Boldness and exploration are linked to shell morph but not environmental context in the snail *Cepaea nemoralis*

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Abstract

1 - Understanding the maintenance of individual behavioural variation (or animal personalities) in populations, and predicting its consequences, are key challenges in behavioural ecology.

2 - As individuals vary in their phenotype and experienced environment, they may experience different selective pressures favouring different optimal behaviours. Studying the (genetic) association between repeatable behaviour and other traits under selection may shed light on these selective pressures.

3 - We used the model snail *Cepaea nemoralis* to examine whether individual behavioural variation is associated with variation in 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.

4 - We show that there are animal personalities in *C. nemoralis*, as both behaviours were repeatable at the individual level. Behavioural variation 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 behaviour 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.

5 - We discuss how these results are compatible with (but do not confirm) the pace of life syndrome hypothesis, and what they 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 behaviour, 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 behaviour in response to environmental changes.

Keywords animal personality; behavioural syndromes; multivariate multilevel model ; shell colour; temperature

Introduction

A key question in behavioural ecology, and more broadly in evolutionary ecology, is how to explain the persistence of variation in phenotypic traits. Although behaviour 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 behaviours to environmental conditions would be adaptive, and the ability to tune behaviour to conditions may itself also vary among individuals (variation in "behavioural reaction norms"; Dingemanse, Kazem, Réale, & Wright, 2010). Moreover, behaviours 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 behavioural phenotypes that are on display in populations (N. A. Dochtermann & Dingemanse, 2013).

State-dependent behaviour is often invoked as one of the key mechanisms/frameworks potentially explaining both adaptive correlations/ feedbacks between behaviours and other traits, and the maintenance of individual behavioural variation (Sih et al., 2015; Wolf & McNamara, 2012; Wolf & Weissing, 2010). If costs and benefits of behaviours 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 behaviour as well (Wolf & Weissing, 2010). The pace-of-life hypothesis, which ties several axes of behavioural 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 behavioural changes or morphological defences,

leading to a positive association between risk-taking behaviour and morphological defence (e.g. Ahlgren, Chapman, Nilsson, & Brönmark, 2015). Quantitative genetics and/or experimental evolution approaches may provide evidence of the evolution of state-behaviour 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 colour (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 colour (Kerkvliet, Boer, Schilthuizen, & Kraaijeveld, 2017; Richards et al., 2013).

In *C. nemoralis*, lighter coloured 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 colour 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 behaviour (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 behavioural syndromes. In particular, individuals are generally assayed once, meaning separating within- from-among individual variation, and individual variation in average behaviour 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 behavioural analyses, meaning there is often no way to determine how behaviour responds to selection pressures on shell colour.

In this context, we investigated the existence and magnitude of personality variation and behavioural syndromes in *C. nemoralis*, how behaviour 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:

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

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

117 (iii) As boldness has survival costs likely due to predation (Hulthén et al., 2017; Smith & Blumstein,
118 2008), we can expect boldness to be counter-selected in habitat × morph combinations more
119 exposed to predation, or an association between boldness and non-behavioural defence traits
120 compensating for these costs. Predictions here differ depending on the importance of frequency-
121 dependency versus crypsis in shaping predation: we should expect the rarer morphs to be bolder, if
122 frequency-dependent predation drives the evolution of shell morphs, while we should expect the less
123 conspicuous snails to be bolder if crypsis is prominent. Unbanded snails are expected to be more
124 cryptic to avian predators, especially on dry vegetation (Surmacki et al., 2013). On the other hand,
125 the phenotypic compensation hypothesis predicts that bolder morphs should have better defended
126 shells (Ahlgren et al., 2015). In *Cepaea nemoralis*, this leads to the prediction that snails with
127 increased number of bands, which have on average thicker shells (Rosin et al., 2013), would be
128 bolder.

129 **Methods**

130 *Sampled sites and maintenance under laboratory conditions*

131 Snails were sampled in fall 2016 in and close to the village of Arçais, France (Fig. 1C), located roughly
132 in the middle of the recorded latitudinal range of *Cepaea nemoralis* (GBIF Secretariat, 2019). We
133 studied two sites located about 2 km apart and differing in terms of vegetation cover. One was a
134 garden with few isolated trees, and thus under relatively direct sun exposure all year long (hereafter
135 the "open habitat"; approximate location: 46° 17' 50"N, 0° 41' 30" W, Fig. 1D). The other was a 200
136 by 150 m deciduous forested lot, and thus fully shaded a large part of the year, especially the hottest
137 spring and summer months ("shaded habitat"; approximately 46° 18' 01" N, 0° 42' 56" W, Fig. 1E).
138 We only sampled snails with the three most abundant shell banding patterns: shells with no bands,
139 three bands on the lower side of the shell, and five bands (Fig. 1B). Following previous authors (e.g.
140 Kavaliers, 1992), we here focused for simplicity solely on band presence, and thus sampled only
141 snails with yellow background shells, which are the most common in the study region (Silvertown et
142 al., 2011; A. Ansart, personal observations) and on which the contrast between shell background and
143 dark bands is the strongest. Only adult snails were selected (recognizable by a reflected "lip" on their
144 shell opening). Sampling for the present study was targeted and adjusted in the field to obtain
145 roughly equal numbers of each banding pattern from both landscapes; it therefore did not allow us
146 to make inferences on their relative abundances. The same sites were however sampled again in
147 2018 for a separate experiment (M. Dahirel and A. Ansart, unpublished data), this time with random
148 sampling with respect to banding pattern. As in previous studies (e.g. Schilthuizen, 2013) and
149 reflecting potential thermal selection, the darker five-banded snails were more frequent in the
150 shaded habitat than in the open habitat (22.3 vs. 13.5 %; see Supplementary Material S1).

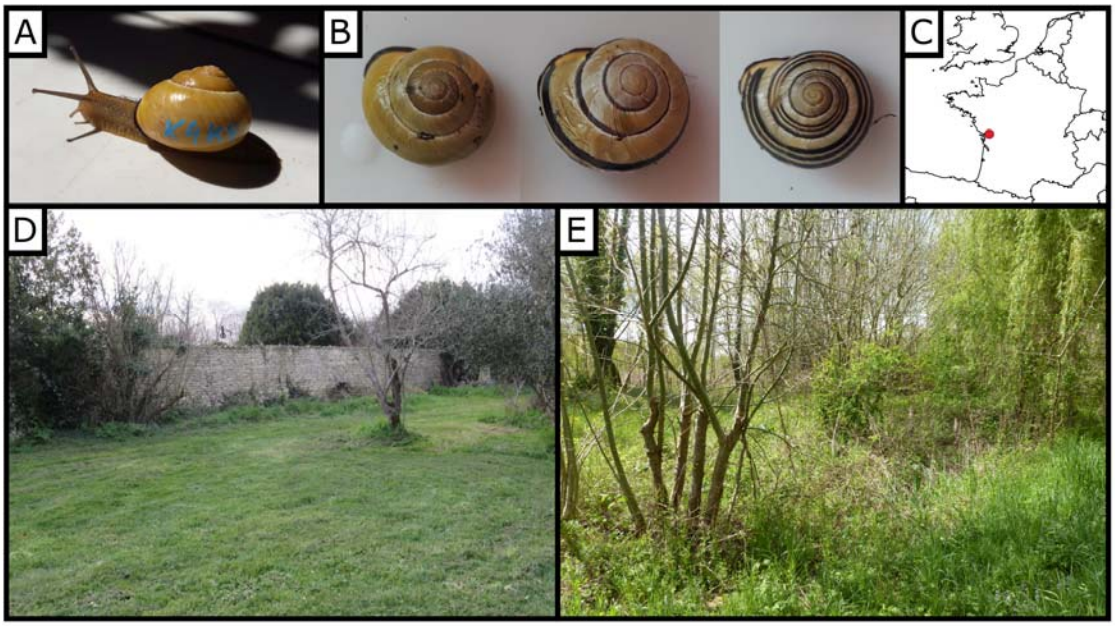


Figure 1. *Study species and sites. (A) An unbanded yellow* Cepaea nemoralis*, showing the position of individual paint marks on the shell (B) Representative shells of the three studied morphs as seen from above: yellow unbanded, three-banded, and five-banded snails (C) Study sites location in France;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

We then kept snails under winter dormancy conditions (6 ± 1°C, no food or water sources) until March 2017, about 3 weeks before the start of the experiment. We then divided them in groups of 15 individuals from the same landscape, 5 of each shell phenotype. Groups were kept under controlled conditions (20 ± 1°C, L:D 16:8) in 8.5 × 15 × 12 cm polyethylene boxes lined with 1-2 cm of soil kept humid at the bottom. Snails had *ad libitum* access to prepared snail food (cereal flour supplemented with calcium, Hélinove, Saint Paul en Pareds, France). We gave each snail a unique ID written on the side of their shell with a paint marker (uni Posca, Mitsubishi Pencil Co., Ltd, Tokyo, Japan; Henry & Jarne, 2007). A total of 360 snails (60 for each habitat × shell phenotype combination) were used in the experiments described below.

Behavioural tests: boldness

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

180 *Behavioural tests: exploration/speed*

181 We studied snail movement at four temperatures within the activity range of *C. nemoralis* (Cameron,
182 1970): 15, 18, 22 and 25 °C. All tests were again performed by the same operator (V.G.). Movement
183 tests started 7 days after the last boldness test for a given individual, successive movement tests
184 were separated by 24h. Half of the boxes, equally distributed between landscapes of origin, were
185 tested in increasing temperature order (from 15 to 25 °C), the other half in decreasing order (25°C to
186 15°). Twenty-four hours before a given test, we placed snails and their box at the testing
187 temperature for habituation, using temperature-controlled cabinets (ET 619-4, Lovibond, Dortmund,
188 Germany). For testing, each snail was placed individually at the center of a clean 25 × 25 cm
189 polyethylene box (height: 9 cm) and left free to move. Snails were deemed active once they had
190 moved more than 2 cm away from their starting point. We used the time snails took to move more
191 than 10 cm from their starting point, minus the time taken to start activity, as our exploration metric,

192 with lower times for snails that moved away faster. We stopped observations after 20 min post-
193 activity. This metric was chosen for its ease of implementation; we acknowledge that it conflates
194 exploration of the environment *stricto sensu* with movement speed (as both slow-moving individuals
195 and thorough explorers would have higher first-passage times).

196 *Ethical note*

197 This study complies with all relevant national and international laws, and the ASAB/ABS Guidelines
198 for the use of animals (2019) were adhered to as closely as possible. Potentially stressful
199 experimental treatments (boldness experiment) were limited to the shortest possible time to elicit
200 the behaviours of interest. No ethical board recommendation or administrative authorization was
201 needed to work on or sample *Cepaea nemoralis*. The marking method used is non-invasive and has
202 minimal to no documented effects on life-history traits (Henry & Jarne, 2007).

203 *Statistical analyses*

204 We analysed snail behavioural data in a Bayesian multilevel/mixed model framework, using Stan
205 (Carpenter et al., 2017), with R (version 3.5; R Core Team, 2019) and the `brms` R package (Bürkner,
206 2017) as frontends.

207 We used a multivariate generalized linear multilevel model to estimate the effect of shell phenotype
208 and environment on behaviour, quantify behavioural (co)variances and partition them across
209 hierarchical levels (inter-box and inter-individual variation) (Dingemanse & Dochtermann, 2013;
210 Thomas M. Houslay & Wilson, 2017). We did not estimate within-individual trait correlations, as
211 exploration and boldness were tested independently at the within-individual level (that is, boldness
212 measure 1 had no stronger "link" to speed measure 1 than boldness measure 2; scenario 4 of table 2
213 in Dingemanse & Dochtermann, 2013).

214 Boldness and exploration were analysed assuming a lognormal distribution to account for the
215 skewed distribution of time to event data. We accounted for the fact that monitoring was stopped

before some individuals could express the behaviour of interest by including a censored data indicator in the model. Fixed effects for both behaviours 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 / speed). The model for exploration additionally included a test temperature effect as well as interactions between this effect, shell banding and landscape effects. Categorical variables (shell banding, landscape of origin) were converted to centred dummy variables, and numeric variables (test order, temperature) were centred and scaled, following Schielzeth (2010). This has two benefits. First, it makes 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 the 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, 2016). 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 behaviour and thermal behavioural reaction norms as well as the box- and individual-level covariances among them (Dingemanse & Dochtermann, 2013). We present a formal write-up of the model as Supplementary Material S2.

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 could actually be observed 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 suggestions by McElreath (2016): a Normal(0,1) prior for the other fixed effects, an Exponential(λ = 1) prior for both random effect and distributional standard deviations, and a LKJ(η = 2) prior for the random effects correlation matrices.

We partitioned total phenotypic variation V_P for each behaviour into the following components: $V_P = V_F + V_I + V_B + V_R$, 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_R is the 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.

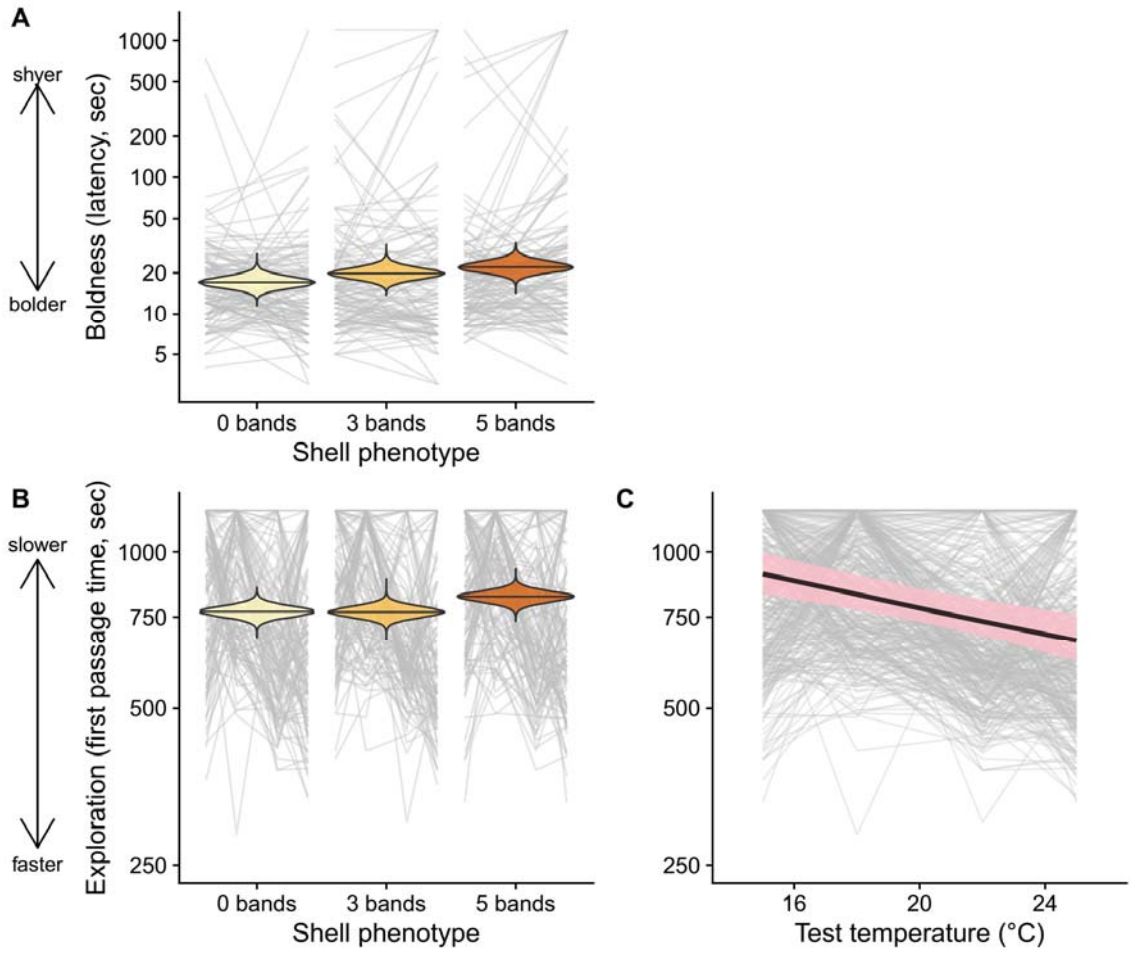
We ran four chains for 20000 iterations, with the first half of each chain used for warmup. We checked mixing graphically and confirmed chain convergence using the improved $\widehat{R}$ statistic by Vehtari et al. (2019). The chains were run longer than the default number of iterations (2000), to ensure effective sample size was satisfactory for all parameters (both bulk- and tail-effective sample sizes sensu Vehtari et al., 2019 > 1000). All credible intervals given are highest posterior density intervals, full posterior density distributions are presented as Supplementary Material S3.

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, see also full posterior distributions in Supplementary Material S3).

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 behaviours (Table 2). Including fixed effect variation due to 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 behaviours. Average exploration and boldness were positively correlated at the individual level (Table 3, Fig. 3). 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).



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

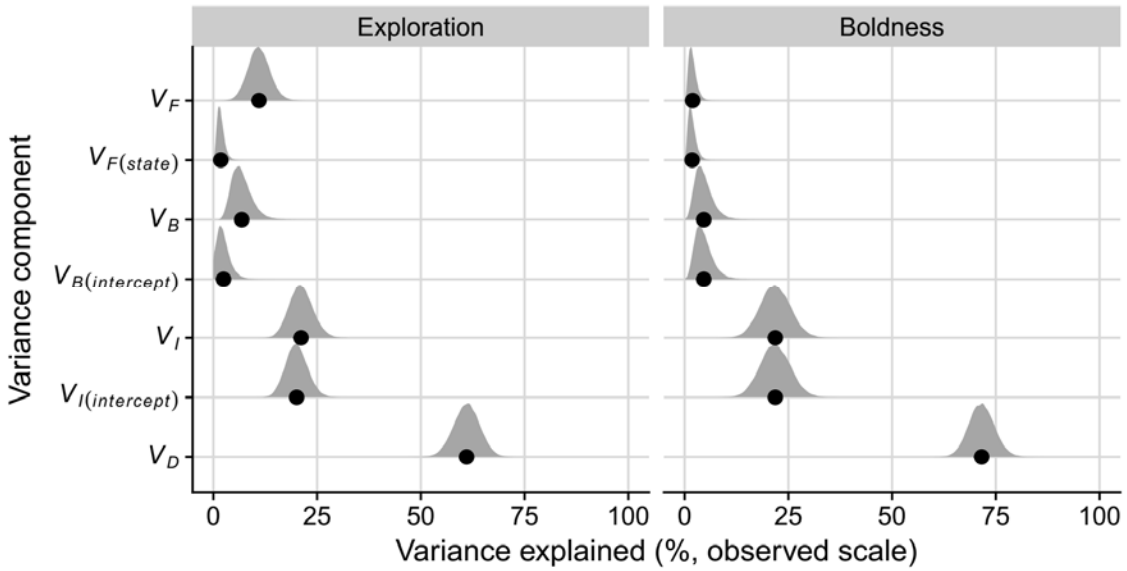

Figure 3. *Mean (points) and posteriors for the proportion of variance explained by the different variance components. See Table 2 or Methods for the names of the variance components.*

Discussion

We showed that behaviours linked to boldness and exploration/activity are repeatable in *Cepaea nemoralis*, confirming again that personality variation is widespread in animals, even in invertebrates (Kralj-Fišer & Schuett, 2014). This result has implications for the evolutionary potential of behaviours in *C. nemoralis,* given repeatability sets the higher limit for the heritability of behaviours (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 behaviour can shape effective thermal tolerance (Abram et al., 2017) or vulnerability to predation (e.g. Hulthén et al., 2017), we believe these behavioural differences must be taken in account when discussing the evolution of shell colour in this model species.

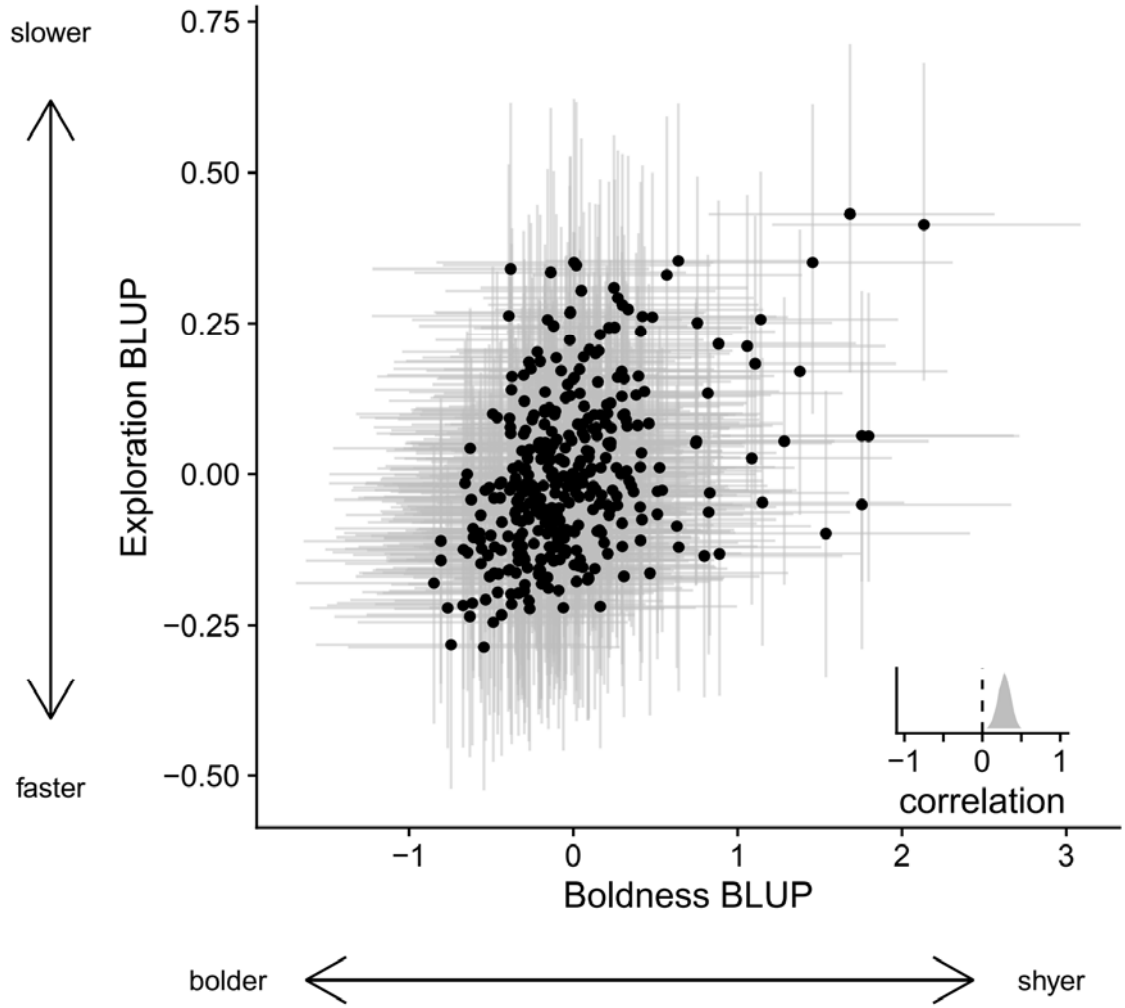

Figure 4. *Correlation between individual-level random effects for boldness and exploration, illustrated by plotting their respective Best Linear Unbiased Predictors and 95% credible intervals. Inset: posterior distribution of the correlation coefficient. BLUPs are plotted, and correlation estimated,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

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

behavioural 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 level (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 behavioural syndrome was integrated into a broader pace of life syndrome *sensu* Réale et al. (2010) by linking behavioural 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 and longevity over their entire life. There is however some indications in the literature that more active/ mobile snails are faster-growing (Oosterhoff, 1977), as predicted by the pace-of-life syndrome hypothesis. At the morph level, it appears that contrary to behaviours, shell morphs do not differ much in terms of average fecundity or growth rate (Oosterhoff, 1977; Wolda, 1967). They however differ markedly in their physiology, based on their response to pharmaceutical assays: the morphs we show here to be faster/bolder also have more responsive endogeneous opioid systems (Kavaliers, 1992). Further research is needed to understand the drivers of these correlations and their consequences (Royauté et al., 2018; Wright et al., 2019).

Five-banded snails, which have been shown to have on average more resistant shells against rodent attacks (Rosin et al., 2013), were shyer than unbanded snails (Fig. 2). At first glance, these results go against the phenotypic compensation hypothesis which predicts boldness should be associated with better defences against predators, in particular thicker shells, mitigating the costs of risk taking behaviour (Ahlgren et al., 2015; Hulthén Kaj, Chapman Ben B., Nilsson P. Anders, Hollander Johan, & Brönmark Christer, 2014; Trovo & Chapman, 2016). However, birds, in particular thrushes (genus *Turdus*) are likely more important predators than rodents (Rosin, Olborska, Surmacki, & Tryjanowski, 2011)**;** given they are visual predators, shell visual characteristics may be more important than structural resistance in influencing behavioural response to predation. Both frequency-dependent predation and direct visual selection have historically been invoked as explanations for predator-dependent morph variation in *Cepaea* (Jones et al., 1977; Ożgo, 2009). More recently, visual

345 selection explanations have received increased support from an experiment using models of avian
346 vision to rigorously test how thrushes actually see different shell morphs (Surmacki et al., 2013). In
347 both our test sites, the boldest morph (unbanded shell) is the least conspicuous (based on Surmacki
348 et al., 2013), not the rarest. This supports crypsis-based explanations over frequency-dependent
349 selection, under the assumption that phenotypes already more at risk of predation should be shyer
350 given boldness increases predation risk (Hulthén et al., 2017). We must nonetheless remember that
351 (i) our knowledge of how thrushes actually perceive snails is very limited (Surmacki et al., 2013), (ii)
352 we only tested a small set of the available morphs, which do not include the rarest background
353 colours (pink and brown), and (iii) shell banding is a trait under multiple selection pressures, including
354 thermal selection (see below).

355 Exploration speed was temperature-dependent: as expected from an ectothermic species, snails
356 were on average faster at higher temperatures (Fig. 2). The temperature reaction norm of
357 exploration was remarkably conserved among individuals (most of the inter-individual variance V_I
358 was due to differences in average behaviour, rather than in temperature slopes; Table 2, Fig. 3). In
359 addition, there was surprisingly no evidence that behavioural differences among morphs are
360 influenced by the thermal environment, whether we consider the previously experienced
361 environment (no habitat × morph interaction) or the current environment (no effect of morph
362 identity on thermal reaction norms) (Table 1). This is despite abundant evidence in the literature for
363 thermal selection on shell morphs, based on field comparisons (Kerstes et al., 2019; for this study,
364 see Methods; e.g. Richardson, 1974; Schilthuizen, 2013), but also experimental evidence of both
365 survival (Lamotte, 1959; Tilling, 1983) and fecundity (Wolda, 1967) thermal selection. In addition,
366 studies giving snails a choice between multiple temperatures show snail morphs do have different
367 thermal preferences that align with expectations based on thermal selection (Kavaliers, 1992). Some
368 studies suggest that snails use shade and humidity just as much (and potentially more) as
369 temperature as cues to adjust their behaviour to microclimate (Ożgo & Kubea, 2005; Rosin et al.,
370 2018). Our exploration tests were short, under standardised lighting conditions and with no water,

371 and snails were brought back to favourable humidity soon after. It is possible longer experiments, or
372 experiments comparing the responses of snails from different habitats to realistic climate variation
373 (including shade and/or humidity) would yield different responses. Maybe more importantly, we only
374 tested temperatures favourable for activity, i.e. the limited part of the thermal niche closer to the
375 optimum. Morph differences in behaviour might be stronger closer to critical minimal or maximal
376 temperature thresholds (Tilling, 1983). This can be investigated by using a wider range of
377 temperatures and expanding the reaction norm approach used here to either a character state
378 approach (e.g. T. M. Houslay, Earley, Young, & Wilson, 2019) or a non-linear reaction norm approach
379 (Arnold, Kruuk, & Nicotra, 2019); both would account for the typical non-linearity of complete
380 thermal performance curves (Arnold et al., 2019). It is very important to note, however, that these
381 results do not mean populations from landscapes differing in sun exposure are identical in behaviour,
382 even for the range of situations we tested. Indeed, because morphs differ in their behaviour, and
383 because morph frequencies differ among landscapes (see Methods), the average snail from a sun
384 exposed population may well be bolder and more active than its counterpart from a shaded
385 population.

386 In any case, the links between behaviours and morphs we observed are conserved across contexts,
387 despite (apparent) selection on shell morph. While this is not a definite proof by itself, we consider
388 this a first hint in favour of a genetic association between morphs and behaviours that cannot be
389 easily broken by environmental changes, in this model species. In addition to studies aiming to
390 confirm these behavioural traits are heritable, further research into the physiological underpinnings
391 of behavioural differences between morphs (building on e.g. Kavaliers, 1992) and of shell colour and
392 pattern determination (Kerkvliet et al., 2017) should help confirm (or infirm) this putative genetic
393 correlation and elucidate its proximate basis.

394 Assuming this genetic link is confirmed, any discussion about how selection on morph may influence
395 the evolution of behaviour (or vice versa) must be tempered by the fact that the greater part of the

396 repeatable inter-individual variation in behaviour was not actually explained by shell morph (see Fig.
397 3, Table 1). It is in a way unsurprising, as we did not expect a single discrete trait to entirely constrain
398 individual behavioural variation. Indeed, the expression of animal personalities can be influenced by
399 many unobserved drivers and state variables which should have a priori limited links to shell morph
400 and its own drivers (Burns et al., 2012; Petelle, Martin, & Blumstein, 2019; Sih et al., 2015; Wright et
401 al., 2019). Furthermore, some level of stochastic behavioural individuality may be inevitable even in
402 the total absence of meaningful genetic and environmental variation (Bierbach, Laskowski, & Wolf,
403 2017). What must be noted, though, is that some of this "remaining" individual variation may still,
404 actually, relate to shell morph. Indeed, because of dominance within loci and especially epistatic
405 relationships among loci, individuals that share the same shell phenotype may actually vary greatly in
406 terms of underlying genotype at morph-determining loci (e.g. having one dominant allele at the
407 "band presence" locus leads to total band absence and masks variation at all other banding genes;
408 Jones et al., 1977). However, while much is known of among-morph variation in thermal tolerance,
409 life history, physiology (Kavaliers, 1992; Kerstes et al., 2019; Lamotte, 1959; Oosterhoff, 1977;
410 Richardson, 1974; Tilling, 1983; Wolda, 1967), nothing as far as we can tell is known about within-
411 morph, but among-genotype variation. Investigations using individuals of known genotype obtained
412 through repeated crosses or, as our knowledge of the actual molecular underpinnings increases,
413 through direct genotyping (Gonzalez, Aramendia, & Davison, 2019; Kerkvliet et al., 2017), may shed
414 light on this "hidden" genetic variation and whether it contributes to the persistence of animal
415 personalities.

416 Increased boldness and activity have been tied to higher probability of dispersal in many species
417 (Cote, Clobert, Brodin, Fogarty, & Sih, 2010), including land snails (Dahirel et al., 2017), and non-
418 random dispersal is now acknowledged as a potentially widespread force behind population
419 phenotypic divergence (Edelaar & Bolnick, 2012; Jacob, Bestion, Legrand, Clobert, & Cote, 2015).
420 Bolder animals are thought to trade increased reproductive success against a greater predation risk
421 (but see Moiron, Laskowski, & Niemelä, 2019; Smith & Blumstein, 2008); predation is generally

422 considered a key driver of morphological differences in *Cepaea*, and plays a key role in dispersal
423 across taxa (Fronhofer et al., 2018). Although active dispersal can safely be dismissed as a driver of
424 continental-scale differences in morph frequencies, our results point to *Cepaea* as a good model to
425 understand how existing behavioural differences may drive local-scale morphological differences
426 (and vice versa). By building on, and complementing, a decades-long history of evolutionary research,
427 this will help us better understand the role of behaviour, and constraints on behavioural variation, in
428 shaping responses to rapid environmental changes (Candolin & Wong, 2012), including landscape
429 alteration and climate change.

430 **Author contributions**

431 AA and MD conceived the study and designed the experimental protocol; AA selected landscapes and
432 collected individuals in the field; VG maintained snails in the lab and collected experimental data,
433 with input from MD; MD and VG analysed data; MD led the writing of the manuscript. All authors
434 contributed critically to the draft and gave final approval for publication.

435 **Data accessibility**

436 Data and reproducible script will be made publicly available on Dryad upon final acceptance.

437 **References**

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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 centred and scaled, and categorical variables converted to centred dummy variables; the intercept then refers to the behaviour of an hypothetical "average" snail.

	Mean effect (95% credible interval)	
	Exploration	Boldness
Fixed effects: main effects		
Intercept	6.670 (6.630 ; 6.700)	2.970 (2.820 ; 3.130)
banding = 3 bands	-0.002 (-0.063 ; 0.058)	0.149 (-0.059 ; 0.358)
banding = 5 bands	**0.066 (0.003 ; 0.124)**	**0.260 (0.054 ; 0.466)**
landscape of origin = shaded	0.056 (-0.017 ; 0.126)	0.199 (-0.105 ; 0.488)
test temperature	**-0.111 (-0.150 ; -0.072)**	--
test order	**0.036 (0.006 ; 0.067)**	0.080 (-0.033 ; 0.196)
Fixed effects: interactions		
banding = 3bands x landscape = shaded	-0.071 (-0.191 ; 0.049)	0.157 (-0.257 ; 0.553)
banding = 5bands x landscape = shaded	-0.008 (-0.127 ; 0.114)	0.239 (-0.153 ; 0.653)
banding = 3bands x temperature	0.002 (-0.039 ; 0.042)	--
banding = 5bands x temperature	0.013 (-0.027 ; 0.054)	--
landscape = shaded x temperature	-0.052 (-0.128 ; 0.026)	--
banding = 3bands x landscape = shaded x temperature	-0.023 (-0.106 ; 0.056)	--
banding = 5bands x landscape = shaded x temperature	0.020 (-0.064 ; 0.099)	--

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. Note that the total variances VP are higher than the empirically observed variances. This is because the latter are underestimated, due to censoring.

	Mean effect (95% credible interval)	
	Exploration	Boldness
Variance partitioning (observed scale)		
Fixed effects V_F	13440 (6375 ; 21026)	49 (7 ; 107)
- explained by state	2171 (368 ; 4354)	46 (5 ; 103)
Box-level V_B	8365 (2913 ; 14964)	124 (12; 296)
- random intercept only	3004 (0 ; 6962)	124 (12; 296)
Individual V_I	25668 (18036 ; 33721)	538 (263; 863)
- random intercept only	24371 (1791 ; 31959)	538 (263; 863)
Residual V_D	73946 (63551 ; 84559)	1778 (953 ; 2779)
Total variance V_P	121420 (102049 ; 141006)	2488 (1348 ; 3927)
Repeatabilities (observed scale)		
$R_{(within\text{-}state)}$	0.201 (0.150 ; 0.253)	0.219 (0.148 ; 0.290)
$R_{(total)}$	0.219 (0.167 ; 0.273)	0.237 (0.166 ; 0.307)
$R_{(within\text{-}state)}$ / $R_{(total)}$	0.918 (0.842 ; 0.985)	0.922 (0.841 ; 0.990)

Table 3. Random effect correlation matrices (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	1	0.134 (-0.469 ; 0.695)	0.434 (-0.012 ; 0.848)
Exploration, intercept	**0.282 (0.095 ; 0.459)**	1	-0.212 (-0.740 ; 0.350)
Exploration, temperature slope	-0.223 (-0.783 ; 0.316)	0.334 (-0.214 ; 0.836)	1

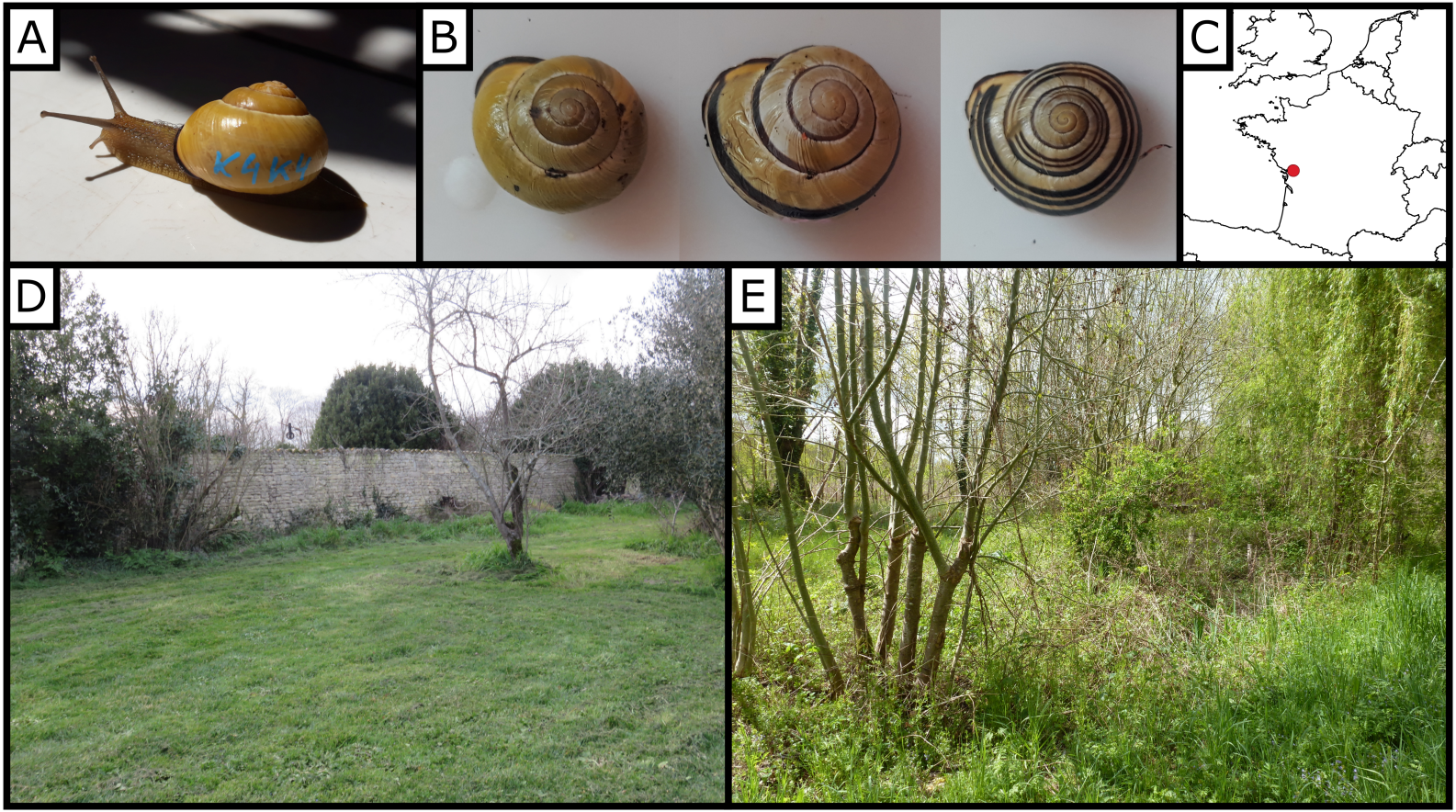
666 **Figure legends**

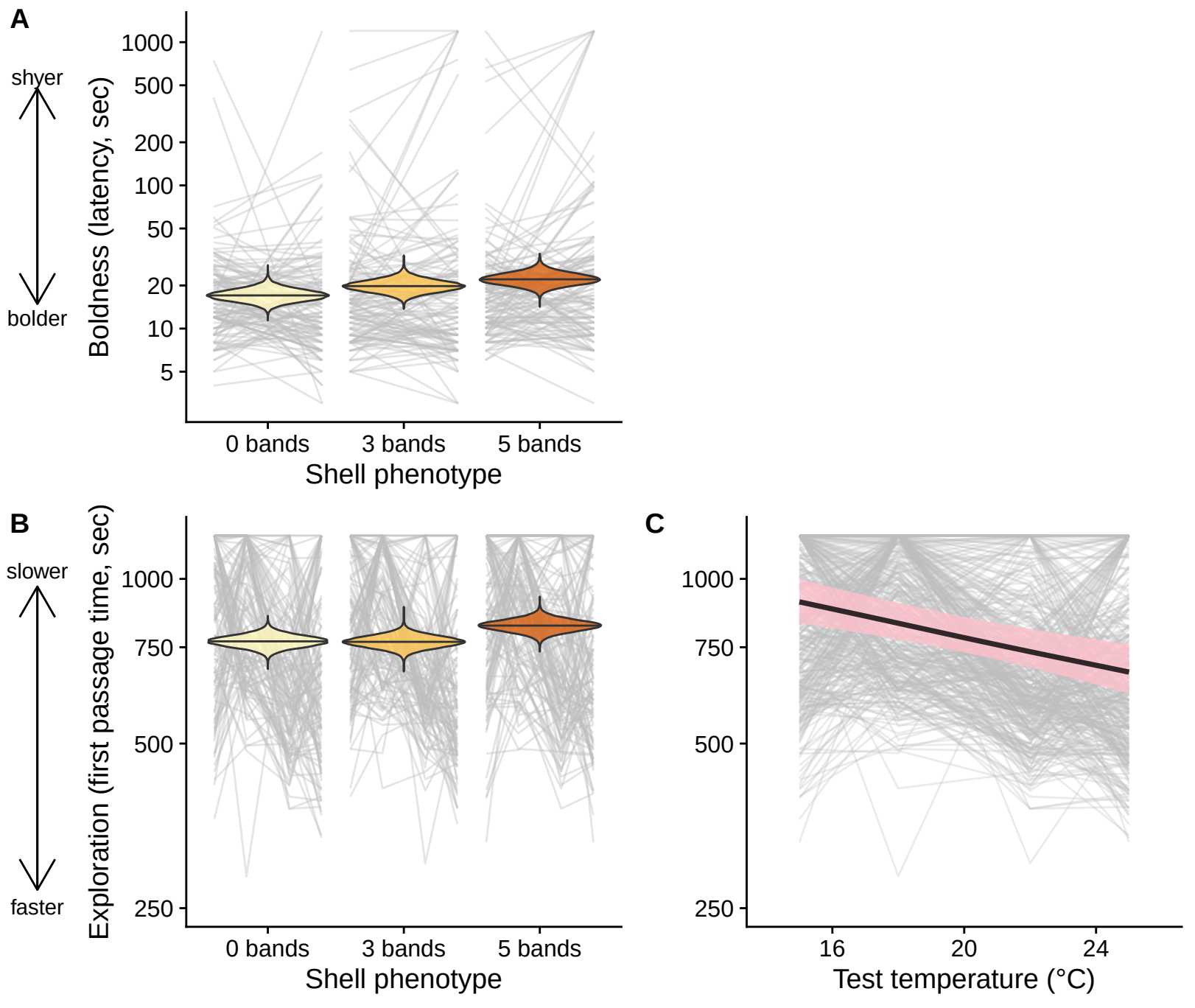
667 **Figure 1.** Study species and sites. (A) An unbanded yellow *Cepaea nemoralis*, showing the position of
668 individual paint marks on the shell (B) Representative shells of the three studied morphs as seen
669 from above: yellow unbanded, three-banded, and five-banded snails (C) Study sites location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

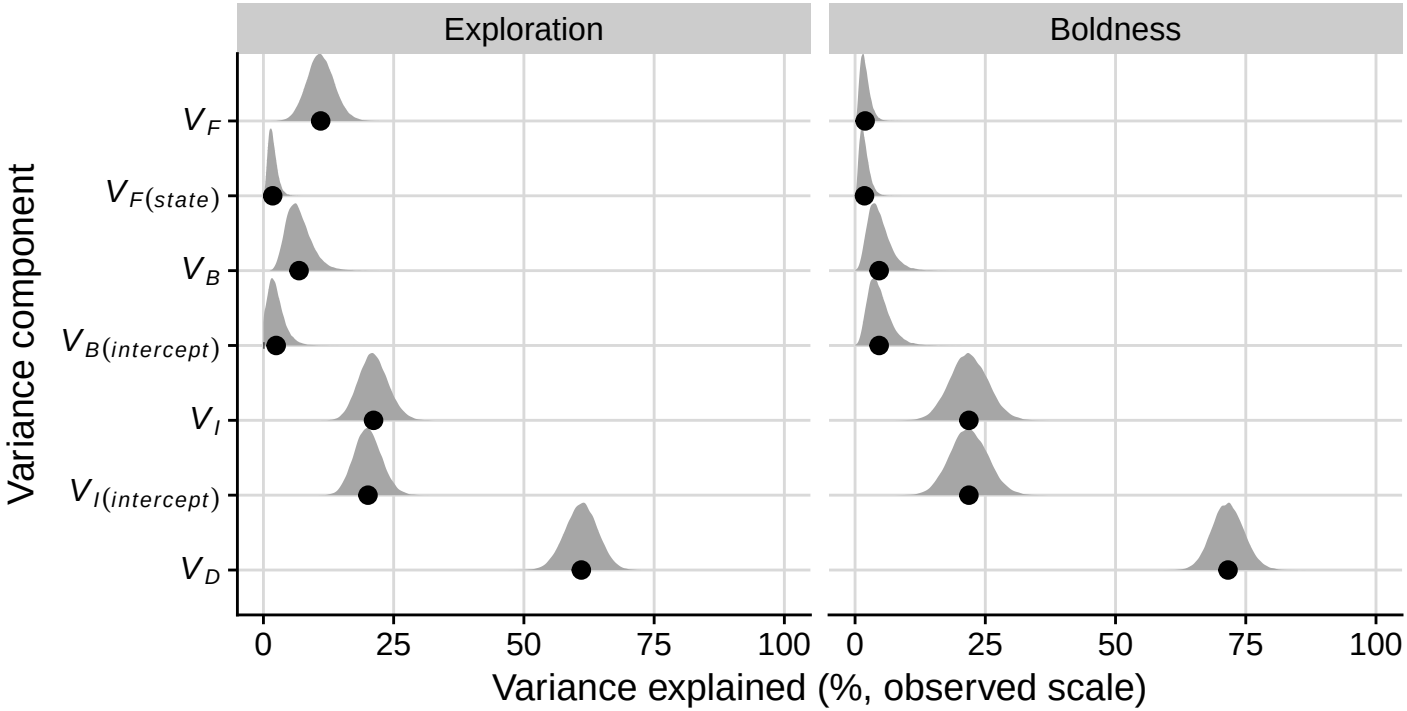
671 **Figure 2.** (A;B) posterior distributions of median boldness (A) and exploration (B) in relation to shell
672 morph. The model estimates the mean log-latencies which corresponds to the medians on the
673 observed latencies scale. (C) mean and 95% credible band for the relationship between exploration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

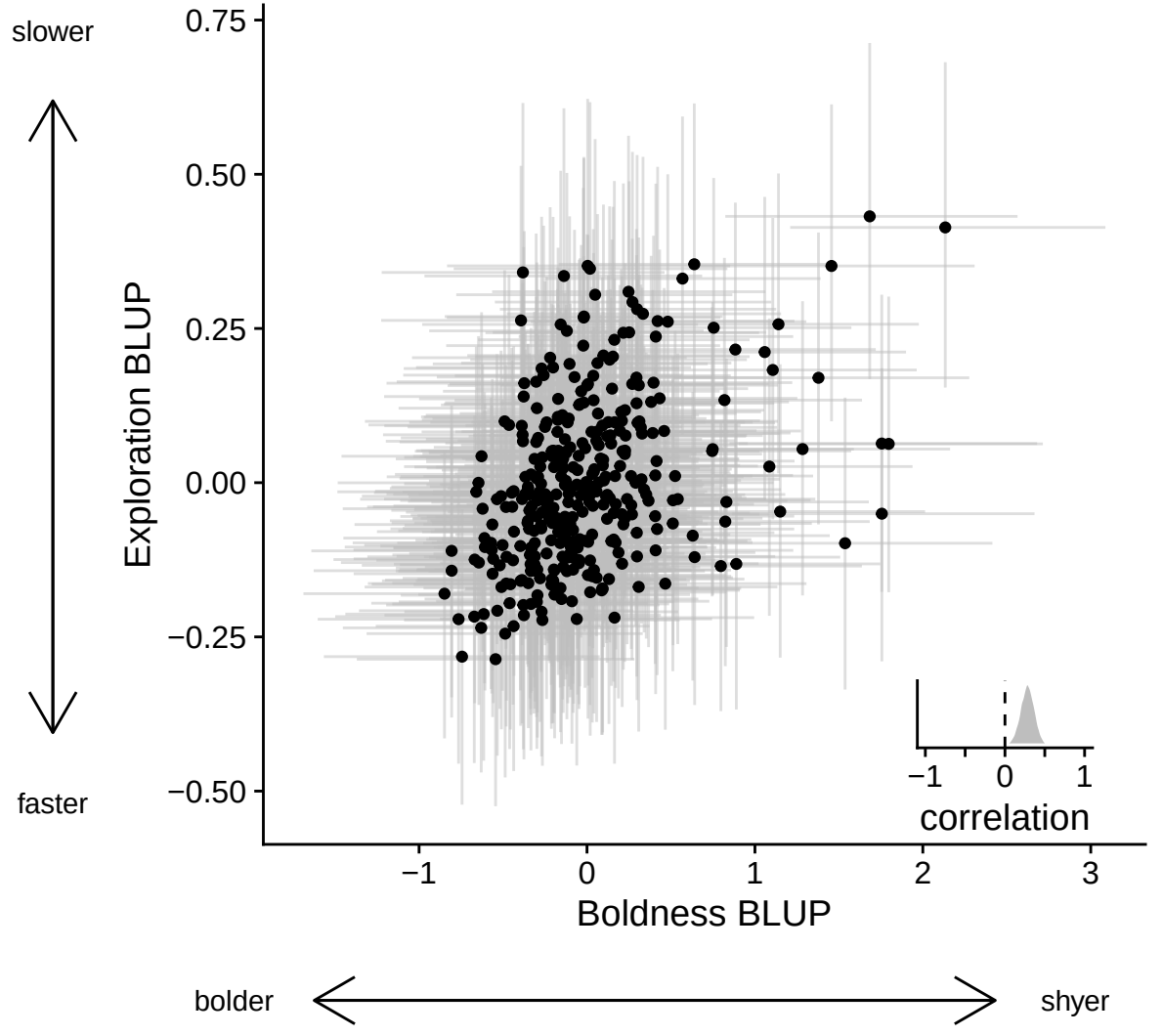
676 **Figure 3.** Mean (points) and posteriors for the proportion of variance explained by the different
677 variance components. See Table 2 or Methods for the names of the variance components.

678 **Figure 4.** Correlation between individual-level random effects for boldness and exploration,
679 illustrated by plotting their respective Best Linear Unbiased Predictors and 95% credible intervals.
680 Inset: posterior distribution of the correlation coefficient. BLUPs are plotted, and correlation
681 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
Shell phenotype
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
16
20
24
Test temperature (°C)


Exploration
Boldness
Variance component
V_F
$V_{F(state)}$
V_B
$V_{B(intercept)}$
V_I
$V_{I(intercept)}$
V_D
0
25
50
75
100
Variance explained (%, observed scale)


slower
faster
0.75
0.50
0.25
0.00
−0.25
−0.50
Exploration BLUP
−1
0
1
2
3
Boldness BLUP
−1
0
1
correlation
bolder
shyer