but not short time scales (Harrison et al., 2019). Finally, some level of stochastic behavioral  
431 individuality is inevitable even in the total absence of meaningful genetic and environmental  
432 variation (Bierbach, Laskowski, & Wolf, 2017). What must be noted, though, is that some of this  
433 “remaining” among-individual variation may still, actually, relate to shell morph. Indeed, because of  
434 dominance within loci and especially epistatic relationships among loci, individuals that share the  
435 same shell phenotype may actually vary greatly in terms of underlying shell genotype (e.g. having  
436 one dominant allele at the « band presence » locus leads to total band absence and masks variation  
437 at all other banding genes; Jones et al., 1977). However, while much is known about among-morph  
438 variation in thermal tolerance, life history, physiology (Kavaliers, 1992; Kerstes et al., 2019; Lamotte,  
439 1959; Oosterhoff, 1977; Richardson, 1974; Tilling, 1983; Wolda, 1967), we know nothing, as far as we  
440 can tell, about within-morph, but among-genotype variation. Investigations using individuals of  
441 known genotype obtained through repeated crosses or, as our knowledge of the actual molecular  
442 underpinnings increases, through direct genotyping (Gonzalez, Aramendia, & Davison, 2019;  
443 Kerkvliet et al., 2017), may shed light on this “hidden” genetic variation and whether it contributes to  
444 the persistence of morph-related behavior differences.

445 Increased boldness and exploration have been tied to a higher probability of dispersal in many  
446 species (Cote, Clobert, Brodin, Fogarty, & Sih, 2010), including land snails (Dahirel et al., 2017), and  
447 non-random dispersal is now acknowledged as a potentially widespread force behind population  
448 phenotypic divergence (Edelaar & Bolnick, 2012; Jacob, Bestion, Legrand, Clobert, & Cote, 2015).  
449 Bolder animals are often thought to trade increased success against a greater predation risk (Hulthén  
450 et al., 2017; but see Moiron, Laskowski, & Niemelä, 2020); predation is generally considered a key  
451 driver of morphological differences in *Cepaea*, and plays a key role in dispersal across taxa (Fronhofer  
452 et al., 2018). Although active dispersal can safely be dismissed as a driver of continental-scale  
453 differences in morph frequencies, our results point to *Cepaea* as a good model to understand how  
454 existing behavioral differences may drive local-scale morphological differences (and vice versa). By  
455 building on, and complementing, a decades-long history of evolutionary research, this will help us  
456 better understand the role of behavior, and constraints on behavioral variation, in shaping responses  
457 to rapid environmental changes (Candolin & Wong, 2012), including landscape alteration and climate  
458 change.

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- 718
- 719

720 **Tables**

721 **Table 1:** Estimated fixed effect parameters of the model explaining exploration and boldness  
 722 latencies (mean and 95% credible intervals). Continuous explanatory variables are centered and  
 723 scaled, and categorical variables converted to centered dummy variables; the intercept then refers to  
 724 the behavior of a hypothetical "average" snail.

	Mean effect (95% credible interval)	
	Exploration	Boldness
<i>Fixed effects: main effects</i>		
Intercept (log-latency of an "average" individual)	6.67 (6.63 ; 6.70)	2.98 (2.83 ; 3.13)
banding = 3 bands	-0.00 (-0.06 ; 0.06)	0.15 (-0.06 ; 0.36)
banding = 5 bands	<b>0.07 (0.01 ; 0.13)</b>	<b>0.26 (0.05 ; 0.47)</b>
landscape of origin = shaded	0.06 (-0.02 ; 0.13)	0.20 (-0.10 ; 0.50)
test temperature	<b>-0.11 (-0.15 ; -0.07)</b>	--
test order	<b>0.04 (0.00 ; 0.07)</b>	0.08 (-0.04 ; 0.19)
<i>Fixed effects: interactions</i>		
banding = 3bands × landscape = shaded	-0.07 (-0.19 ; 0.05)	0.16 (-0.25 ; 0.56)
banding = 5bands × landscape = shaded	-0.01 (-0.13 ; 0.11)	0.24 (-0.16 ; 0.65)
banding = 3bands × temperature	0.00 (-0.04 ; 0.04)	--
banding = 5bands × temperature	0.01 (-0.03 ; 0.05)	--
landscape = shaded × temperature	-0.05 (-0.13 ; 0.03)	--
banding = 3bands × landscape = shaded × temperature	-0.02 (-0.10 ; 0.06)	--
banding = 5bands × landscape = shaded × temperature	0.02 (-0.06 ; 0.10)	--

725

726 **Table 2.** Variance partitioning and repeatabilities. Estimated variances and 95% credible interval are  
 727 obtained from a multivariate mixed model. Variances are estimated on the observed scale *sensu de*  
 728 Villemereuil et al (2016). Variances are rounded to the nearest unit. Readers looking at the data may  
 729 note that the total variances  $V_P$  are higher than the empirically observed variances. This is because  
 730 the latter are underestimated, due to censoring.

	Posterior mean (95% credible interval)	
	Exploration	Boldness
<i>Variance partitioning (observed scale, in sec<sup>2</sup>)</i>		
Fixed effects $V_F$	13556 (6349 ; 21112)	49 (6 ; 110)
- explained by state	2185 (329 ; 4360)	46 (4 ; 105)
Among boxes $V_B$	8468 (2984 ; 15132)	128 (12; 307)
- random intercept only	3102 (0 ; 7101)	128 (12; 307)
Among individuals $V_I$	25677 (17966 ; 33628)	542 (263; 875)
- random intercept only	24346 (17322 ; 32035)	542 (263; 875)
Residual $V_D$	73976 (63439 ; 84520)	1795 (966 ; 2816)
Total variance $V_P$	121676 (102632 ; 141659)	2513 (1334 ; 3960)
<i>Repeatabilities (observed scale)</i>		
$R_{(within-state)}$	0.20 (0.15 ; 0.25)	0.22 (0.15 ; 0.29)
$R_{(total)}$	0.22 (0.17 ; 0.27)	0.24 (0.17 ; 0.31)
$R_{(within-state)} / R_{(total)}$	0.92 (0.84 ; 0.98)	0.92 (0.84 ; 0.99)

731

732



733 **Table 3.** Random effect correlation matrices (latent scale, mean and 95% credible intervals). Box-  
734 level correlations are above the diagonal, individual-level correlations below the diagonal.

	Boldness, intercept	Exploration, intercept	Exploration, temperature slope
Boldness, intercept		0.12 (-0.42 ; 0.63)	0.38 (-0.05 ; 0.79)
Exploration, intercept	<b>0.28 (0.10 ; 0.46)</b>		-0.19 (-0.69 ; 0.33)
Exploration, temperature slope	-0.19 (-0.67 ; 0.32)	0.29 (-0.24 ; 0.76)	

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736

737 **Figure legends**

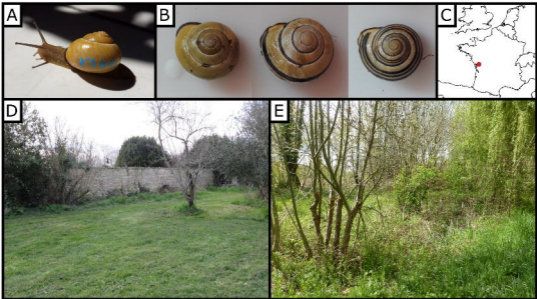
738 **Figure 1.** Study species and sites. (A) An unbanded yellow *Cepaea nemoralis*, showing the position of  
739 individual paint marks on the shell (B) Representative shells of the three studied morphs as seen  
740 from above: yellow unbanded, three-banded, and five-banded snails (C) Study sites location in  
741 France; the open habitat (D) and the shaded habitat (E) are separated by about 2 km. Photographs  
742 were taken during winter, when snails were collected.

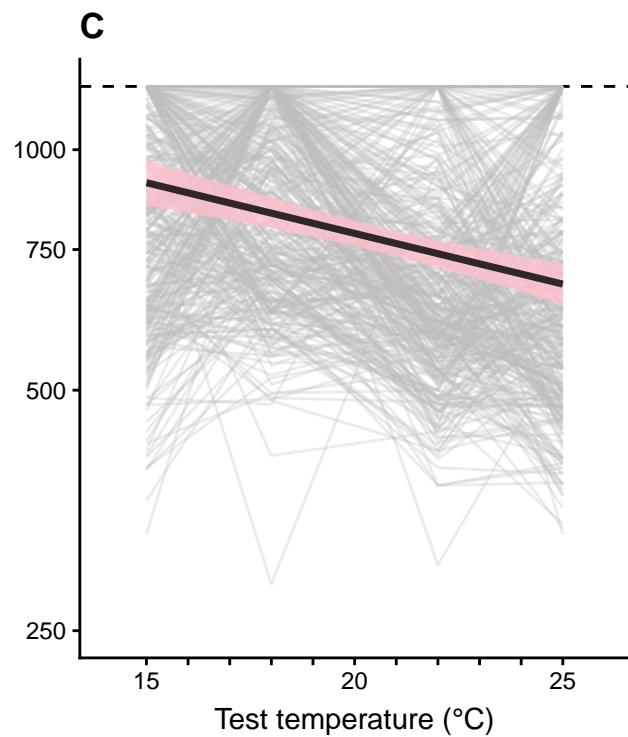
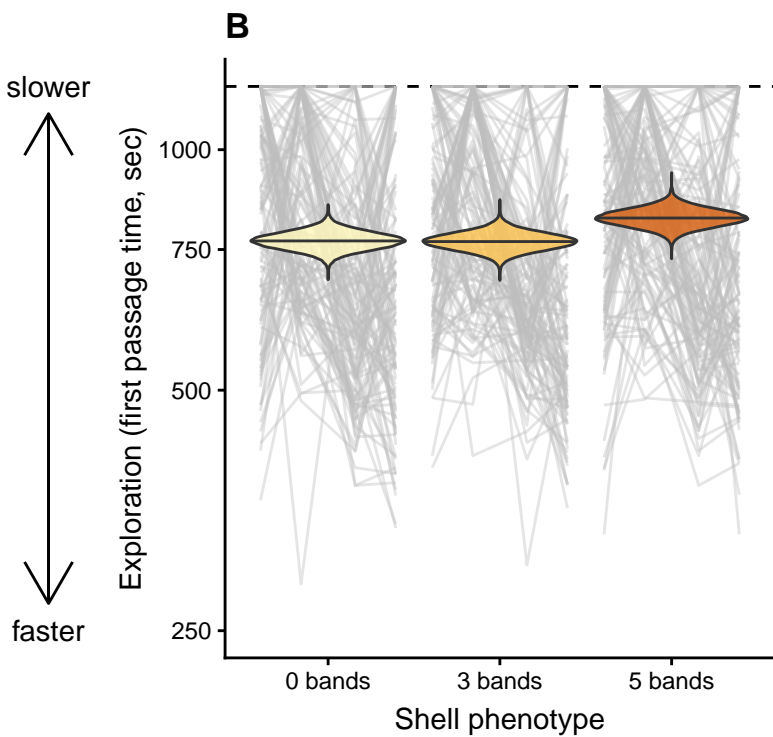
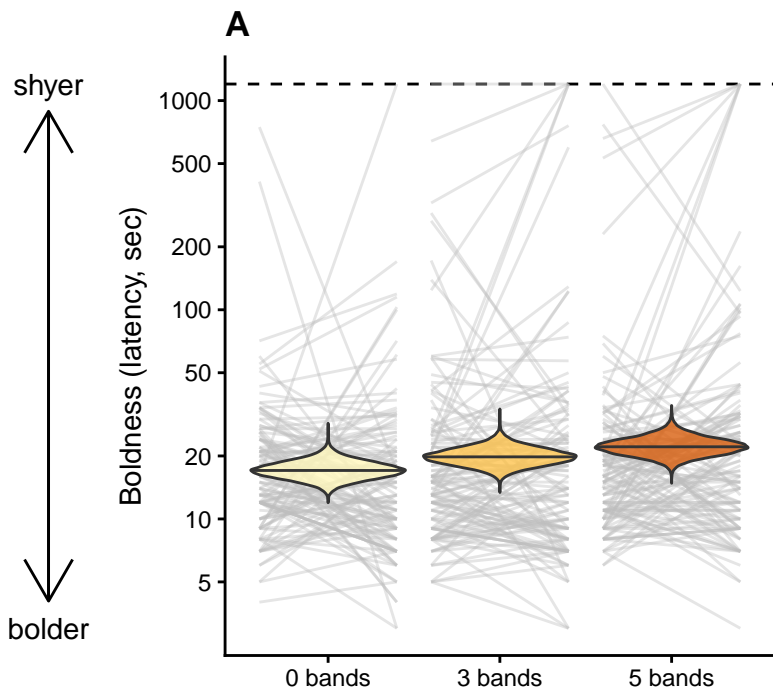
743 **Figure 2.** (A; B) posterior distributions of median boldness (A) and exploration (B) in relation to shell  
744 morph. The model estimates the mean log-latencies, which correspond to the medians on the  
745 observed latencies scale. (C) Mean and 95% credible band for the relationship between exploration  
746 latency and test temperature. Grey lines connect trials from the same individual. Values are plotted  
747 on a log-transformed axis. N = 360 individuals (60 per landscape × morph combination)

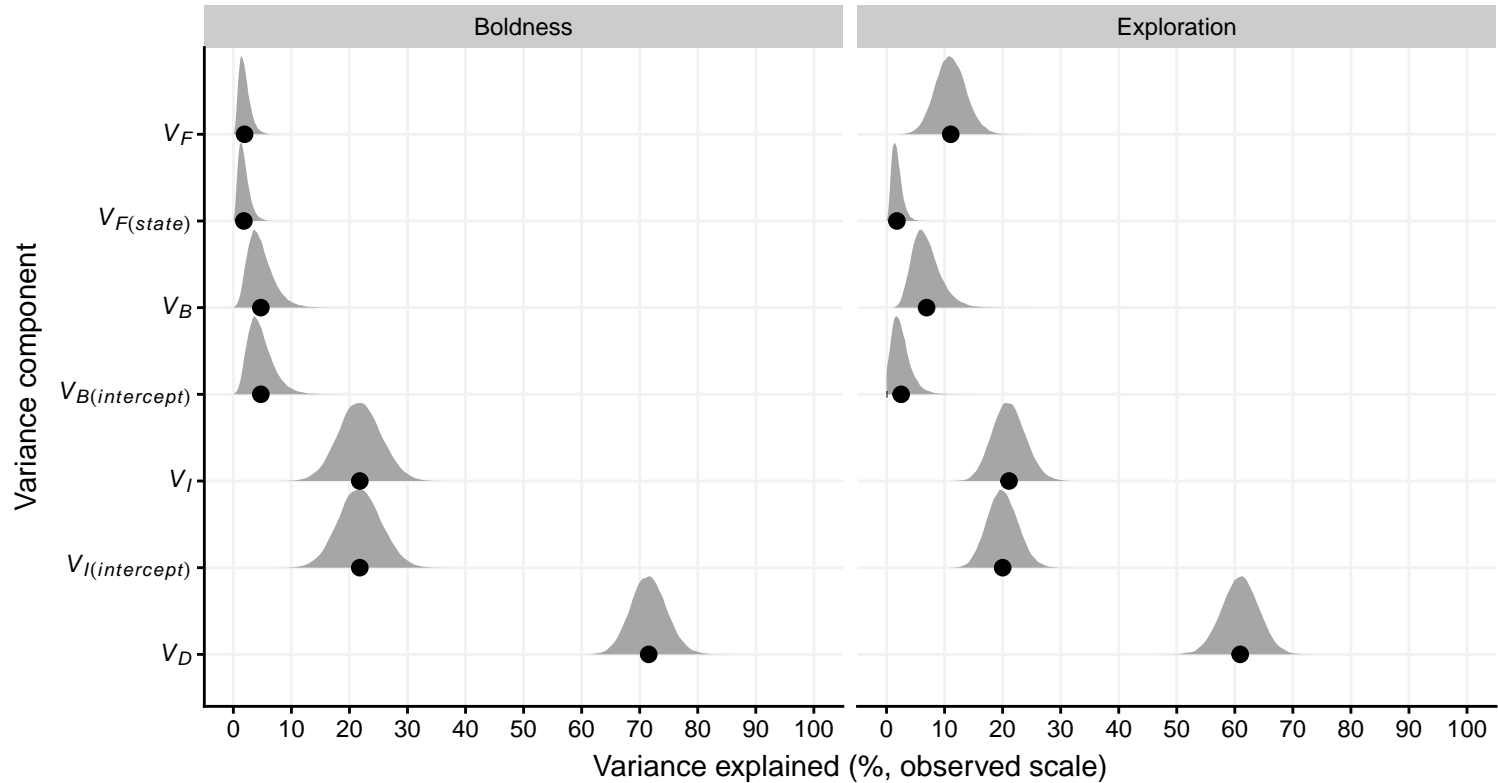
748 **Figure 3.** Mean (points) and posteriors for the proportion of variance explained by the different  
749 variance components. For boldness,  $V_B$  and  $V_{B(intercept)}$  are exactly equal by definition (same for  $V_I$  and  
750  $V_{I(intercept)}$ ); see Methods and Table 2 for details on this and the names of the variance components.

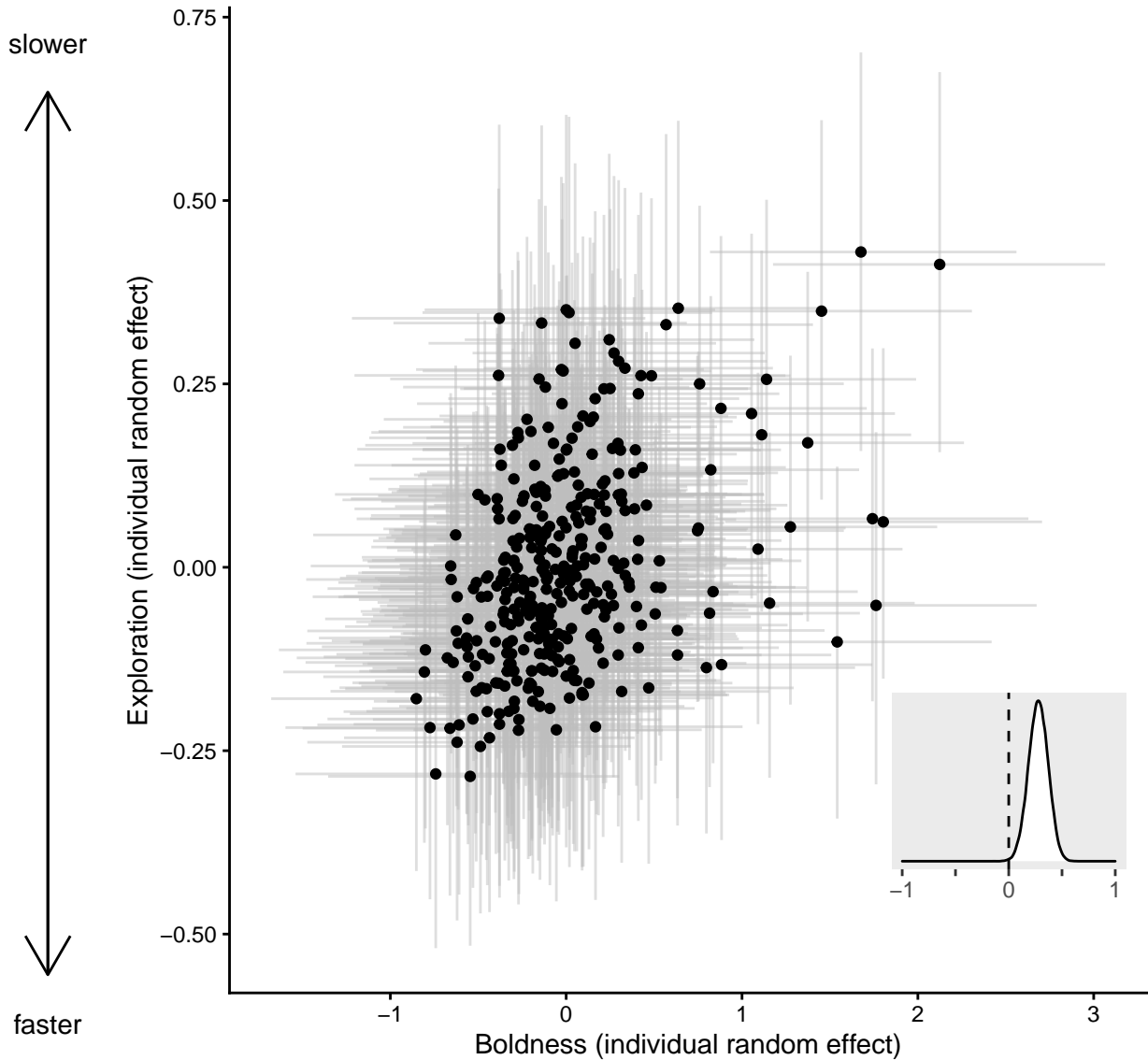
751 **Figure 4.** Correlation between individual-level random effects for boldness and exploration,  
752 illustrated by plotting their respective Best Linear Unbiased Predictors and 95% credible intervals.  
753 Inset: posterior distribution of the correlation coefficient. BLUPs are plotted, and correlation  
754 estimated, on the latent log scale.

755









slower

Exploration (individual random effect)

faster

Boldness (individual random effect)

bolder

shyer