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

Running title: Personality and shell morph in snails

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Conflicts of interest

The authors have no conflict of interest to declare.

Data accessibility

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

Abstract

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

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

Introduction

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

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

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

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

In *C. nemoralis*, lighter-colored shells absorb less heat and allow snails to maintain a lower body temperature (Heath, 1975) and higher water content (Chang, 1991). Many studies have shown that lighter (vs. darker) snails have a selective advantage in hotter/sunnier (vs. colder/shaded) environments, whether one looks at continental-scale latitudinal clines (Jones et al., 1977; Silvertown 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 (Ożgo, Liew, Webster, & Schilthuizen, 2017; Ożgo & 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; Ożgo & 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 ± 1°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 ± 1°C, L:D 16:8) in 8.5 × 15 × 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 × 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 Dahirel 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 (≈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

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

Behavioral tests: exploration/speed

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

Ethical note and compatibility with reporting guidelines

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

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

Statistical analyses

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

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

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

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

We used a Normal(μ = ln(400), σ = 0.5) prior for the fixed effects intercepts (mean log- latencies), so that ~99% of the probability mass was within the range of latencies that was observable during the experiment (i.e. 0 to 1200 sec, see above), but not excluding larger values, because of censoring. We set the other priors to be weakly informative and follow some suggestions by McElreath (2020): a Normal(0,1) prior for the other fixed effects, a half-Normal(0, 1) prior for both random effect and distributional standard deviations. For the random effects correlation matrices, we use an LKJ(η = 3) prior, as it helps reach convergence faster than McElreath (2020)'s η = 2 default. Note that our choice here is more skeptical of high correlations and thus penalizes against our hypotheses of interest (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 $R_{(within\text{-}state)} = V_{I(intercept)} / V_P$, 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].

Results

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

Morphs also varied in average boldness (Table 1, Fig. 2), with morph-specific intercepts for 0, 3 and 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 snails were bolder than five-banded snails (mean difference: -0.26 [-0.47, -0.05]); three-banded snails presenting intermediate values, with no clear difference with either extreme morph. Again, there was no evidence for landscape or landscape × morph effects.

Both exploration and boldness were repeatable at the individual level, with average repeatabilities in the same range for both behaviors (Table 2). Including fixed effect variation due to individual state (morph and landscape of origin) in the calculation only slightly increased repeatabilities. Indeed, the proportion of persistent among-individual variation attributable to fixed effects was different from zero but small, with over 90% of individual-level variation attributable to other, unmeasured sources (Fig. 3, Table 2). Among-individual variation in temperature slopes was minimal, with variation in intercepts explaining 98% [89%, 100%] of the average exploration V_I (Fig. 3, Table 2). Accordingly, we find no clear evidence that the level of among-individual variation changes across the temperature 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; Dahirel 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 (Ożgo, 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; Ożgo & 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; Ożgo, 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 ×
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 (Ożgo & 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.

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

References

Abram, P. K., Boivin, G., Moiroux, J., & Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: Unifying thermal physiology and behavioural plasticity. *Biological Reviews*, *92*(4), 1859–1876. doi: 10.1111/brv.12312

Ahlgren, J., Chapman, B. B., Nilsson, P. A., & Brönmark, C. (2015). Individual boldness is linked to protective shell shape in aquatic snails. *Biology Letters*, *11*(4), 20150029. doi: 10.1098/rsbl.2015.0029

Arnold, P. A., Kruuk, L. E. B., & Nicotra, A. B. (2019). How to analyse plant phenotypic plasticity in response to a changing climate. *New Phytologist*, *222*(3), 1235–1241. doi: 10.1111/nph.15656

ASAB, & ABS. (2020). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour*, *159*, I–XI. doi: 10.1016/j.anbehav.2019.11.002

Bierbach, D., Laskowski, K. L., & Wolf, M. (2017). Behavioural individuality in clonal fish arises despite near-identical rearing conditions. *Nature Communications*, *8*, 15361. doi: 10.1038/ncomms15361

Brommer, J. E. (2013). Variation in plasticity of personality traits implies that the ranking of personality measures changes between environmental contexts: Calculating the cross-environmental correlation. *Behavioral Ecology and Sociobiology*, *67*(10), 1709–1718. doi: 10.1007/s00265-013-1603-9

Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*(1), 1–28. doi: 10.18637/jss.v080.i01

Burns, J. G., Svetec, N., Rowe, L., Mery, F., Dolan, M. J., Boyce, W. T., & Sokolowski, M. B. (2012). Gene–environment interplay in *Drosophila melanogaster*: Chronic food deprivation in early life affects adult exploratory and fitness traits. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(Suppl 2), 17239–17244. doi: 10.1073/pnas.1121265109

Cain, A. J., & Sheppard, P. M. (1954). Natural selection in *Cepaea*. *Genetics*, *39*(1), 89–116.

Cameron, R. A. D. (1970). The effect of temperature on the activity of three species of helicid snail (Mollusca: Gastropoda). *Journal of Zoology*, *162*(3), 303–315. doi: 10.1111/j.1469-7998.1970.tb01267.x

Cameron, R. A. D., & Carter, M. A. (1979). Intra- and interspecific effects of population density on growth and activity in some helicid land snails (Gastropoda: Pulmonata). *Journal of Animal Ecology*, *48*(1), 237–246. doi: 10.2307/4111

Candolin, U., & Wong, B. B. M. (Éds.). (2012). *Behavioural responses to a changing world: Mechanisms and consequences* (1st edition). Oxford: Oxford University Press.

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., … Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, *76*(1), 1–32. doi: 10.18637/jss.v076.i01

Chang, H.-W. (1991). Activity and weight loss in relation to solar radiation in the polymorphic land snail *Cepaea nemoralis*. *Journal of Zoology*, *225*(2), 213–225. doi: 10.1111/j.1469-7998.1991.tb03812.x

Cloyed, C. S., Dell, A. I., Hayes, T., Kordas, R. L., & O'Gorman, E. J. (2019). Long-term exposure to higher temperature increases the thermal sensitivity of grazer metabolism and movement. *Journal of Animal Ecology*, *0*(0). doi: 10.1111/1365-2656.12976

Cook, L. M. (2008). Variation with habitat in *Cepaea nemoralis*: The Cain & Sheppard diagram. *Journal of Molluscan Studies*, *74*(3), 239–243. doi: 10.1093/mollus/eyn011

Cornwell, T. O., McCarthy, I. D., & Biro, P. A. (2020). Integration of physiology, behaviour and life history traits: Personality and pace of life in a marine gastropod. *Animal Behaviour*, *163*, 155–162. doi: 10.1016/j.anbehav.2020.03.009

Cornwell, T. O., McCarthy, I. D., Snyder, C. R. A., & Biro, P. A. (2019). The influence of environmental gradients on individual behaviour: Individual plasticity is consistent across risk and temperature gradients. *Journal of Animal Ecology*, *88*(4), 511–520. doi: 10.1111/1365-2656.12935

Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1560), 4065–4076. doi: 10.1098/rstb.2010.0176

Dahirel, M., Vong, A., Ansart, A., & Madec, L. (2017). Individual boldness is life stage-dependent and linked to dispersal in a hermaphrodite land snail. *Ecological Research*, *32*, 751–755. doi: 10.1007/s11284-017-1484-x

Davison, A., Jackson, H. J., Murphy, E. W., & Reader, T. (2019). Discrete or indiscrete? Redefining the colour polymorphism of the land snail *Cepaea nemoralis*. *Heredity*, 1. doi: 10.1038/s41437-019-0189-z

De Winter, G., Ramalho Martins, H., Trovo, R. A., & Chapman, B. B. (2016). Knights in shining armour are not necessarily bold: Defensive morphology correlates negatively with boldness, but positively with activity, in wild threespine stickleback, *Gasterosteus aculeatus*. *Evolutionary Ecology Research*, *17*, 1–12.

Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*(1), 39–54. doi: 10.1111/1365-2656.12013

Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution*, *25*(2), 81–89. doi: 10.1016/j.tree.2009.07.013

Dingemanse, N. J., & Wright, J. (2020). Criteria for acceptable studies of animal personality and behavioural syndromes. *Ethology*, *126*(9), 865–869. doi: 10.1111/eth.13082

DiRienzo, N., & Aonuma, H. (2017). Individual differences are consistent across changes in mating status and mediated by biogenic amines. *Behavioral Ecology and Sociobiology*, *71*(8), 118. doi: 10.1007/s00265-017-2345-x

Dochtermann, N. A., & Dingemanse, N. J. (2013). Behavioral syndromes as evolutionary constraints. *Behavioral Ecology*, *24*(4), 806–811. doi: 10.1093/beheco/art002

Edelaar, P., & Bolnick, D. I. (2012). Non-random gene flow: An underappreciated force in evolution and ecology. *Trends in Ecology & Evolution*, *27*(12), 659–665. doi: 10.1016/j.tree.2012.07.009

Fronhofer, E. A., Legrand, D., Altermatt, F., Ansart, A., Blanchet, S., Bonte, D., … Cote, J. (2018). Bottom-up and top-down control of dispersal across major organismal groups. *Nature Ecology & Evolution*, *2*(12), 1859–1863. doi: 10.1038/s41559-018-0686-0

Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in Bayesian workflow. *Journal of the Royal Statistical Society: Series A (Statistics in Society)*, *182*(2), 389–402. doi: 10.1111/rssa.12378

GBIF Secretariat. (2020). Cepaea nemoralis *(Linnaeus, 1758)* in *GBIF Backbone Taxonomy. Checklist dataset accessed via GBIF.org on 2020-08-11*. Consulté à l'adresse https://doi.org/10.15468/39omei

Gonzalez, D. R., Aramendia, A. C., & Davison, A. (2019). Recombination within the *Cepaea nemoralis* supergene is confounded by incomplete penetrance and epistasis. *Heredity*, 1. doi: 10.1038/s41437-019-0190-6

Goodchild, C. G., Schmidt, L. M., & DuRant, S. E. (2020). Evidence for the 'behavioural character' hypothesis: Does boldness programme disparate antipredator strategies? *Animal Behaviour*, *164*, 123–132. doi: 10.1016/j.anbehav.2020.04.010

Harrison, P. M., Keeler, R. A., Robichaud, D., Mossop, B., Power, M., & Cooke, S. J. (2019). Individual differences exceed species differences in the movements of a river fish community. *Behavioral Ecology*, arz076. doi: 10.1093/beheco/arz076

Heath, D. J. (1975). Colour, sunlight and internal temperatures in the land-snail *Cepaea nemoralis* (L.). *Oecologia*, *19*(1), 29–38. doi: 10.1007/BF00377587

Henry, P.-Y., & Jarne, P. (2007). Marking hard-shelled gastropods: Tag loss, impact on life-history traits, and perspectives in biology. *Invertebrate Biology*, *126*(2), 138–153. doi: 10.1111/j.1744-7410.2007.00084.x

Houslay, T. M., Earley, R. L., Young, A. J., & Wilson, A. J. (2019). Habituation and individual variation in the endocrine stress response in the Trinidadian guppy (*Poecilia reticulata*). *General and Comparative Endocrinology*, *270*, 113–122. doi: 10.1016/j.ygcen.2018.10.013

Houslay, Thomas M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology. *Behavioral Ecology*, *28*(4), 948–952. doi: 10.1093/beheco/arx023

Hulthén, K., Chapman, B. B., Nilsson, P. A., Hansson, L.-A., Skov, C., Brodersen, J., … Brönmark, C. (2017). A predation cost to bold fish in the wild. *Scientific Reports*, *7*(1), 1239. doi: 10.1038/s41598-017-01270-w

Jacob, S., Bestion, E., Legrand, D., Clobert, J., & Cote, J. (2015). Habitat matching and spatial heterogeneity of phenotypes: Implications for metapopulation and metacommunity functioning. *Evolutionary Ecology*, *29*(6), 851–871. doi: 10.1007/s10682-015-9776-5

Johnson, P. C. D. (2014). Extension of Nakagawa & Schielzeth's R^2_{GLMM} to random slopes models. *Methods in Ecology and Evolution*, *5*(9), 944–946. doi: 10.1111/2041-210X.12225

Jones, J. S. (1982). Genetic differences in individual behaviour associated with shell polymorphism in the snail *Cepaea nemoralis*. *Nature*, *298*(5876), 749–750. doi: 10.1038/298749a0

Jones, J. S., Leith, B. H., & Rawlings, P. (1977). Polymorphism in *Cepaea*: A problem with too many solutions? *Annual Review of Ecology and Systematics*, *8*, 109–143. JSTOR. Consulté à l'adresse JSTOR.

Kavaliers, M. (1992). Opioid systems, behavioral thermoregulation and shell polymorphism in the land snail, *Cepaea nemoralis*. *Journal of Comparative Physiology B*, *162*(2), 172–178. doi: 10.1007/BF00398344

Kay, M. (2019). *tidybayes: Tidy data and geoms for Bayesian models*. doi: 10.5281/zenodo.1308151

Kerkvliet, J., Boer, T. de, Schilthuizen, M., & Kraaijeveld, K. (2017). Candidate genes for shell colour polymorphism in *Cepaea nemoralis*. *PeerJ*, *5*, e3715. doi: 10.7717/peerj.3715

Kern, E. M. A., Robinson, D., Gass, E., Godwin, J., & Langerhans, R. B. (2016). Correlated evolution of personality, morphology and performance. *Animal Behaviour*, *117*, 79–86. doi: 10.1016/j.anbehav.2016.04.007

Kerstes, N. A. G., Breeschoten, T., Kalkman, V. J., & Schilthuizen, M. (2019). Snail shell colour evolution in urban heat islands detected via citizen science. *Communications Biology*, *2*(1), 264. doi: 10.1038/s42003-019-0511-6

Kralj-Fišer, S., Hebets, E. A., & Kuntner, M. (2017). Different patterns of behavioral variation across and within species of spiders with differing degrees of urbanization. *Behavioral Ecology and Sociobiology*, *71*(8), 125. doi: 10.1007/s00265-017-2353-x

Kralj-Fišer, S., & Schuett, W. (2014). Studying personality variation in invertebrates: Why bother? *Animal Behaviour*, *91*, 41–52. doi: 10.1016/j.anbehav.2014.02.016

Kuo, C.-Y., Irschick, D. J., & Lailvaux, S. P. (2015). Trait compensation between boldness and the propensity for tail autotomy under different food availabilities in similarly aged brown anole lizards. *Functional Ecology*, *29*(3), 385–392. doi: 10.1111/1365-2435.12324

Lamotte, M. (1959). Polymorphism of natural populations of *Cepaea nemoralis*. *Cold Spring Harbor Symposia on Quantitative Biology*, *24*(0), 65–86. doi: 10.1101/SQB.1959.024.01.009

McElreath, R. (2020). *Statistical rethinking: A Bayesian course with examples in R and Stan* (2nd edition). Boca Raton, USA: Chapman and Hall/CRC.

Moiron, M., Laskowski, K. L., & Niemelä, P. T. (2020). Individual differences in behaviour explain variation in survival: A meta-analysis. *Ecology Letters*, *23*(2), 399–408. doi: 10.1111/ele.13438

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

Niemelä, P. T., & Dingemanse, N. J. (2018). On the usage of single measurements in behavioural ecology research on individual differences. *Animal Behaviour*, *145*, 99–105. doi: 10.1016/j.anbehav.2018.09.012

Oosterhoff, L. M. (1977). Variation in growth rate as an ecological factor in the landsnail *Cepaea nemoralis* (L.). *Netherlands Journal of Zoology*, *27*(1), 1–132. doi: 10.1163/002829677X00072

Ożgo, M. (2009). Current problems in the research of *Cepaea* polymorphism. *Folia Malacologica*, *16*(2), 55–60. doi: 10.12657/folmal.016.009

Ozgo, M., & Kinnison, M. T. (2008). Contingency and determinism during convergent contemporary evolution in the polymorphic land snail, *Cepaea nemoralis*. *Evolutionary Ecology Research*, *10*, 721–733.

Ożgo, M., & Kubea, A. (2005). Humidity and the effect of shell colour on activity of *Cepaea nemoralis* (Linnaeus, 1758). *Folia Malacologica*, *13*(3).

Ożgo, M., Liew, T.-S., Webster, N. B., & Schilthuizen, M. (2017). Inferring microevolution from museum collections and resampling: Lessons learned from *Cepaea*. *PeerJ*, *5*, e3938. doi: 10.7717/peerj.3938

Ożgo, M., & Schilthuizen, M. (2012). Evolutionary change in *Cepaea nemoralis* shell colour over 43 years. *Global Change Biology*, *18*(1), 74–81. doi: 10.1111/j.1365-2486.2011.02514.x

Pedersen, T. L. (2019). *patchwork: The composer of plots*. Consulté à l'adresse https://CRAN.R-project.org/package=patchwork

Petelle, M. B., Martin, J. G. A., & Blumstein, D. T. (2019). Mixed support for state maintaining risky personality traits in yellow-bellied marmots. *Animal Behaviour*, *150*, 177–188. doi: 10.1016/j.anbehav.2019.02.008

R Core Team. (2020). R: a language and environment for statistical computing (Version 4.0.0). Vienna, Austria: R Foundation for Statistical Computing. Consulté à l'adresse https://www.R-project.org/

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1560), 4051–4063. doi: 10.1098/rstb.2010.0208

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291–318. doi: 10.1111/j.1469-185X.2007.00010.x

Richards, P. M., Liu, M. M., Lowe, N., Davey, J. W., Blaxter, M. L., & Davison, A. (2013). RAD-Seq derived markers flank the shell colour and banding loci of the *Cepaea nemoralis* supergene. *Molecular Ecology*, *22*(11), 3077–3089. doi: 10.1111/mec.12262

Richardson, A. M. M. (1974). Differential climatic selection in natural population of land snail *Cepaea nemoralis*. *Nature*, *247*(5442), 572. doi: 10.1038/247572a0

Rosin, Z. M., Kobak, J., Lesicki, A., & Tryjanowski, P. (2013). Differential shell strength of *Cepaea nemoralis* colour morphs—Implications for their anti-predator defence. *Naturwissenschaften*, *100*(9), 843–851. doi: 10.1007/s00114-013-1084-8

Rosin, Z. M., Kwieciński, Z., Lesicki, A., Skórka, P., Kobak, J., Szymańska, A., … Tryjanowski, P. (2018). Shell colour, temperature, (micro)habitat structure and predator pressure affect the behaviour of *Cepaea nemoralis*. *The Science of Nature*, *105*(5), 35. doi: 10.1007/s00114-018-1560-2

Rosin, Z. M., Lesicki, A., Kwieciński, Z., Skórka, P., & Tryjanowski, P. (2017). Land snails benefit from human alterations in rural landscapes and habitats. *Ecosphere*, *8*(7), e01874. doi: 10.1002/ecs2.1874

Rosin, Z. M., Olborska, P., Surmacki, A., & Tryjanowski, P. (2011). Differences in predatory pressure on terrestrial snails by birds and mammals. *Journal of Biosciences*, *36*(4), 691–699. doi: 10.1007/s12038-011-9077-2

Royauté, R., Berdal, M. A., Garrison, C. R., & Dochtermann, N. A. (2018). Paceless life? A meta-analysis of the pace-of-life syndrome hypothesis. *Behavioral Ecology and Sociobiology*, *72*(3), 64. doi: 10.1007/s00265-018-2472-z

Santostefano, F., Wilson, A. J., Niemelä, P. T., & Dingemanse, N. J. (2017). Behavioural mediators of genetic life-history trade-offs: A test of the pace-of-life syndrome hypothesis in field crickets. *Proc. R. Soc. B*, *284*(1864), 20171567. doi: 10.1098/rspb.2017.1567

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. doi: 10.1111/j.2041-210X.2010.00012.x

Schilthuizen, M. (2013). Rapid, habitat-related evolution of land snail colour morphs on reclaimed land. *Heredity*, *110*(3), 247–252.

Seaman, B., & Briffa, M. (2015). Parasites and personality in periwinkles (*Littorina littorea*): Infection status is associated with mean-level boldness but not repeatability. *Behavioural Processes*, *115*, 132–134. doi: 10.1016/j.beproc.2015.03.014

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *The Quarterly Review of Biology*, *79*(3), 241–277. doi: 10.1086/422893

Sih, A., Mathot, K. J., Moirón, M., Montiglio, P.-O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state–behaviour feedbacks: A review and guide for empiricists. *Trends in Ecology & Evolution*, *30*(1), 50–60. doi: 10.1016/j.tree.2014.11.004

Silvertown, J., Cook, L., Cameron, R., Dodd, M., McConway, K., Worthington, J., … Juan, X. (2011). Citizen science reveals unexpected continental-scale evolutionary change in a model organism. *PLOS ONE*, *6*(4), e18927. doi: 10.1371/journal.pone.0018927

Surmacki, A., Ożarowska-Nowicka, A., & Rosin, Z. M. (2013). Color polymorphism in a land snail *Cepaea nemoralis* (Pulmonata: Helicidae) as viewed by potential avian predators. *Die Naturwissenschaften*, *100*(6), 533–540. doi: 10.1007/s00114-013-1049-y

Tilling, S. M. (1983). An experimental investigation of the behaviour and mortality of artificial and natural morphs of *Cepaea nemoralis* (L.). *Biological Journal of the Linnean Society*, *19*(1), 35–50. doi: 10.1111/j.1095-8312.1983.tb00775.x

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., & Bürkner, P.-C. (2020). Rank-normalization, folding, and localization: An improved \widehat{R} for assessing convergence of MCMC. *Bayesian Analysis*. doi: 10.1214/20-BA1221

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

Villemereuil, Pierre de, Schielzeth, H., Nakagawa, S., & Morrissey, M. (2016). General methods for evolutionary quantitative genetic inference from Generalized Mixed Models. *Genetics*, *204*(3), 1281–1294. doi: 10.1534/genetics.115.186536

Webster, M. M., & Rutz, C. (2020). How STRANGE are your study animals? *Nature*, *582*(7812), 337–340. doi: 10.1038/d41586-020-01751-5

Welter-Schultes, F. (2012). *European non-marine molluscs, a guide for species identification*. Göttingen: Planet Poster Editions.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., … Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, *4*(43), 1686. doi: 10.21105/joss.01686

Wilson, A. J. (2018). How should we interpret estimates of individual repeatability? *Evolution Letters*, *2*(1), 4–8. doi: 10.1002/evl3.40

Wolda, H. (1967). The effect of temperature on reproduction in some morphs of the landsnail *Cepaea nemoralis* (L.). *Evolution*, *21*(1), 117–129. doi: 10.1111/j.1558-5646.1967.tb00135.x

Wolf, M., & McNamara, J. M. (2012). On the evolution of personalities via frequency-dependent selection. *The American Naturalist*, *179*(6), 679–692. doi: 10.1086/665656

Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 3959–3968. doi: 10.1098/rstb.2010.0215

Wright, J., Bolstad, G. H., Araya-Ajoy, Y. G., & Dingemanse, N. J. (2019). Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. *Biological Reviews*, *94*(1), 230–247. doi: 10.1111/brv.12451

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
Fixed effects: main effects		
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	**0.07 (0.01 ; 0.13)**	**0.26 (0.05 ; 0.47)**
landscape of origin = shaded	0.06 (-0.02 ; 0.13)	0.20 (-0.10 ; 0.50)
test temperature	**-0.11 (-0.15 ; -0.07)**	--
test order	**0.04 (0.00 ; 0.07)**	0.08 (-0.04 ; 0.19)
Fixed effects: interactions		
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

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

	Posterior mean (95% credible interval)	
	Exploration	Boldness
Variance partitioning (observed scale, in sec²)		
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)
Repeatabilities (observed scale)		
$R_{(within\text{-}state)}$	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)
$R_{(within\text{-}state)}$ / $R_{(total)}$	0.92 (0.84 ; 0.98)	0.92 (0.84 ; 0.99)

Table 3. Random effect correlation matrices (latent scale, mean and 95% credible intervals). Box-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	**0.28 (0.10 ; 0.46)**		-0.19 (-0.69 ; 0.33)
Exploration, temperature slope	-0.19 (-0.67 ; 0.32)	0.29 (-0.24 ; 0.76)	

737 **Figure legends**

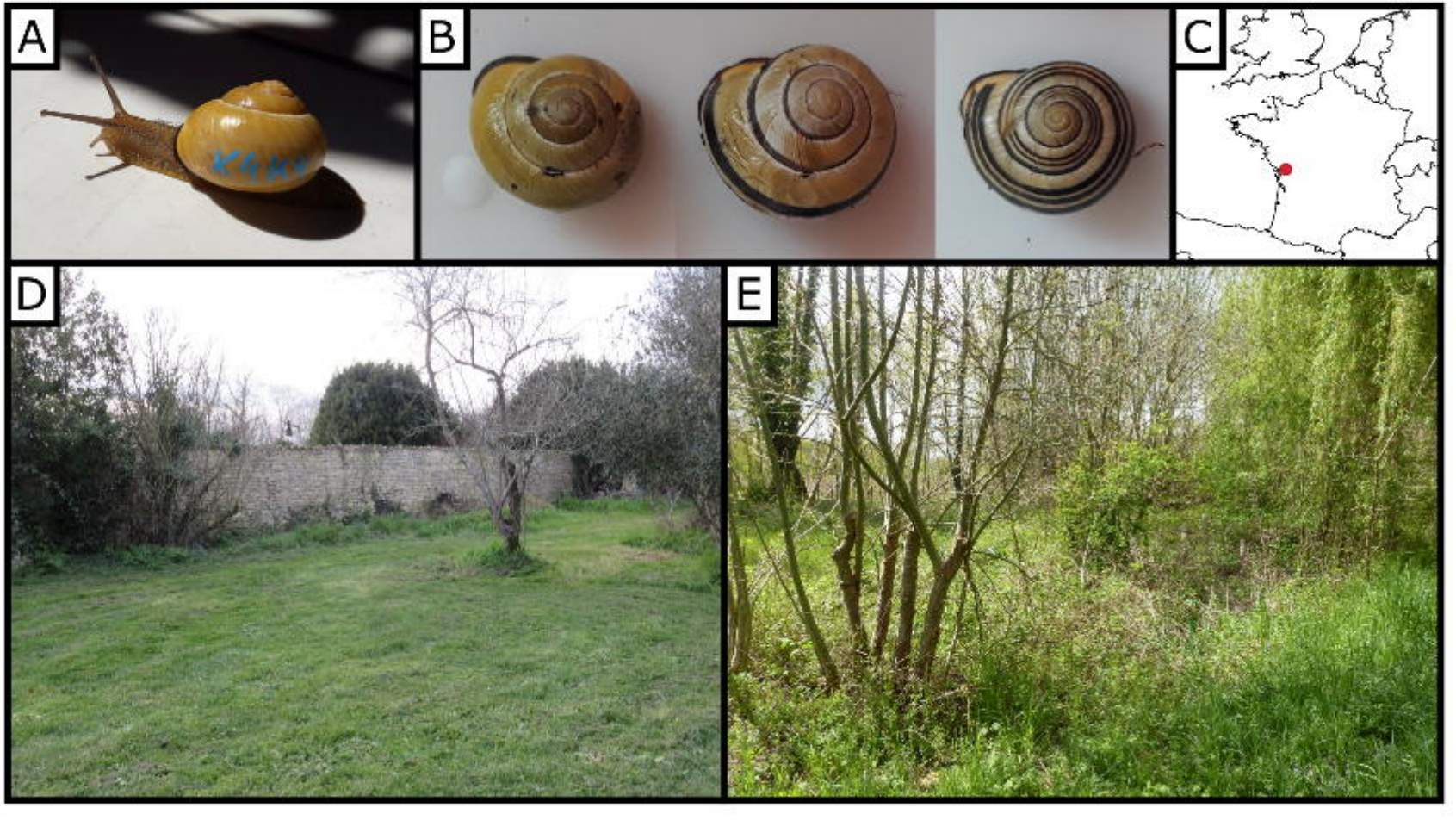
738 **Figure 1.** Study species and sites. (A) An unbanded yellow *Cepaea nemoralis*, showing the position of
739 individual paint marks on the shell (B) Representative shells of the three studied morphs as seen
740 from above: yellow unbanded, three-banded, and five-banded snails (C) Study sites location 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.

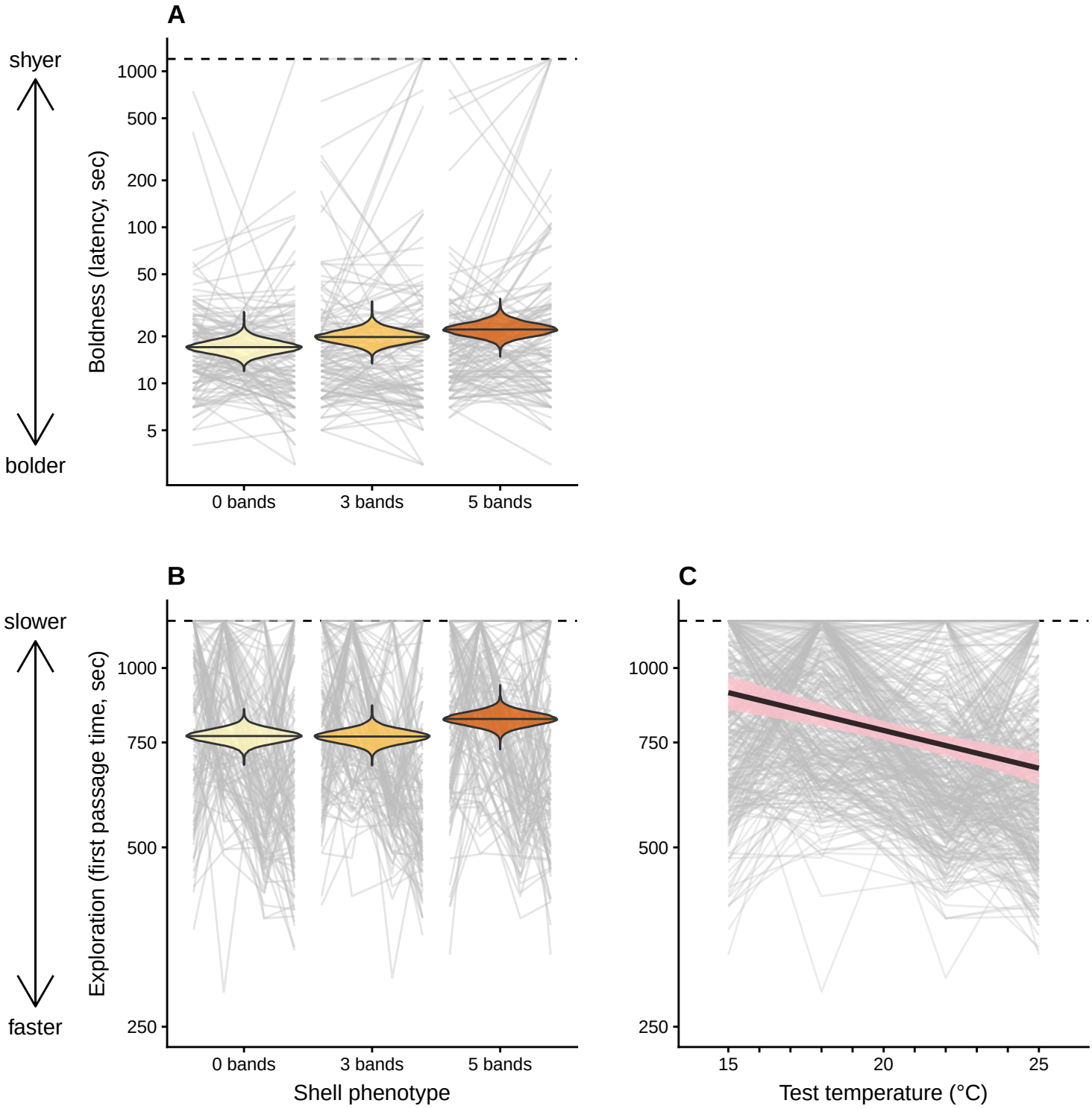
743 **Figure 2.** (A; B) posterior distributions of median boldness (A) and exploration (B) in relation to shell
744 morph. The model estimates the mean log-latencies, which correspond to the medians on the
745 observed latencies scale. (C) Mean and 95% credible band for the relationship between exploration
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)

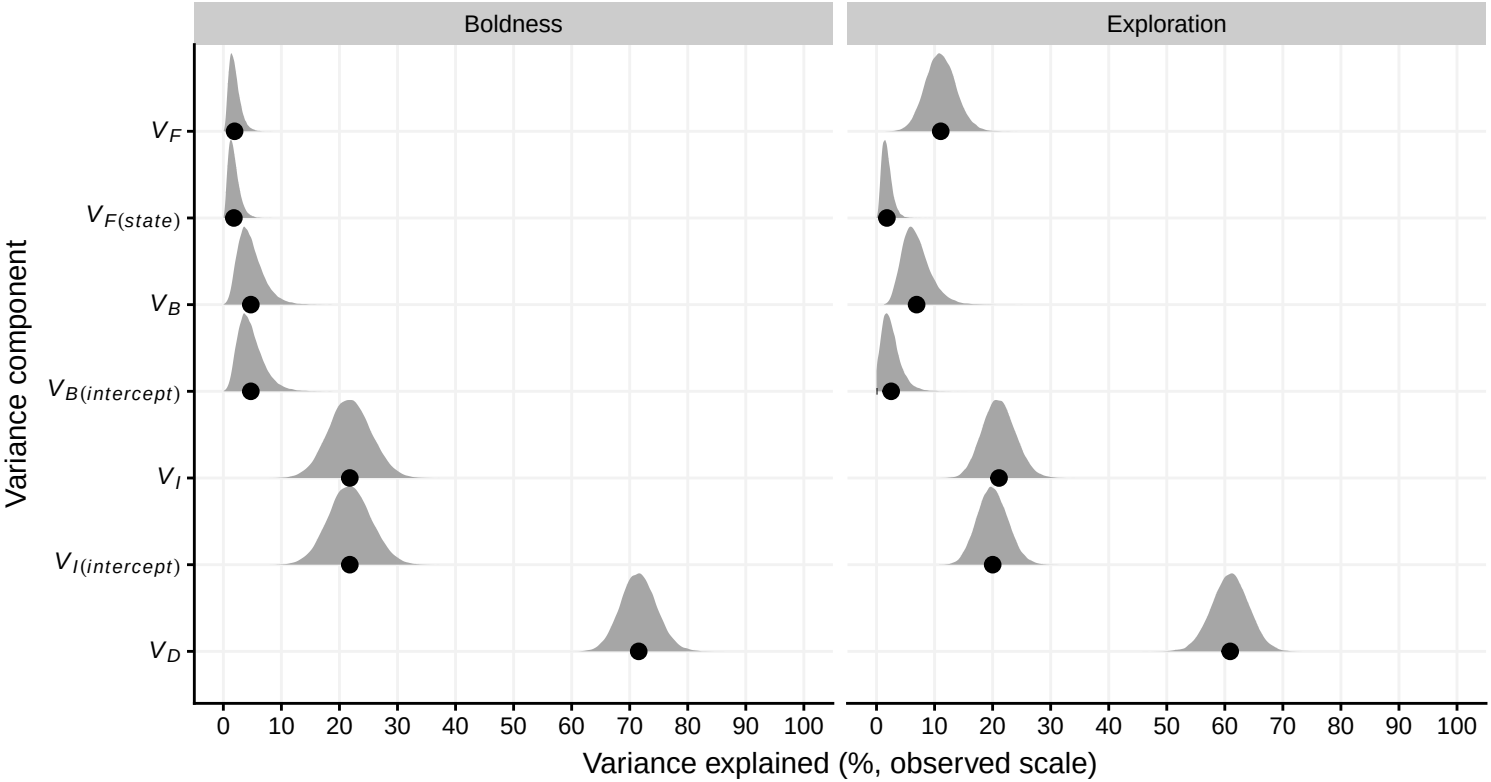
748 **Figure 3.** Mean (points) and posteriors for the proportion of variance explained by the different
749 variance components. For boldness, V_B and $V_{B(intercept)}$ are exactly equal by definition (same for V_I and
750 $V_{I(intercept)}$); see Methods and Table 2 for details on this and the names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

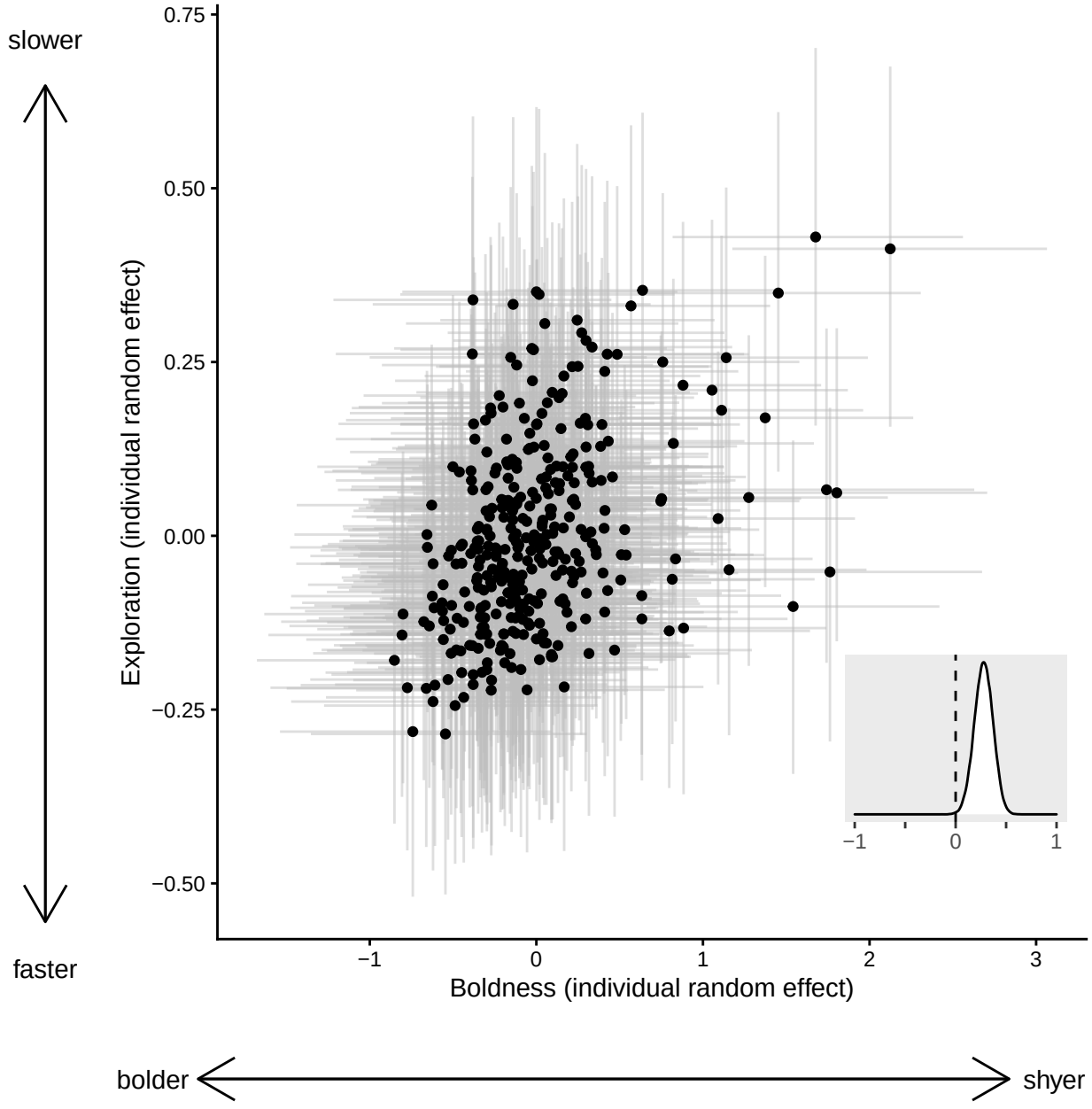
751 **Figure 4.** Correlation between individual-level random effects for boldness and exploration,
752 illustrated by plotting their respective Best Linear Unbiased Predictors and 95% credible intervals.
753 Inset: posterior distribution of the correlation coefficient. BLUPs are plotted, and correlation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

755


A
B
C
D
E


A
shyer
bolder
Boldness (latency, sec)
1000
500
200
100
50
20
10
5
0 bands
3 bands
5 bands
B
slower
faster
Exploration (first passage time, sec)
1000
750
500
250
0 bands
3 bands
5 bands
Shell phenotype
C
1000
750
500
250
15
20
25
Test temperature (°C)


Boldness
Exploration
Variance component
V_F
$V_{F(state)}$
V_B
$V_{B(intercept)}$
V_I
$V_{I(intercept)}$
V_D
0 10 20 30 40 50 60 70 80 90 100
Variance explained (%, observed scale)


slower
faster
0.75
0.50
0.25
0.00
−0.25
−0.50
Exploration (individual random effect)
−1
0
1
2
3
Boldness (individual random effect)
−1
0
1
bolder
shyer