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 individual behavioral variation (or animal personalities) in populations, and predicting its consequences, are key challenges in behavioral ecology. Studying the association between repeatable behavior and other traits under selection may shed light on these selective pressures. We used the model snail *Cepaea nemoralis* to examine whether individual behavioral is associated with shell morph, a key trait that has been extensively studied in relation to 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 contrasted thermal environments. We show that both behaviors were repeatable at the individual level in *C. nemoralis*. Behavior was associated with shell morph, with the darker morph (five-banded) being consistently shyer and slower to explore. There was no evidence that experienced thermal environment influenced behavior at the individual level, whether we considered past environment or experimental temperature. Boldness and exploration were correlated at the individual level in a common syndrome. 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 results 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 actually 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 inter-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 also vary among individuals (variation in "behavioral reaction norms"; Dingemanse, Kazem, Réale, & Wright, 2010). Moreover, behaviors are often correlated together and with other traits in 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 individual behavioral variation (Sih et al., 2015; Wolf & McNamara, 2012; Wolf & Weissing, 2010). If costs and benefits of behaviors vary depending on individual state variables, including morphology, size, past experienced environment… which may be less labile or even fixed at the individual level, then we should expect individuals differing in state to adaptively differ in behavior 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 common 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 morphological defenses (e.g. Ahlgren, Chapman, Nilsson, & Brönmark, 2015). 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 some species in which this may be difficult, we believe a fruitful alternative may be to study the association between personality and state traits already known to be fully genetically determined with little to no plasticity, and to study it across a range of environments known to select on the state variable.

The grove snail *Cepaea nemoralis* (Linnaeus 1758) (family Helicidae) has a long history as a model in evolutionary biology, in relation to its conspicuous shell polymorphism (reviewed by Jones, Leith, & Rawlings, 1977; Ożgo, 2009)(Fig. 1A-B). Genetic variation in terms of 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 in Mendelian terms (Jones et al., 1977). 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 (darker) snails are as a consequence selectively advantaged in hotter/sunnier (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; Ozgo & Kinnison, 2008; Schilthuizen, 2013), or historical comparisons in the context of climate change (Ożgo, Liew, Webster, & Schilthuizen, 2017; Ożgo & Schilthuizen, 2012). Local variations in morph frequencies have also been tied to predation pressure, with both frequency-dependent and crypsis-based visual selection thought to play a role (Jones et al., 1977; Surmacki, Ożarowska-Nowicka, & Rosin, 2013, and references therein; but see Cook, 2008). In addition to visual selection,

there are indications that shell color morphs vary in the physical resistance they oppose to predators, possibly because pigments (e.g. melanins) also influence the structural properties of shells (Kerkvliet et al., 2017; Williams, 2017). For instance, shells with more dark bands are more resistant to crushing in the areas of the shell attacked by rodent predators (Rosin, Kobak, Lesicki, & Tryjanowski, 2013).

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

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

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

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

124 (iii) As boldness may increase predation risk (Hulthén et al., 2017; Smith & Blumstein, 2008), we can
125 expect boldness to be counter-selected in habitat × morph combinations more exposed to predation,
126 or an association between boldness and non-behavioral defense traits compensating for these costs.
127 Predictions here differ depending on the importance of frequency-dependency versus crypsis in
128 shaping predation: we should expect the rarer morphs to be bolder, if frequency-dependent
129 predation drives the evolution of shell morphs, while we should expect the less conspicuous snails to
130 be bolder if crypsis is prominent. Unbanded snails are expected to be more cryptic to avian
131 predators, especially on dry vegetation (Surmacki et al., 2013). On the other hand, the phenotypic
132 compensation hypothesis predicts that bolder morphs should have better defended shells (Ahlgren
133 et al., 2015). In *Cepaea nemoralis*, this leads to the prediction that snails with increased number of
134 bands, which have on average thicker shells (Rosin et al., 2013), would be bolder.

135 **Methods**

136 *Sampled sites and snail maintenance under laboratory conditions*

137 Snails were sampled in fall 2016 in and close to the village of Arçais, France (Fig. 1C), located roughly
138 in the middle of the recorded latitudinal range of *Cepaea nemoralis* (GBIF Secretariat, 2020). We
139 studied two sites located about 2 km apart and differing in terms of vegetation cover. One was a
140 garden with few isolated trees, and thus under relatively direct sun exposure all year long (hereafter
141 the "open habitat"; approximate location: 46° 17' 50"N, 0° 41' 30" W, Fig. 1D). The other was a 200

142 by 150 m deciduous forested lot, and thus fully shaded a large part of the year, especially the hottest
143 spring and summer months ("shaded habitat"; approximately 46° 18' 01" N, 0° 42' 56" W, Fig. 1E).
144 We only sampled snails with the three most abundant shell banding patterns: shells with no bands,
145 three bands on the lower side of the shell, and five bands (Fig. 1B). Following previous authors (e.g.
146 Kavaliers, 1992), we here focused for simplicity solely on band presence, and thus sampled only
147 snails with yellow background shells, which are the most common in the study region (Silvertown et
148 al., 2011; personal observations) and on which the contrast between shell background and dark
149 bands is the strongest. Only adult snails were selected (recognizable by a reflected "lip" on their shell
150 opening). Sampling for the present study was targeted and adjusted in the field to obtain roughly
151 equal numbers of each banding pattern from both landscapes; it therefore did not allow us to make
152 inferences on their relative abundances. The same sites were however sampled again in 2018 for a
153 separate experiment, this time with random sampling with respect to banding pattern. As in previous
154 studies (e.g. Schilthuizen, 2013) and reflecting potential thermal selection, the darker five-banded
155 snails were more frequent in the shaded habitat than in the open habitat (22.3 vs. 13.5 %; see
156 Supplementary Material S1).

157 We then kept snails under winter dormancy conditions (6 ± 1°C, no food or water sources) until
158 March 2017, about 3 weeks before the start of the experiment. We then divided them in groups of
159 15 individuals from the same landscape, 5 (randomly chosen) of each shell phenotype. Groups were
160 kept under controlled conditions (20 ± 1°C, L:D 16:8) in 8.5 × 15 × 12 cm polyethylene boxes lined
161 with 1-2 cm of soil kept humid at the bottom. Snails had *ad libitum* access to prepared snail food
162 (cereal flour supplemented with calcium, Hélinove, Saint Paul en Pareds, France) in a Petri dish. We
163 gave each snail a unique ID written on the side of their shell with a paint marker (uni Posca,
164 Mitsubishi Pencil Co., Ltd, Tokyo, Japan; Henry & Jarne, 2007). A total of 360 snails (60 for each
165 habitat × shell phenotype combination) were used in the experiments described below. By necessity,
166 the observer (see below) was not blind to individual habitat of origin/phenotype; note that the
167 analyst (MD) did not contribute to the actual observations.

168 *Behavioral tests: boldness*

169 We studied boldness using simulated predator attacks as in Dahirel et al. (2017). All tests were done
170 by the same operator (V.G.) to avoid effects of inter-experimenter variability. Snails were assayed
171 during the last four hours of the photophase. To stimulate activity, we first placed them in a Petri
172 dish with water for 5 minutes, before putting them on individual clean glass plates. After snails had
173 moved at least one shell length (≈20 mm) from their starting position, the operator used a pipette tip
174 to pinch them for 5 seconds on the right side of the foot. Preliminary tests confirmed that this was
175 the shortest time needed to ensure all snails retracted fully in their shell. We then recorded the time
176 snails took to exit the shell and resume activity after the attack (from retraction to the full extension
177 of all tentacles out of the shell), as our measure of boldness (snails with shorter latencies being
178 considered bolder). We stopped observations after 20 min. Snails from the same test box were
179 tested on the same day, and replaced in their box after testing. To estimate the repeatability of
180 boldness, snails were tested a second time after seven days, using the same protocol. The initial
181 order in which groups were tested within a sequence was random; this order was conserved for all
182 subsequent tests.

183 *Behavioral tests: exploration/speed*

184 We studied snail movement at four temperatures within the activity range of *C. nemoralis* (Cameron,
185 1970): 15, 18, 22 and 25 °C. All tests were again performed by the same operator (V.G.). Movement
186 tests started 7 days after the last boldness test for a given individual, successive movement tests
187 were separated by 24h. Half of the boxes, equally distributed between landscapes of origin, were
188 tested in increasing temperature order (from 15 to 25 °C), the other half in decreasing order (25°C to
189 15°). Twenty-four hours before a given test, we placed snails and their box at the testing
190 temperature for habituation, using temperature-controlled cabinets (ET 619-4, Lovibond, Dortmund,
191 Germany). For testing, each snail was placed individually at the center of a clean 25 × 25 cm
192 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 times 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 *stricto sensu* with movement speed (as both slow-moving individuals and thorough explorers would have higher first-passage times).

Ethical note

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).

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 and environment on behavior, quantify behavioral (co)variances and partition them across hierarchical levels (inter-box and inter-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

217 “link” to speed measure 1 than boldness measure 2; scenario 4 of table 2 in Dingemanse &
218 Dochtermann, 2013). We present a full write-up of the model as Supplementary Material S2; a verbal
219 description follows below.

220 Boldness and exploration were analyzed assuming a lognormal distribution to account for the
221 skewed distribution of time to event data. We accounted for the fact that monitoring was stopped
222 before some individuals could express the behavior of interest by including a censored data indicator
223 in the model. Fixed effects for both behaviors included shell banding (three-level categorical
224 variable), landscape of origin (binary variable), and their interaction, as well as test order (1 or 2 for
225 boldness, 1 to 4 for exploration / speed). The model for exploration additionally included a test
226 temperature effect as well as interactions between this effect, shell banding and landscape effects.
227 Categorical variables (shell banding, landscape of origin) were converted to centered dummy
228 variables, and numeric variables (test order, temperature) were centered, following Schielzeth
229 (2010)(temperature was additionally scaled to unit 1SD). This has two benefits. First, it makes main
230 effect coefficients directly interpretable even in the presence of interactions (Schielzeth, 2010).
231 Second, for categorical variables, having the intercept on an “average” rather than on one arbitrary
232 default category avoids the problem of putting a more precise prior on the reference category (which
233 would be defined by the intercept only) than on the others (which would be defined by the intercept
234 and one or several other coefficients)(McElreath, 2020). Random effects included box-level and
235 individual-level intercepts as well as, in the case of exploration, the associated slopes for
236 temperature. This allowed us to estimate among-box and among-individual variation in mean
237 behavior and thermal behavioral reaction norms as well as the box- and individual-level covariances
238 among them (Dingemanse & Dochtermann, 2013).

239 We used a Normal(μ = ln(400), σ = 0.5) prior for the fixed effects intercepts (mean log- latencies), so
240 that ~99% of the probability mass was within the range of latencies that could actually be observed
241 by design during the experiment (i.e. 0 to 1200 sec, see above), but not totally 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 a 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).

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

We ran four chains for 12000 iterations, with the first 2000 iterations of each chain used for warmup. We checked mixing graphically and confirmed chain convergence using the improved $\widehat{R}$ statistic by Vehtari et al. (2020). The chains were run longer than the default number of iterations (2000), to ensure effective sample size was satisfactory for all parameters (both bulk- and tail-effective sample sizes sensu Vehtari et al., 2020 > 1000). All credible intervals given are highest posterior density intervals.

Results

Exploration was influenced by shell morph (Table 1, Fig. 2). Five-banded snails were on average slower to explore their surroundings than either unbanded or three-banded snails (Fig.2). Snails also became slower as tests went on (Table 1). There was no clear evidence of a landscape of origin effect. Snails explored faster with increasing temperature (Table 1, Fig. 2). 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). Unbanded snails were bolder than five-banded snails, with three-banded snails presenting intermediate values. Again, there was no evidence for landscape of origin, 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 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). Variation among boxes was small but non negligible, in the same range as the proportion of variation explained by fixed effects for both behaviors. Average exploration and boldness were positively correlated at the individual level (Table 3, Fig. 4). There was no evidence that individual-

level variation in responses to temperature was correlated with either mean exploration times or mean boldness (Table 3). There was no evidence for box-level correlations among traits (Table 3).

Discussion

We showed that behaviors linked to boldness and exploration/activity are repeatable in *Cepaea nemoralis*, confirming once again that personality variation is common even in invertebrates (Kralj-Fišer & Schuett, 2014). This result has implications for the evolutionary potential of behaviors in *C. nemoralis*, given repeatability sets the higher limit for the heritability of behaviors (Ned A. Dochtermann, Schwab, & Sih, 2015). Additionally, we demonstrated that these traits are positively correlated in a common syndrome, and that their expression varies depending on shell banding, a Mendelian trait that has been the focus on much research in this species in relation to predation and thermal selection (Ożgo, 2009). Given how behavior can shape effective thermal tolerance (Abram et al., 2017) or vulnerability to predation (e.g. Hulthén et al., 2017), we believe these behavioral differences must be taken in account when discussing the evolution of shell color in this model species.

Unbanded snails were both bolder and explored faster than five-banded snails (Table 1, Fig. 2). Three-banded snails behaved similarly to unbanded snails with respect to boldness (but were intermediate between unbanded and five-banded snails for exploration). This shows the "effectively unbanded" category sometimes used in *Cepaea* studies (Cain & Sheppard, 1954) has at least some behavioral relevance (that category groups together snails with little to no banding on the side of their shell exposed to the sun). Exploration and boldness were positively correlated both at the among-individual (Table 2) and among-morph levels (the shyest morph was also the slowest, Fig. 2). At the individual level, while some clutches were laid during the experiments, we were not able to test if this behavioral syndrome was integrated into a broader pace of life syndrome *sensu* Réale et al. (2010) by linking behavioral and life history variation. Indeed, we were unable to ascertain the maternal and especially paternal origin of most clutches, and were not able to follow snail fecundity

318 or longevity over their entire life. There is however some indications in the literature that more
319 active/ mobile snails are faster-growing (Oosterhoff, 1977), as predicted by the pace-of-life syndrome
320 hypothesis. At the morph level, it appears that contrary to behaviors, shell morphs do not differ
321 much in terms of average fecundity or growth rate (Oosterhoff, 1977; Wolda, 1967). They however
322 differ markedly in their physiology, based on their response to pharmaceutical assays: the morphs
323 we show here to be faster/bolder also have more responsive endogeneous opioid systems (Kavaliers,
324 1992). Further research is needed to understand the drivers of these correlations and their
325 consequences (Royauté et al., 2018; Wright et al., 2019).

326 Five-banded snails, which have been shown to have on average more resistant shells against rodent
327 attacks (Rosin et al., 2013), were shyer than unbanded snails (Fig. 2). At first glance, these results go
328 against the phenotypic compensation hypothesis which predicts boldness should be associated with
329 better defenses against predators, in particular thicker shells, mitigating the costs of risk taking
330 behavior (Ahlgren et al., 2015; De Winter, Ramalho Martins, Trovo, & Chapman, 2016; Hulthén,
331 Chapman, Nilsson, Hollander, & Brönmark, 2014). However, birds, in particular thrushes (genus
332 *Turdus*) are likely more important predators than rodents (Rosin, Olborska, Surmacki, & Tryjanowski,
333 2011); given they are visual predators, shell visual characteristics may be more important than
334 structural resistance in influencing behavioral response to predation. Both frequency-dependent
335 predation and direct visual selection have historically been invoked as explanations for predator-
336 dependent morph variation in *Cepaea* (Jones et al., 1977; Ożgo, 2009), but discussions often used
337 human vision as a baseline. More recently, visual selection explanations have received increased
338 support from an experiment using models of avian vision to rigorously test how thrushes actually see
339 different shell morphs (Surmacki et al., 2013). In both our test sites, the boldest morph (unbanded
340 shell) is the least conspicuous (based on Surmacki et al., 2013), not the rarest. This supports crypsis-
341 based explanations over frequency-dependent selection, under the assumption that phenotypes
342 already more at risk of predation should be shyer given boldness increases predation risk (Hulthén et
343 al., 2017). We must nonetheless remember that (i) our knowledge of how thrushes actually perceive

344 snails is very limited (Surmacki et al., 2013), (ii) we only tested a small set of the available morphs,
345 which do not include the rarest background colors (pink and brown), and (iii) shell banding is a trait
346 under multiple selection pressures, including thermal selection (see below).

347 Exploration speed was temperature-dependent: as expected from an ectothermic species, snails
348 were on average faster at higher temperatures (Fig. 2). The temperature reaction norm of
349 exploration was remarkably conserved among individuals (most of the inter-individual variance V_I
350 was due to differences in average behavior, rather than in temperature slopes; Table 2, Fig. 3). In
351 addition, there was surprisingly no evidence that behavioral differences among morphs are
352 influenced by the thermal environment, whether we consider the previously experienced
353 environment (no habitat × morph interaction) or the current environment (no effect of morph
354 identity on thermal reaction norms) (Table 1). This is despite abundant evidence in the literature for
355 thermal selection on shell morphs, based on field comparisons (Kerstes et al., 2019; for this study,
356 see Methods; e.g. Richardson, 1974; Schilthuizen, 2013), but also experimental evidence of both
357 survival (Lamotte, 1959; Tilling, 1983) and fecundity (Wolda, 1967) thermal selection. In addition,
358 studies giving snails a choice between multiple temperatures show snail morphs do have different
359 thermal preferences that align with expectations based on thermal selection (Kavaliers, 1992). Some
360 studies suggest that snails use shade and humidity just as much (and potentially more) as
361 temperature as cues to adjust their behavior to microclimate (Ożgo & Kubea, 2005; Rosin et al.,
362 2018). Our exploration tests were short, under standardized lighting conditions and with no water,
363 and snails were brought back to favorable humidity soon after. It is possible longer experiments, or
364 experiments comparing the responses of snails from different habitats to realistic climate variation
365 (including shade and/or humidity) would yield different responses. Maybe more importantly, we only
366 tested temperatures favorable for activity, i.e. the limited part of the thermal niche closer to the
367 optimum. Morph differences in behavior might be stronger closer to critical minimal or maximal
368 temperature thresholds (Tilling, 1983). This can be investigated by using a wider range of
369 temperatures and expanding the reaction norm approach used here to either a character state

370 approach (e.g. Houslay, Earley, Young, & Wilson, 2019) or a non-linear reaction norm approach
371 (Arnold, Kruuk, & Nicotra, 2019); both would account for the typical non-linearity of complete
372 thermal performance curves (Arnold et al., 2019). It is very important to note, however, that these
373 results do not mean populations from landscapes differing in sun exposure are identical in behavior,
374 even for the range of situations we tested. Indeed, because morphs differ in their behavior, and
375 because morph frequencies differ among landscapes (see Methods), the average snail from a sun
376 exposed population may well be bolder and more active than its counterpart from a shaded
377 population.

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

386 Assuming this genetic link is confirmed, any discussion about how selection on morph may influence
387 the evolution of behavior (or vice versa) must be tempered by the fact that the greater part of the
388 repeatable inter-individual variation in behavior was not actually explained by shell morph (see Fig. 3,
389 Table 1). It is in a way unsurprising, as we did not expect a single discrete trait to entirely constrain
390 individual behavioral variation. Indeed, the expression of animal personalities can be influenced by
391 many unobserved drivers and state variables which should have a priori limited links to shell morph
392 and its own drivers (Burns et al., 2012; Petelle, Martin, & Blumstein, 2019; Sih et al., 2015; Wright et
393 al., 2019). Furthermore, some level of stochastic behavioral individuality is inevitable even in the
394 total absence of meaningful genetic and environmental variation (Bierbach, Laskowski, & Wolf,

395 2017). What must be noted, though, is that some of this "remaining" individual variation may still,
396 actually, relate to shell morph. Indeed, because of dominance within loci and especially epistatic
397 relationships among loci, individuals that share the same shell phenotype may actually vary greatly in
398 terms of underlying genotype at morph-determining loci (e.g. having one dominant allele at the
399 « band presence » locus leads to total band absence and masks variation at all other banding genes;
400 Jones et al., 1977). However, while much is known of among-morph variation in thermal tolerance,
401 life history, physiology (Kavaliers, 1992; Kerstes et al., 2019; Lamotte, 1959; Oosterhoff, 1977;
402 Richardson, 1974; Tilling, 1983; Wolda, 1967), nothing as far as we can tell is known about within-
403 morph, but among-genotype variation. Investigations using individuals of known genotype obtained
404 through repeated crosses or, as our knowledge of the actual molecular underpinnings increases,
405 through direct genotyping (Gonzalez, Aramendia, & Davison, 2019; Kerkvliet et al., 2017), may shed
406 light on this "hidden" genetic variation and whether it contributes to the persistence of morph-
407 related behavior differences.

408 Increased boldness and activity have been tied to higher probability of dispersal in many species
409 (Cote, Clobert, Brodin, Fogarty, & Sih, 2010), including land snails (Dahirel et al., 2017), and non-
410 random dispersal is now acknowledged as a potentially widespread force behind population
411 phenotypic divergence (Edelaar & Bolnick, 2012; Jacob, Bestion, Legrand, Clobert, & Cote, 2015).
412 Bolder animals are thought to trade increased success against a greater predation risk (Hulthén et al.,
413 2017; but see Moiron, Laskowski, & Niemelä, 2020; Smith & Blumstein, 2008); predation is generally
414 considered a key driver of morphological differences in *Cepaea*, and plays a key role in dispersal
415 across taxa (Fronhofer et al., 2018). Although active dispersal can safely be dismissed as a driver of
416 continental-scale differences in morph frequencies, our results point to *Cepaea* as a good model to
417 understand how existing behavioral differences may drive local-scale morphological differences (and
418 vice versa). By building on, and complementing, a decades-long history of evolutionary research, this
419 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.

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Tables

Table 1: Estimated fixed effect parameters of the model explaining exploration and boldness latencies (mean and 95% credible intervals). Continuous explanatory variables are centered and scaled, and categorical variables converted to centered dummy variables; the intercept then refers to 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)	6.670 (6.630 ; 6.700)	2.980 (2.830 ; 3.140)
banding = 3 bands	-0.002 (-0.064 ; 0.057)	0.149 (-0.054 ; 0.358)
banding = 5 bands	**0.066 (0.004 ; 0.125)**	**0.260 (0.059 ; 0.472)**
landscape of origin = shaded	0.056 (-0.017 ; 0.128)	0.196 (-0.108 ; 0.483)
test temperature	**-0.112 (-0.150 ; -0.072)**	--
test order	**0.036 (0.006 ; 0.067)**	0.079 (-0.033 ; 0.198)
Fixed effects: interactions		
banding = 3bands × landscape = shaded	-0.071 (-0.191 ; 0.048)	0.157 (-0.247 ; 0.561)
banding = 5bands × landscape = shaded	-0.008 (-0.130 ; 0.114)	0.239 (-0.164 ; 0.644)
banding = 3bands × temperature	0.002 (-0.039 ; 0.042)	--
banding = 5bands × temperature	0.013 (-0.028 ; 0.053)	--
landscape = shaded × temperature	-0.053 (-0.130 ; 0.023)	--
banding = 3bands × landscape = shaded × temperature	-0.023 (-0.107 ; 0.056)	--
banding = 5bands × landscape = shaded × temperature	0.020 (-0.063 ; 0.101)	--

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	13596 (6340 ; 21088)	49 (6 ; 108)
- explained by state	2179 (337 ; 4332)	46 (4 ; 103)
Box-level V_B	8439 (2782 ; 15010)	128 (12; 310)
- random intercept only	3085 (0 ; 7028)	128 (12; 310)
Individual V_I	25748 (18111 ; 33850)	542 (260; 867)
- random intercept only	24400 (17412 ; 32270)	542 (260; 867)
Residual V_D	73943 (63481 ; 84587)	1795 (970 ; 2851)
Total variance V_P	121726 (102528 ; 141858)	2514 (1356 ; 4010)
Repeatabilities (observed scale)		
$R_{(within\text{-}state)}$	0.200 (0.150 ; 0.253)	0.218 (0.147 ; 0.290)
$R_{(total)}$	0.218 (0.165 ; 0.271)	0.236 (0.166 ; 0.307)
$R_{(within\text{-}state)}$ / $R_{(total)}$	0.918 (0.842 ; 0.984)	0.923 (0.841 ; 0.989)

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		0.119 (-0.402 ; 0.653)	0.384 (-0.059 ; 0.780)
Exploration, intercept	**0.279 (0.096 ; 0.457)**		-0.184 (-0.688 ; 0.326)
Exploration, temperature slope	-0.202 (-0.681 ; 0.312)	0.286 (-0.207 ; 0.785)	

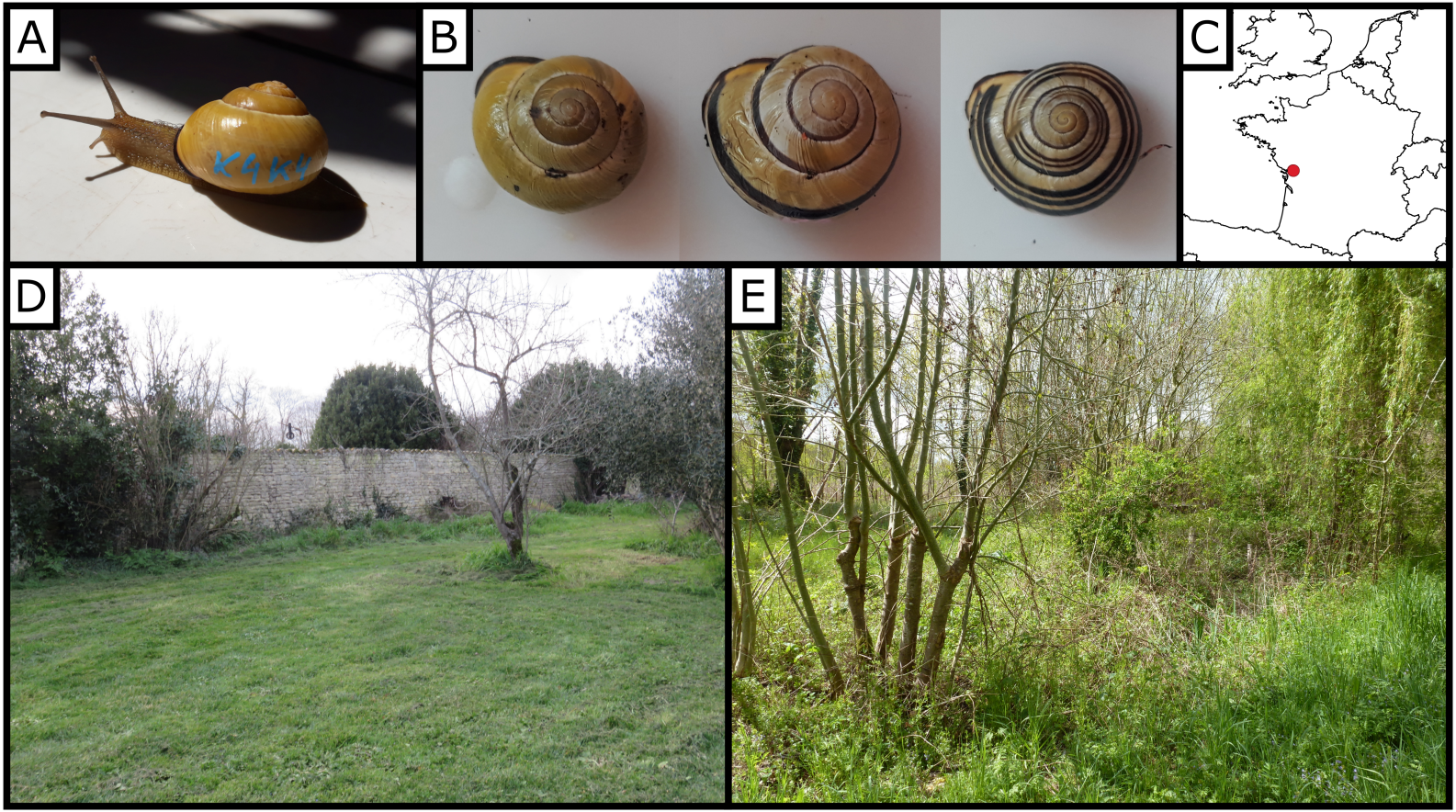
Figure legends

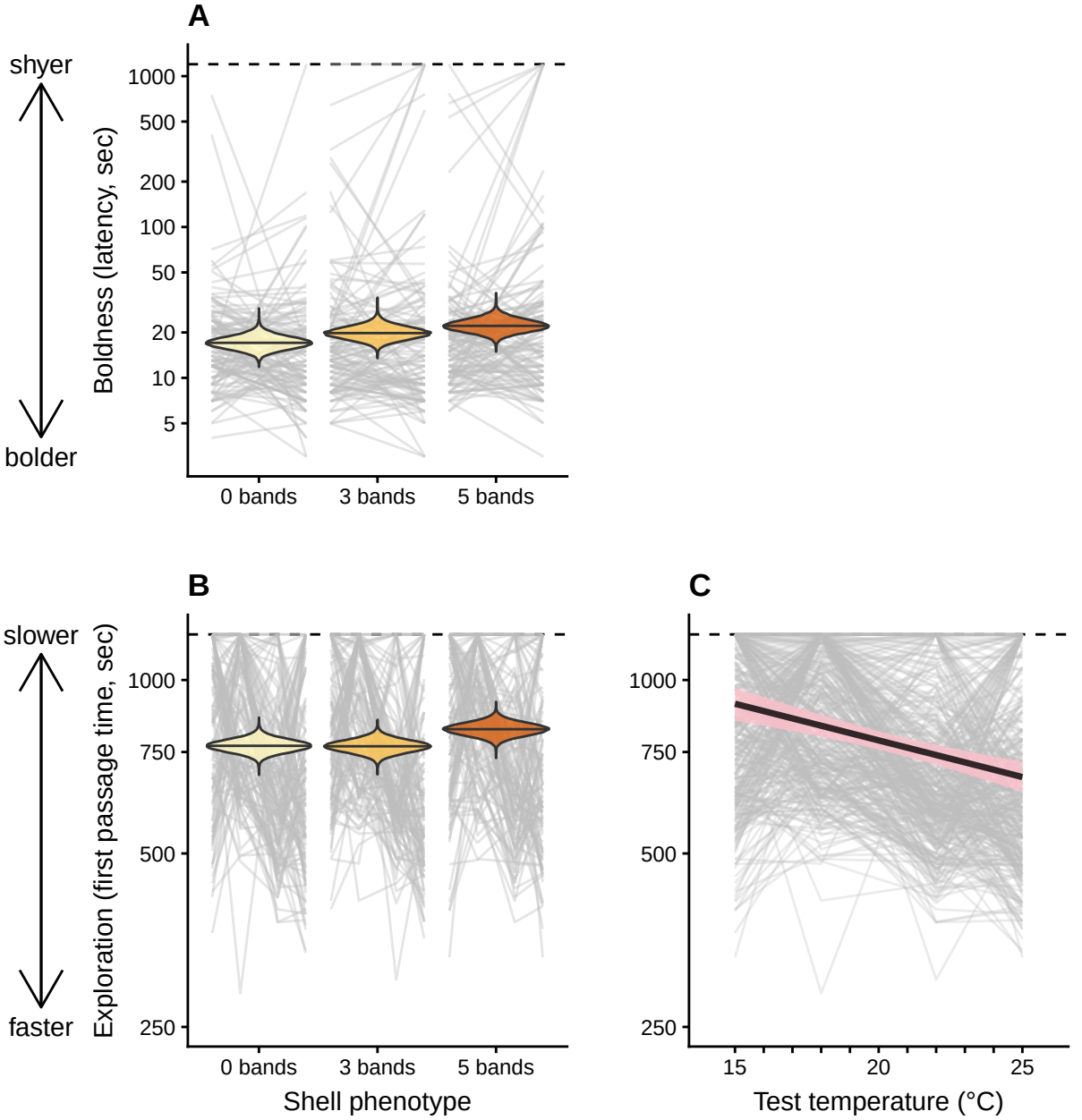
Figure 1. Study species and sites. (A) An unbanded yellow *Cepaea nemoralis*, showing the position of individual paint marks on the shell (B) Representative shells of the three studied morphs as seen from above: yellow unbanded, three-banded, and five-banded snails (C) Study sites location in France;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

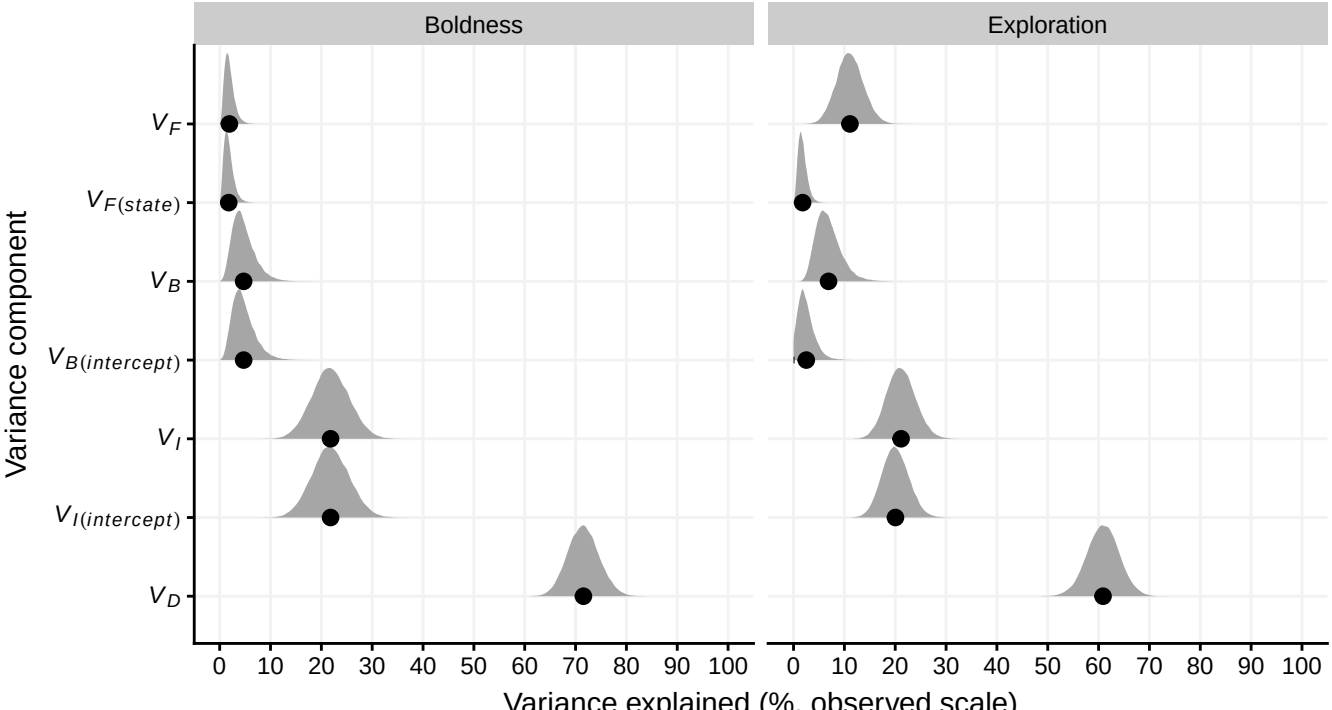
Figure 2. (A;B) posterior distributions of median boldness (A) and exploration (B) in relation to shell morph. The model estimates the mean log-latencies, which correspond to the medians on the observed latencies scale. (C) Mean and 95% credible band for the relationship between exploration latency and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

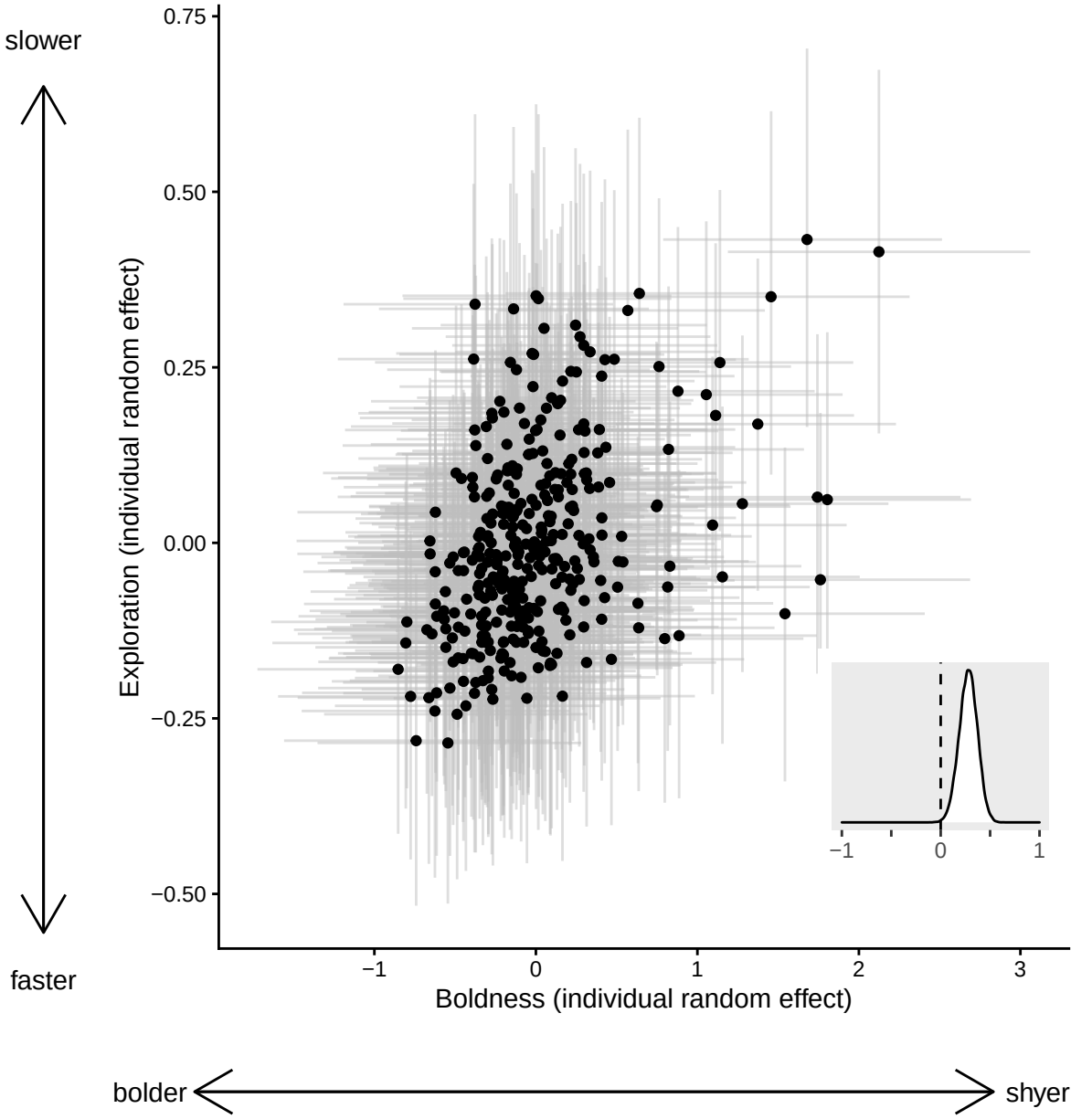
Figure 3. Mean (points) and posteriors for the proportion of variance explained by the different variance components. See Table 2 or Methods for the names of the variance components.

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


A
K4K4
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