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1 **Increased population density depresses activity but does not influence**
2 **emigration in the snail *Pomatias elegans***

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7 **Abstract**

8 Dispersal is a key trait linking ecological and evolutionary dynamics, allowing organisms to optimize
9 fitness expectations in spatially and temporally heterogeneous environments. Some organisms can
10 either actively disperse or reduce activity in response to challenging conditions, and both responses
11 may be under a trade-off. To understand how such organisms respond to changes in environmental
12 conditions, we studied emigration (the first step of dispersal) and activity behaviour in the
13 gonochoric land snail *Pomatias elegans*, a litter decomposer that can reach very high local densities,
14 over most of the range of ecologically relevant densities. We found that crowding had no detectable
15 effect on emigration tendency in this species, contrary to previous results in many hermaphroditic
16 snails. *Pomatias elegans* is nonetheless able to detect population density; we show they reduce
17 activity rather than increase dispersal in response to crowding. We propose that limiting activity may
18 be more advantageous than moving away in species with especially poor movement abilities, even by
19 land mollusc standards, like *P. elegans*. Interestingly, emigration and activity were positively
20 correlated independently of density; this dispersal syndrome may reflect an underlying pace-of-life
21 syndrome, and is compatible with a dispersal-dormancy trade-off, which would require further
22 investigation. Additionally, we found snails with heavier shells relative to their size tended to be less
23 mobile, which may reflect physical and metabolic constraints on movement and/or survival during
24 inactivity. We finally discuss how the absence of density-dependent dispersal may explain why *P.*
25 *elegans* is often found at very high local densities, and the possible consequences of this behaviour
26 for ecosystem functioning and litter decomposition.

27 **Keywords**

28 Defence, dispersal syndromes, ecosystem functioning, gastropod, sex-biased dispersal

29

30 **Introduction**

31 Dispersal, i.e. movement potentially leading to gene flow in space, is a key organismal trait
32 influencing and linking ecological and evolutionary dynamics in sometimes complex ways (Ronce,
33 2007; Clobert *et al.*, 2012; Bonte & Dohirel, 2017). As the cost-benefit balance of dispersal is
34 expected to vary depending on individual phenotype and experienced conditions, dispersal is often
35 highly context- and phenotype-dependent (Bowler & Benton, 2005; Clobert *et al.*, 2012; Baines,
36 Ferzoco & McCauley, 2019; Endriss *et al.*, 2019). Complexity is even added when one considers that
37 dispersal can be seen as a three-step process (emigration, transfer, immigration), and that different
38 factors can have different levels of influence at each step (Matthysen, 2012). It has been
39 hypothesized (e.g. Matthysen, 2012; Bonte & Dohirel, 2017), that this multicausality of dispersal is
40 why even well-studied environmental factors may lead to very different dispersal responses
41 depending on populations and species. To understand the context-dependency of dispersal, it is thus
42 necessary to study a broader range of life histories and contexts, including organisms that may have
43 alternative strategies to escape negative environmental conditions, e.g. dormancy (Buoro & Carlson,
44 2014).

45 The effects of population density on dispersal, and especially emigration, are likely among the most
46 studied of all dispersal drivers (Bowler & Benton, 2005; Matthysen, 2005; Harman *et al.*, 2020).
47 However, while emigration increasing with density and competition would be a straightforward
48 expectation, and is supported by theory (Travis, Murrell & Dytham, 1999; Rodrigues & Johnstone,
49 2014), empirical results are actually much more idiosyncratic both within and among species:
50 positive density-dependent, negative density-dependent and density-independent emigration seem
51 to occur at broadly similar frequencies (Jacob *et al.*, 2019; Harman *et al.*, 2020). Explanations for this
52 variability typically invoke multicausality and interactions with other traits, such as sociality (with
53 more social species/individuals in a species less likely to leave large groups, leading to negative
54 density-dependent dispersal; Serrano *et al.*, 2003; Cote & Clobert, 2007), body size (as larger and
55 smaller individuals do not feel competition with the same intensity; e.g. Baines *et al.*, 2019), or sex
56 and sex-ratio (as competition for resources and for partners interact; De Meester & Bonte, 2010;
57 Hovestadt, Mitesser & Poethke, 2014), among many others. Despite the large amount of studies, we
58 are still far from integrating them into a general understanding of density-dependent dispersal: a
59 possible reason is that invertebrates and especially non-arthropod invertebrates are under-
60 represented in the published literature (Harman *et al.*, 2020), meaning we have only explored a
61 narrow part of the trait combinations that may interact with, and shape, the density-dependence of
62 dispersal.

63 The land winkle *Pomatias elegans* (Müller 1774)(Fig. 1A), is a common gastropod species in forests
64 and hedgerows across Europe (Kerney & Cameron, 1999; Falkner *et al.*, 2001; Welter-Schultes, 2012).
65 As a caenogastropod, it has separate sexes, contrary to the majority of land molluscs which are
66 hermaphrodite (Barker, 2001). Its active dispersal capacities are poorly studied but expected to be
67 very low, even by molluscan standards (Kramarenko, 2014); average dispersal distances after 42 days
68 are below 20 cm, according to one of the only (indirect) records available in the peer-reviewed
69 literature (Pfenninger, 2002). Like many other land snails (Cook, 2001; Falkner *et al.*, 2001), it is able
70 to survive up to several months under unfavourable conditions by strongly reducing its activity
71 (sometimes down to dormancy; Kilian, 1951; Falkner *et al.*, 2001). *P. elegans* is often distributed in a
72 very aggregated way across landscapes, and when a population is present, local densities can vary by
73 several orders of magnitude, from less than one to several hundred individuals.m⁻² (Pfenninger,
74 2002). When it is present, *P. elegans* plays a key role in ecosystem functioning, by decomposing litter
75 and altering its chemical and physical characteristics (Coulis *et al.*, 2009; De Oliveira, Hättenschwiler
76 & Handa, 2010).

77 We here tested the hypothesis that emigration (the first step of dispersal) and activity were density-
78 dependent in *P. elegans*. We tested both activity and actual emigration for two reasons. We
79 expected dispersers to be more active than residents, density being equal, in agreement with general
80 predictions on behavioural syndromes (Cote *et al.*, 2010; Réale *et al.*, 2010). However, the two traits
81 may not be interchangeable, and divergent responses between the two may help understand how *P.*
82 *elegans* cope with high densities. For instance, if activity merely is a correlate of dispersal, or vice-
83 versa (for instance if dispersal is just a “by-product” of routine movement; Van Dyck & Baguette,
84 2005), we would expect activity to respond to density in the same way as emigration. If reduced
85 activity is also an alternative coping strategy in the face of stress, we may expect instead a
86 depression of activity in response to density (Cameron & Carter, 1979). In accordance with the
87 phenotypic compensation hypothesis, which predicts that risk-taking behaviour should be associated
88 with morphological traits limiting vulnerability to predators (e.g. Ahlgren *et al.*, 2015), we also
89 expected dispersers/active individuals to be better defended, by having heavier shells. Finally, we
90 accounted for sex differences, given sex-biased dispersal is often observed in other taxa with
91 separated sexes (Trochet *et al.*, 2016).

92 **Material and methods**

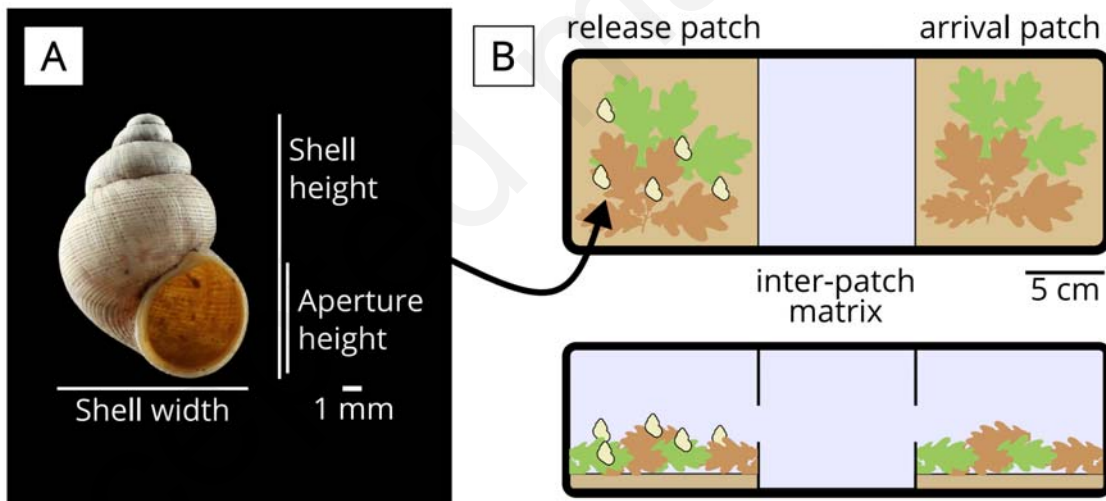
93 We collected *Pomatias elegans* snails in spring 2017 in leaf litter and at the bottom of calcareous
94 walls (Falkner *et al.*, 2001) in Arcais, France (approximate location: 46°17'60"N, 0°41'21"W). They
95 were then kept under controlled conditions (20°C, L:D 16:8) in plastic boxes (25 × 25 × 9 cm, about

96 500 snails.m⁻²) with a 1 cm layer of soil and a roughly 2-3 cm thick layer of leaf litter collected in
97 urban and suburban woodlots and hedgerows on and close to the University of Rennes Beaulieu
98 campus (predominantly oaks *Quercus robur* L. 1753 and *Q. petraea* (Matt.) Liebl. 1784, and beech
99 *Fagus sylvatica* L. 1753). We provided humidity by watering soil and litter every 10 to 15 days.

100 *Dispersal experiment*

101 In June 2017, we created two-patch systems by adapting the system we developed for slugs in
102 Fronhofer et al. (2018), but with a shorter inter-patch gap and longer dispersal period to account for
103 the more limited dispersal capacities of *P. elegans* (Fig. 1B). We divided 32 × 12 cm² transparent
104 plastic boxes (height: 9 cm) in two 12 × 12 cm² patches (“release” and “arrival”) and one central 10 ×
105 12 cm matrix, using plastified cardboard walls. A 2 × 12 cm² slot was left open in each wall to allow
106 snails to leave and enter patches. Both patches were filled with watered soil and litter as in
107 maintenance boxes (see above), while the matrix was kept dry and empty. Experiments were done
108 under controlled conditions (20°C, L:D 16:8).

109



110

111 **Figure 1.** (A) *Pomatias elegans* shell showing the measurements used in the present study. (B)
112 Diagram of the experimental two-patch system, showing (to scale) the release and arrival patches
113 containing litter and soil, and the empty matrix in-between. Top: viewed from above; bottom: side
114 view. Credits: snail photograph – Armelle Ansart; derived snail silhouette – Maxime Dahirel
115 (deposited in phylopic.org); *Quercus robur* leaves silhouette – Ferran Sayol, available in phylopic.org
116 under Public Domain Dedication 1.0 license.

117

118

119 We then placed between 1 and 30 snails in each “release” patch, and first closed the patches for 24 h
120 to let the snails habituate. We then let them free to move for 4 days, and recorded which snails
121 stayed in their release patch (hereafter “residents”) and which snails emigrated to the arrival patch.
122 No snails were found in the matrix between the two patches, and no snails died during the
123 experiment. We tested the following group sizes: 1, 2, 3, 4, 5, 10, 15, 20, and 30 snails per box, with
124 respectively 30, 20, 10, 9, 6, 4, 3, 3, and 2 replicates (total: 371 snails in 87 replicates). We chose
125 these replicate numbers to have at least 30 individuals and 2 replicates per group size. We focused
126 our replication effort more on individuals than boxes (although we did both to some extent), as we
127 were interested in individual traits both as responses and covariates (see Statistical analyses), so a
128 substantial number of individuals at each density was needed. The selected group sizes correspond
129 to initial densities ranging from 69.4 to 2083.3 snails.m⁻² (taking only release patch surface area into
130 account), and likely provide a good coverage of natural densities. Indeed, densities of up to 1072
131 detected snails.m⁻² have been found using 25 × 25 cm² quadrats in natural populations (Pfenninger,
132 2002), and a separate study indicates this species has a field detectability in the 0.5 to 0.9 range
133 when hand collected (Albano *et al.*, 2015), possibly because many individuals may have buried
134 themselves in the substrate at any one time (Falkner *et al.*, 2001). We aimed and managed to ensure
135 balanced sex ratios across densities (in line with natural populations; Boycott, 1916); see
136 **Supplementary Material 1** for a description of the sexing procedure, including both (shell
137 morphology-based) putative sexing before the experiment and (dissection-based) confirmatory
138 sexing after. Tests were spread haphazardly over the month due to logistical constraints (start dates
139 ranging from June 2 to June 26); no reproduction was observed during this interval.

140 *Post-dispersal phenotyping*

141 Within 24h after dispersal tests, we placed each snail on a small (8 cm diameter) clean patch of wet
142 substrate (synthetic upholstery foam) and recorded the latency to activity, snails being defined as
143 active if their operculum was open and both their foot and tentacles were visible out of the shell.
144 Experiments were done under controlled (20°C) temperature conditions, always during the “light”
145 period. All snails that had not moved after 20 minutes remained inactive, operculum closed, for at
146 least two hours, indicating they were not simply slower individuals, but actually behaved differently
147 from the active ones. Indeed, a limited number was further monitored and remained fully inactive
148 even after 7 hours. We therefore analysed activity as a binary variable (active within 20 minutes/ not
149 active for at least two hours). After sexing by dissection (see **Supplementary Material 1**), shells were
150 dried at room temperature before being weighed twice (to the nearest 0.1 mg; CP224S scale,

151 Sartorius, Göttingen, Germany). Twenty-four out of 371 shells were partly broken during dissection
152 and could not be weighed.

153 *Statistical analyses*

154 All analyses were done in a Bayesian framework, using the probabilistic language Stan, which uses a
155 variant of Hamiltonian Monte Carlo (NUTS) as an MCMC method to obtain satisfactory posterior
156 samples in a much lower number of iterations than other methods (Carpenter *et al.*, 2017; Stan
157 Development Team, 2018). We created our Stan models using R (R Core Team, 2020) and the *brms*
158 package (Bürkner, 2017) as front-ends; this allows models to be specified using R formula syntax.
159 Scripting, analysis and plotting relied on the *tidybayes*, *bayesplot*, and *patchwork* packages, as well as
160 the *tidyverse* family of packages (Gabry *et al.*, 2019; Kay, 2019; Pedersen, 2019; Wickham *et al.*,
161 2019).

162 We used a multivariate generalized linear mixed model (GLMM) framework (Dingemanse &
163 Dochtermann, 2013), which allowed us not only to draw inferences on dispersal and activity, but also
164 on their correlations with each other and with (relative) shell mass, while handling missing shell mass
165 data by in-model imputation (McElreath, 2020). A full write-up of the model is given in
166 **Supplementary Material 2**. Briefly, we analysed the probability of dispersing and the probability of
167 activity as individual-level binary variables (dispersed/did not disperse; active/not active) using
168 Bernoulli GLMMs with a logit link. We tested whether dispersal or activity state depended on
169 experienced population density, sex and body size (defined as $\ln(\text{shell height})$); **Fig. 1**). The models
170 also included random effects of date, experimental box, as well as a random effect of individual
171 identity. Importantly, the latter was set to be identical (same values) in both the dispersal and
172 activity models. In effect, this means it corresponds to a latent individual “behaviour” variable that
173 would influence both dispersal and activity. This allowed us to estimate the effect of dispersal on
174 activity (and vice-versa), while accounting for the fact both are estimated with uncertainty and the
175 causal path from one to the other is unknown. We can then easily obtain the (logit) activity
176 probability for, for instance, an average disperser by adding (on the logit scale) the average value of
177 the latent behavioural variable for a disperser to the overall average $\text{logit}(\text{activity probability})$. The
178 same principle applies to get the average dispersal probability of an active individual. Note that using
179 instead dispersal status as a covariate in a univariate activity model leads to the exact same
180 inferences (**Supplementary Material 3**); it however prevents us from doing the analyses described in
181 the next few sentences. To be able to separate the effects of relative shell mass from those of body
182 size, we used a third submodel. We fitted a linear mixed model in which $\ln(\text{Shell mass})$ was a function
183 of $\ln(\text{Shell height})$, sex, and a random effect of individual identity. The use of repeated measures (see

184 “Post-dispersal phenotyping”) of shell mass allowed us here to separate individual variation from
185 residual error, and facilitated the estimation of the former. Finally, individual-level random effects
186 were included in a variance-covariance matrix, allowing us to evaluate the correlation between
187 “relative” shell mass (i.e. after accounting for body size and sex) and the latent behavioural variable.
188 All continuous variables were centred and scaled to unit standard deviation (**Supplementary**
189 **Material 4**), and the “sex” variable was converted to a centred dummy numerical variable (-0.5 =
190 “Male”; +0.5 = “Female”)(Schielzeth, 2010).

191 We set weakly informative priors by following McElreath (2020)’s suggestions for continuous and
192 proportion variables. We used Normal($\mu = 0$, $\sigma = 1.5$) priors for the dispersal and activity fixed effects
193 intercepts, and Normal(0, 1) priors for all the other fixed effects. We set half-Normal(0, 1) priors for
194 all standard deviations (random effects as well as residual variance of shell mass), and LKJ($\eta = 2$)
195 priors for the random effects correlation matrices.

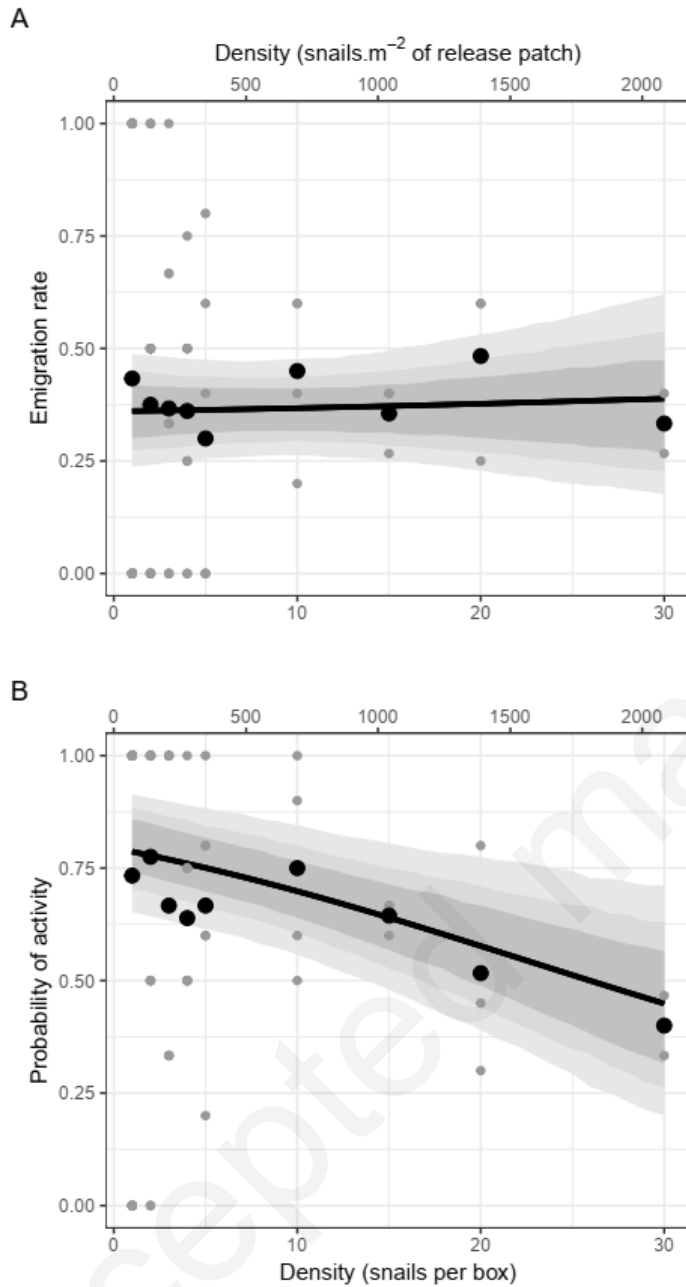
196 We ran four chains for 25000 iterations, with the first 5000 of each chain used for warmup. We
197 checked mixing graphically and confirmed chain convergence using the improved \hat{R} statistic (Vehtari
198 *et al.*, 2020). The chains were run longer than the default number of iterations (2000), to ensure
199 effective sample size was satisfactory for all parameters (bulk- and tail-ESS sensu Vehtari *et al.*, 2020
200 > 1000). All posterior summaries are given as: mean [95% Higher Posterior Density Intervals].

201 **Results**

202 144 snails out of 371 (38.81%) dispersed across all test boxes. There was no detectable effect of box
203 population density (**Fig. 2A**), sex or shell height on emigration probability (**Table 1**).

204 Snails exposed to higher population densities were less likely to be active afterwards (**Table 1, Fig.**
205 **2B**). There were no clear effects of sex or size on activity probability (**Table 1**). The latent behavioural
206 variable was positively associated with both emigration and activity (**Supplementary Material 5**):
207 accordingly, dispersers were 1.23 [1.02; 1.47] times more likely to be active on average, and
208 conversely active individuals were 1.54 [1.04; 2.16] times more likely to have emigrated (**Fig. 3**). This
209 activity-emigration correlation was confirmed by analysing activity in a univariate model with
210 dispersal status as a covariate (**Supplementary Material 3**). After accounting for shell length, sex and
211 measurement error, individual shell mass was negatively correlated with the behavioural latent
212 variable: dispersers/active snails tended to have lighter shells, given their size and sex, than
213 residents/inactive individuals (**Fig. 4, Table 2**).

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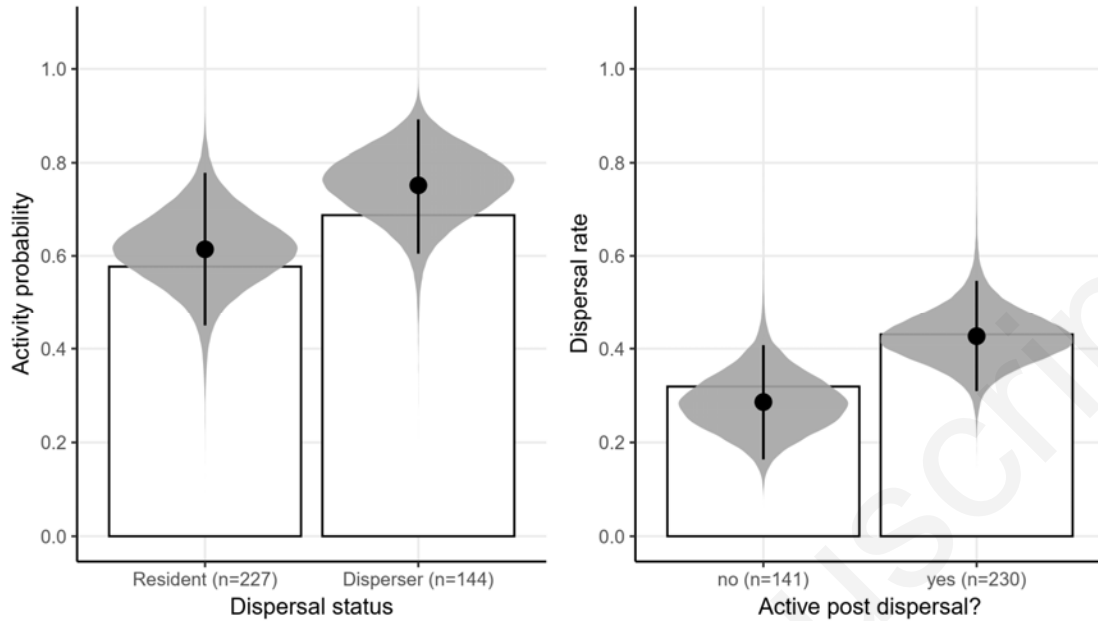


215

216 **Figure 2.** Effect of population density on *Pomatias elegans* dispersal rate (A) and probability of
 217 activity (B) ($N = 371$ snails). Grey points are observed proportions for each test box, black points
 218 averages for each density; black curves give posterior predicted means, grey bands 66, 84 and 95%
 219 credible intervals.

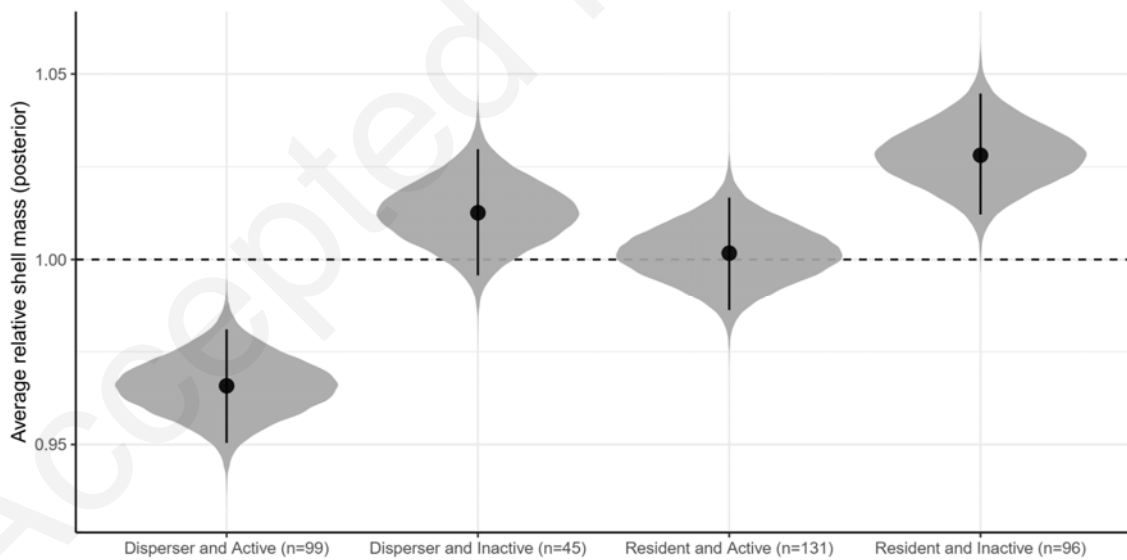
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222

223 **Figure 3.** Relationship between dispersal status and activity post-dispersal. White bars correspond to
 224 observed frequencies, grey “eyes” to posterior predictions based on model intercepts and individual-
 225 level random effects, i.e. averaging out the effects of sex, size and population density (black dots:
 226 posterior means; segments: 95% credible intervals).



227

228 **Figure 4.** Posterior predicted relationship between dispersal status, activity post-dispersal, and mean
 229 predicted shell mass, that is relative to the shell mass predicted for a snail of same shell height and
 230 sex (black dots: posterior means; segments: 95% credible intervals). Posterior pairwise mean
 231 differences are presented in **Supplementary Material 6**.

232 **Table 1.** Posterior means [and 95% credible intervals] for the parameters of the multivariate model
 233 of dispersal, activity and shell mass. Individual-level random effect covariance matrices are in **Table**
 234 **2.** See **Supplementary Material 2** for the full write-up of the model, and **Supplementary Material 4,**
 235 for original means and SDs of transformed variables ($N = 371$ snails, except for Shell mass, $N = 347$
 236 snails, each measured twice)

	Dispersal probability	Activity probability	Shell mass (ln- transformed then scaled)
<i>Fixed effects</i>			
Intercept	-0.54 [-1.04 ; -0.26]	0.74 [0.05 ; 1.49]	-0.01 [-0.09 ; 0.06]
Population density (scaled)	0.04 [-0.38 ; 0.46]	-0.55 [-1.01 ; -0.10]	--
Sex (effect of being female)	-0.16 [-0.79 ; 0.46]	0.23 [-0.42 ; 0.86]	0.18 [-0.02 ; 0.38]
Body size (shell height, ln-transformed then scaled)	0.01 [-0.31 ; 0.33]	0.16 [-0.17 ; 0.51]	0.62 [0.52 ; 0.72]
<i>Random effects (see Table 2 for individual-level effects)</i>			
Date-level variance	0.13 [0.00 ; 0.59]	0.56 [0.00 ; 1.75]	--
Box-level variance	0.52 [0.00 ; 1.33]	0.38 [0.00 ; 1.04]	--
Date-level dispersal-activity correlation		0.13 [-0.69 ; 0.90]	--
Box-level dispersal-activity correlation		0.03 [-0.74 ; 0.73]	--
<i>Residual variance</i>	--	--	8.00×10^{-4} [6.85×10^{-4} ; 9.23×10^{-4}]

237

238 **Table 2.** Individual-level variance-covariance matrix between the latent behavioural variable
 239 (positively correlated with dispersal and activity, see **Fig. 3** and **Supplementary Material 3**) and shell
 240 mass. Posterior means [95% credible interval] are depicted; random effects variances are given on
 241 the diagonal, correlation/covariance on the off diagonal

	Behaviour latent variable	Shell mass
Behaviour latent variable	0.90 [0.08 ; 1.81]	
Shell mass	-0.39 [-0.67 ; -0.12] / -0.25 [-0.41 ; -0.09]	0.54 [0.46 ; 0.63]

242

243 **Discussion**

244 We studied the relationship between *Pomatias elegans* dispersal and population density over most
 245 of the known range of natural densities (Pfenninger, 2002; Albano *et al.*, 2015), yet found no
 246 evidence of density-dependent emigration. There was however a negative relationship between

247 density and activity. Furthermore, we found that emigration, activity and (relative) shell mass co-
248 vary in this species, once density variation is accounted for.

249 We additionally found no evidence of sex bias in dispersal probability or activity. While sex-biased
250 dispersal is abundantly documented in non-molluscan groups (Bowler & Benton, 2005; Trochet *et al.*,
251 2016), there are numerous species with no bias. Broadly, sex-dependent dispersal is predicted to
252 arise when there are sex-differences in spatio-temporal fitness variation due to e.g. sex differences in
253 resource use and/or in local mate competition (Hovestadt *et al.*, 2014; Trochet *et al.*, 2016; Li &
254 Kokko, 2019). Our results, in light of dispersal theory, imply that male and female *P. elegans* use
255 resources similarly and that they do not present polygyny or any mating system leading to
256 predictable sex differences in spatio-temporal fitness variation. While sex ratio is, overall, balanced in
257 this species (Boycott, 1916), the other predictions remain to be tested by the collection of further
258 natural history data. We should additionally note that our experimental setup (one measure of
259 dispersal, after 4 days, and groups that were sex-balanced on average) may not have allowed us to
260 detect finer sex differences in dispersal, i.e. in emigration timing (Li & Kokko, 2019), or conditional
261 strategies dependent on locally experienced sex-ratio (Hovestadt *et al.*, 2014).

262 The absence of density-dependent emigration was more surprising, as many other land mollusc
263 species have been shown to increase emigration and/or dispersal distances in response to population
264 density (Cain & Currey, 1968; Oosterhoff, 1977; Hamilton & Wellington, 1981; Livshits, 1985; Baur,
265 1993; Shachak, Leeper & Degen, 2002; Dahirel *et al.*, 2016). In addition, our experimental design
266 included a (supposedly) costly matrix, which should have made the detection of a positive
267 emigration-density link easier, if it exists (as the dispersal-density reaction norm is predicted to
268 become steeper as costs of dispersal increase; Travis *et al.*, 1999). The costs of competition, which
269 can trigger density-dependent dispersal, are well-documented in land molluscs (Oosterhoff, 1977;
270 Hamilton & Wellington, 1981; Dan & Bailey, 1982). However, density-independent emigration also
271 exists in some mollusc species, in at least some contexts (e.g. Hamilton & Wellington, 1981; Baur,
272 1993). The traditionally expected positive relationship between density and dispersal can be
273 dampened, or even reversed, if for instance species/individuals benefit from group-living (Serrano *et al.*,
274 2003; Bowler & Benton, 2005; Cote & Clobert, 2007). In terrestrial gastropods, individuals may
275 aggregate actively in shelters (and get benefits from this aggregation that go beyond the shelter
276 itself, as the presence of conspecifics may create a favourable microclimate), sometimes following
277 trails to do so (Cook, 2001). However, it is unknown whether *Pomatias elegans* follows trails, and this
278 aggregation behaviour is anyway common to many land molluscs, including species we know show
279 positive density-dependent emigration (Cook, 2001), so it is unlikely to explain alone the density-
280 independence seen in the present study. *P. elegans*, contrary to most land molluscs has separate

281 sexes, and differences in reproductive systems may drive the evolution of different dispersal
282 strategies (Eppley & Jesson, 2008). Indeed, all things equal, hermaphrodites are *a priori* more likely
283 than species with separate sexes to find a mate in small populations (Tomlinson, 1966). This means
284 the density threshold at which the costs of competition outweigh the benefits of grouping (Kim,
285 Torres & Drummond, 2009; Fronhofer, Kropf & Altermatt, 2015) and the costs of dispersal (Bonte *et*
286 *al.*, 2012) is likely lower for hermaphrodites. We hypothesize that context being equal (including e.g.
287 movement costs, or group shelter benefits), this may make hermaphrodites more likely than
288 gonochoric species to exhibit positive density-dependent dispersal over a range of natural densities.
289 In any case, our study shows that further comparisons between hermaphroditic and gonochoric
290 species sharing ecological and life-history characteristics are crucially needed to clarify the role of
291 reproductive system in shaping context-dependent dispersal.

292 Alternatively (but not exclusively), the absence of density response in dispersal may reflect the fact
293 *Pomatias* snails possess other mechanisms to respond to unfavourable densities. Indeed, by contrast
294 with dispersal, activity propensity did decrease with increasing population density (**Fig. 2B**). Like
295 many other shelled land gastropods, *P. elegans* can reduce its activity and even enter dormancy
296 when context is unfavourable (Cook, 2001; Falkner *et al.*, 2001). Activity reduction in response to
297 increased competition has been observed in several species (Oosterhoff, 1977; Cameron & Carter,
298 1979; Dan & Bailey, 1982). This is generally thought to result from interference (mediated through
299 mucus and/or faeces) by the most competitive individuals, which remain active. However, when the
300 experimental/observational setup also allowed for dispersal, species that reduced activity in
301 response to density (e.g. *Cepaea nemoralis*, *Cornu aspersum*, *Xerocrassa seetzenii*) did however also
302 exhibit density-dependent dispersal (Oosterhoff, 1977; Shachak *et al.*, 2002; Dähirel *et al.*, 2016).
303 Given the very limited dispersal capacities of *P. elegans* (Pfenninger, 2002) even compared to other
304 snails (Kramarenko, 2014), the least competitive *Pomatias* snails may well be more successful
305 reducing activity to wait out more favourable conditions, than by attempting to find better by
306 moving away. Indeed, in snails, starvation, a possible result of inactivity, may trigger entry into actual
307 dormancy (Wells, 1944), which can be seen as a form of “dispersal in time” (Buoro & Carlson, 2014).
308 The fact there was no effect of body size on activity suggests the loss of activity is not simply an
309 inhibition of activity by competitive individuals, leading to competitive exclusion. Indeed, in that case
310 we would have expected larger individuals to stay active at high densities while smaller less
311 competitive snails are inhibited (Dan & Bailey, 1982). Given this, and while we need more
312 information to conclude that strongly reduced activity in short-term tests is correlated with long-
313 term dormancy propensity, it is possible that *Pomatias* snails use dormancy as a general “dispersal in
314 time” mechanism, rather than moving away in response to high densities. Note however that we

315 only studied emigration, the first step of dispersal, and density-dependent responses may also
316 happen during transience (Shachak *et al.*, 2002; Poethke, Gros & Hovestadt, 2011; Dahirel *et al.*,
317 2016). In addition, we set within-patch conditions to be standard and favourable; food availability
318 may interact with density and shape dispersal (e.g. Endriss *et al.*, 2019).

319 All three phenotypic traits we studied were linked. First, density being held equal, dispersers were
320 more likely to be active post-dispersal test, and vice versa (**Fig. 3, Supplementary Material 3**). These
321 results line up with predictions on dispersal syndromes and the pace-of-life hypothesis (Cote *et al.*,
322 2010; Réale *et al.*, 2010), which predicts among other things a metabolically-underpinned link
323 between activity and risk taking behaviour (such as dispersal). While, again, more extended
324 assessments of activity are needed to confirm that low activity is correlated to true dormancy, the
325 observed syndrome can also be interpreted as a trade-off between dispersal in space and in time
326 (Buoro & Carlson, 2014), in which individuals that do not disperse are more likely to be dormant at
327 any point in time, even after accounting for density effects. Second, we found that more mobile
328 snails (higher activity and/or dispersal) had on average lighter shells (**Fig. 4, Table 2**), compared to
329 inactive/resident snails. This result goes against our predictions based on the phenotypic
330 compensation hypothesis, which states that risk-taking individuals should have better morphological
331 defences against predators (Hulthén *et al.*, 2014; Ahlgren *et al.*, 2015; Kuo, Irschick & Lailvaux, 2015).
332 However, phenotypic compensation is not a hard rule (De Winter *et al.*, 2016), and while
333 thicker/heavier shells are harder to break (see e.g. Rosin *et al.*, 2013), variation in shell characteristics
334 depends on many abiotic and biotic parameters (Goodfriend, 1986). Indeed, thicker shells may also
335 better conserve humidity (Goodfriend, 1986), which may be adaptive for snails more prone to be
336 inactive for extended periods of time. Heavier shells are likely to increase the costs of movement
337 (Herreid & Full, 1986); given the already high costs of movement in land molluscs (Denny, 1980), this
338 may explain why mobile individuals have lighter shells, despite the potentially increased predation
339 risk. Experimental manipulations of the costs and benefits of heavier shells (by e.g. testing snails
340 under varying humidity conditions, and/or by adding weights to shells), may help disentangle the
341 underpinnings of this dispersal/shell mass syndrome.

342 Although *P. elegans* is overall much less abundant than other macroinvertebrate decomposers at the
343 landscape scale (David, 1999), it can locally reach very high densities (Pfenninger, 2002). Our study
344 shows that increased densities do not trigger increased emigration from crowded into empty
345 habitats in this species. This helps explain the maintenance of this strong spatial heterogeneity and
346 high local densities, as dispersal cannot play its “density-equalizing” role as well. Given
347 decomposition by *P. elegans* can have marked effects on litter characteristics (Coulis *et al.*, 2009; De
348 Oliveira *et al.*, 2010), and facilitate decomposition by other co-occurring macroinvertebrates (De

349 Oliveira *et al.*, 2010), this absence of a common context-dependency in dispersal may have broader
350 implications for local heterogeneity in soil ecosystem functioning and soil communities.

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354 **Data availability**

355 Data and analysis script are archived on GitHub ([https://github.com/mdahirel/pomatias-dispersal-](https://github.com/mdahirel/pomatias-dispersal-2017)
356 [2017](https://github.com/mdahirel/pomatias-dispersal-2017)) and Zenodo (doi: 10.5281/zenodo.3691977) (version v1.2).

357 **References**

- 358 Ahlgren, J., Chapman, B.B., Nilsson, P.A. & Brönmark, C. (2015). Individual boldness is linked to
359 protective shell shape in aquatic snails. *Biol. Lett.* **11**, 20150029.
- 360 Albano, P.G., Strazzari, G., D’Occhio, P. & Succetti, F. (2015). Field estimates of detectability and site
361 occupancy show that northern Italy forest molluscs are spatially rare and poorly detectable.
362 *Ital. J. Zool.* **82**, 592–608.
- 363 Baines, C.B., Ferzoco, I.M.C. & McCauley, S.J. (2019). Phenotype-by-environment interactions
364 influence dispersal. *J. Anim. Ecol.* **88**, 1263–1274.
- 365 Barker, G.M. (2001). Gastropods on land: phylogeny, diversity and adaptive morphology. In *The*
366 *biology of terrestrial molluscs*: 1–146. Barker, G.M. (Ed.). Wallingford, UK: CABI.
- 367 Baur, A. (1993). Effects of food availability and intra-and interspecific interaction on the dispersal
368 tendency in the land snail *Chondrina clienta*. *J. Zool.* **230**, 87–100.
- 369 Bonte, D. & Dahirrel, M. (2017). Dispersal: a central and independent trait in life history. *Oikos* **126**,
370 472–479.
- 371 Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E.,
372 Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V.M., Vandewoestijne, S., Baguette,
373 M., Barton, K., Benton, T.G., Chaput-Bardy, A., Clobert, J., Dytham, C., Hovestadt, T., Meier,
374 C.M., Palmer, S.C.F., Turlure, C. & Travis, J.M.J. (2012). Costs of dispersal. *Biol. Rev.* **87**, 290–
375 312.
- 376 Bowler, D.E. & Benton, T.G. (2005). Causes and consequences of animal dispersal strategies: relating
377 individual behaviour to spatial dynamics. *Biol. Rev.* **80**, 205–225.
- 378 Boycott, A.E. (1916). On sexual characteristics in the shell and radula of *Pomatias elegans* (Müller).
379 *Proc. Malacol. Soc. Lond.* **v.12-13 (1916-1919)**, 127–132.
- 380 Buoro, M. & Carlson, S.M. (2014). Life-history syndromes: Integrating dispersal through space and
381 time. *Ecol. Lett.* **17**, 756–767.

- 382 Bürkner, P.-C. (2017). brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.*
383 **80**, 1–28.
- 384 Cain, A.J. & Currey, J.D. (1968). Ecogenetics of a population of *Cepaea nemoralis* (L.) subject to strong
385 area effects. *Phil. Trans. R. Soc. B* **253**, 447–482.
- 386 Cameron, R.A.D. & Carter, M.A. (1979). Intra- and interspecific effects of population density on
387 growth and activity in some helicid land snails (Gastropoda: Pulmonata). *J. Anim. Ecol.* **48**,
388 237–246.
- 389 Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo,
390 J., Li, P. & Riddell, A. (2017). Stan: a probabilistic programming language. *J. Stat. Softw.* **76**, 1–
391 32.
- 392 Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M. (Eds.). (2012). *Dispersal ecology and evolution*.
393 Oxford, UK: Oxford University Press.
- 394 Cook, A. (2001). Behavioural ecology: on doing the right thing, in the right place at the right time. In
395 *The biology of terrestrial molluscs*: 447–488. Barker, G.M. (Ed.). Wallingford, UK: CABI.
- 396 Cote, J. & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proc. Royal Soc. B*
397 **274**, 383–390.
- 398 Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. (2010). Personality-dependent dispersal:
399 characterization, ontogeny and consequences for spatially structured populations. *Phil.*
400 *Trans. R. Soc. B* **365**, 4065–4076.
- 401 Coulis, M., Hättenschwiler, S., Rapior, S. & Coq, S. (2009). The fate of condensed tannins during litter
402 consumption by soil animals. *Soil Biol. Biochem.* **41**, 2573–2578.
- 403 Dahirel, M., Vardakis, M., Ansart, A. & Madec, L. (2016). Density-dependence across dispersal stages
404 in a hermaphrodite land snail: insights from discrete choice models. *Oecologia* **181**, 1117–
405 1128.
- 406 Dan, N. & Bailey, S.E.R. (1982). Growth, mortality, and feeding rates of the snail *Helix aspersa* at
407 different population densities in the laboratory, and the depression of activity of helicid
408 snails by other individuals, or their mucus. *J. Mollus. Stud.* **48**, 257–265.
- 409 David, J.-F. (1999). Abundance, biomass and functional structure of the saprophagous macrofauna in
410 the litter and soil of Mediterranean oak forests. *Pedobiologia* **43**, 319–327.
- 411 De Meester, N. & Bonte, D. (2010). Information use and density-dependent emigration in an
412 agrobiont spider. *Behav. Ecol.* **21**, 992–998.
- 413 De Oliveira, T., Hättenschwiler, S. & Handa, I.T. (2010). Snail and millipede complementarity in
414 decomposing Mediterranean forest leaf litter mixtures. *Funct. Ecol.* **24**, 937–946.
- 415 De Winter, G., Ramalho Martins, H., Trovo, R.A. & Chapman, B.B. (2016). Knights in shining armour
416 are not necessarily bold: defensive morphology correlates negatively with boldness, but
417 positively with activity, in wild threespine stickleback, *Gasterosteus aculeatus*. *Evol. Ecol. Res.*
418 **17**, 1–12.
- 419 Denny, M. (1980). Locomotion: the cost of gastropod crawling. *Science* **208**, 1288–1290.

- 420 Dingemanse, N.J. & Dochtermann, N.A. (2013). Quantifying individual variation in behaviour: mixed-
421 effect modelling approaches. *J. Anim. Ecol.* **82**, 39–54.
- 422 Endriss, S.B., Vahsen, M.L., Bitume, E.V., Monroe, J.G., Turner, K.G., Norton, A.P. & Hufbauer, R.A.
423 (2019). The importance of growing up: juvenile environment influences dispersal of
424 individuals and their neighbours. *Ecol. Lett.* **22**, 45–55.
- 425 Eppley, S.M. & Jesson, L.K. (2008). Moving to mate: the evolution of separate and combined sexes in
426 multicellular organisms. *J. Evol. Biol.* **21**, 727–736.
- 427 Falkner, G., Obrdlik, P., Castella, E. & Speight, M.C.D. (2001). *Shelled Gastropoda of western Europe*.
428 München, Germany: Friedrich Held Gesellschaft.
- 429 Fronhofer, E.A., Kropf, T. & Altermatt, F. (2015). Density-dependent movement and the
430 consequences of the Allee effect in the model organism *Tetrahymena*. *J. Anim. Ecol.* **84**, 712–
431 722.
- 432 Fronhofer, E.A., Legrand, D., Altermatt, F., Ansart, A., Blanchet, S., Bonte, D., Chaine, A., Dahirel, M.,
433 Laender, F.D., Raedt, J.D., Gesu, L. di, Jacob, S., Kaltz, O., Laurent, E., Little, C.J., Madec, L.,
434 Manzi, F., Masier, S., Pellerin, F., Pennekamp, F., Schtickzelle, N., Therry, L., Vong, A.,
435 Winandy, L. & Cote, J. (2018). Bottom-up and top-down control of dispersal across major
436 organismal groups. *Nature Ecol. Evol.* **2**, 1859–1863.
- 437 Gabry, J., Simpson, D., Vehtari, A., Betancourt, M. & Gelman, A. (2019). Visualization in Bayesian
438 workflow. *J. Royal Stat. Soc. A* **182**, 389–402.
- 439 Goodfriend, G.A. (1986). Variation in land-snail shell form and size and its causes: a review. *Syst. Zool.*
440 **35**, 204–223.
- 441 Hamilton, P.A. & Wellington, W.G. (1981). The effects of food and density of the movement of *Arion*
442 *ater* and *Ariolimax columbianus* (Pulmonata: Stylommatophora) between habitats. *Res.*
443 *Popul. Ecol.* **23**, 299–308.
- 444 Harman, R.R., Goddard, J., Shivaji, R. & Cronin, J.T. (2020). Frequency of occurrence and population-
445 dynamic consequences of different forms of density-dependent emigration. *Am. Nat.* **195**,
446 851–867.
- 447 Herreid, C.F. & Full, R.J. (1986). Energetics of hermit crabs during locomotion: the cost of carrying a
448 shell. *J. Exp. Biol.* **120**, 297–308.
- 449 Hovestadt, T., Mitesser, O. & Poethke, H.-J. (2014). Gender-specific emigration decisions sensitive to
450 local male and female density. *Am. Nat.* **184**, 38–51.
- 451 Hulthén, K., Chapman, B.B., Nilsson, P.A., Hollander, J. & Brönmark, C. (2014). Express yourself: bold
452 individuals induce enhanced morphological defences. *Proc. R. Soc. B* **281**, 20132703.
- 453 Jacob, S., Chaine, A.S., Huet, M., Clobert, J. & Legrand, D. (2019). Variability in dispersal syndromes is
454 a key driver of metapopulation dynamics in experimental microcosms. *Am. Nat.* **194**, 613–
455 626.
- 456 Kay, M. (2019). *tidybayes: tidy data and geoms for Bayesian models*.

- 457 Kerney, M.-P. & Cameron, R.-A.-D. (1999). *Guide des escargots et limaces d'Europe*. Lonay (Suisse):
458 Delachaux et Niestlé.
- 459 Kilian, E.F. (1951). Untersuchungen zur Biologie von *Pomatias elegans* (Müller) und ihrer
460 'Konkrementdrüse.' *Arch. Molluskenkd.* **80**, 1–16.
- 461 Kim, S.-Y., Torres, R. & Drummond, H. (2009). Simultaneous positive and negative density-dependent
462 dispersal in a colonial bird species. *Ecology* **90**, 230–239.
- 463 Kramarenko, S. (2014). Active and passive dispersal of terrestrial mollusks: a review. *Ruthenica* **24**, 1–
464 14.
- 465 Kuo, C.-Y., Irschick, D.J. & Lailvaux, S.P. (2015). Trait compensation between boldness and the
466 propensity for tail autotomy under different food availabilities in similarly aged brown anole
467 lizards. *Funct. Ecol.* **29**, 385–392.
- 468 Li, X.-Y. & Kokko, H. (2019). Intersexual resource competition and the evolution of sex-biased
469 dispersal. *Front. Ecol. Evol.* **7**, 111.
- 470 Livshits, G.M. (1985). Ecology of the terrestrial snail *Brephulopsis bidens* (Pulmonata: Enidae):
471 mortality, burrowing and migratory activity. *Malacologia* **26**, 213–223.
- 472 Matthysen, E. (2005). Density-dependent dispersal in birds and mammals. *Ecography* **28**, 403–416.
- 473 Matthysen, E. (2012). Multicausality of dispersal: a review. In *Dispersal ecology and evolution*: 3–18.
474 Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M. (Eds.). Oxford, UK: Oxford University
475 Press.
- 476 McElreath, R. (2020). *Statistical rethinking: a Bayesian course with examples in R and Stan*. 2nd
477 edition. Boca Raton, USA: Chapman and Hall/CRC.
- 478 Oosterhoff, L.M. (1977). Variation in growth rate as an ecological factor in the landsnail *Cepaea*
479 *nemoralis* (L.). *Neth. J. Zool.* **27**, 1–132.
- 480 Pedersen, T.L. (2019). *patchwork: the composer of plots*.
- 481 Pfenninger, M. (2002). Relationship between microspatial population genetic structure and habitat
482 heterogeneity in *Pomatias elegans* (O.F. Müller 1774) (Caenogastropoda, Pomatiasidae). *Biol.*
483 *J. Linn. Soc.* **76**, 565–575.
- 484 Poethke, H.J., Gros, A. & Hovestadt, T. (2011). The ability of individuals to assess population density
485 influences the evolution of emigration propensity and dispersal distance. *Theor. Biol.* **282**,
486 93–99.
- 487 R Core Team. (2020). *R: a language and environment for statistical computing*. Vienna, Austria: R
488 Foundation for Statistical Computing.
- 489 Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.-O. (2010).
490 Personality and the emergence of the pace-of-life syndrome concept at the population level.
491 *Phil. Trans. R. Soc. B* **365**, 4051–4063.
- 492 Rodrigues, A.M.M. & Johnstone, R.A. (2014). Evolution of positive and negative density-dependent
493 dispersal. *Proc. R. Soc. B* **281**, 20141226.

494 Ronce, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution.
495 *Annu. Rev. Ecol. Evol. Syst.* **38**, 231–253.

496 Rosin, Z.M., Kobak, J., Lesicki, A. & Tryjanowski, P. (2013). Differential shell strength of *Cepaea*
497 *nemoralis* colour morphs—implications for their anti-predator defence. *Naturwissenschaften*
498 **100**, 843–851.

499 Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients.
500 *Methods Ecol. Evol.* **1**, 103–113.

501 Serrano, D., Tella, J.L., Donázar, J.A. & Pomarol, M. (2003). Social and individual features affecting
502 natal dispersal in the colonial lesser kestrel. *Ecology* **84**, 3044–3054.

503 Shachak, M., Leeper, A. & Degen, A. (2002). Effect of population density on water influx and
504 distribution in the desert snail *Trochoidea seetzenii*. *Ecoscience* **9**, 287–292.

505 Stan Development Team. (2018). *RStan: the R interface to Stan*.

506 Tomlinson, J. (1966). The advantages of hermaphroditism and parthenogenesis. *J. Theor. Biol.* **11**, 54–
507 58.

508 Travis, J.M.J., Murrell, D.J. & Dytham, C. (1999). The evolution of density-dependent dispersal. *Proc.*
509 *R. Soc. B* **266**, 1837–1842.

510 Trochet, A., Courtois, E.A., Stevens, V.M., Baguette, M., Chaine, A., Schmeller, D.S., Clobert, J. &
511 Wiens, J.J. (2016). Evolution of sex-biased dispersal. *Q. Rev. Biol.* **91**, 297–320.

512 Van Dyck, H. & Baguette, M. (2005). Dispersal behaviour in fragmented landscapes: routine or special
513 movements? *Basic Appl. Ecol.* **6**, 535–545.

514 Vehtari, A., Gelman, A., Simpson, D., Carpenter, B. & Bürkner, P.-C. (2020). Rank-normalization,
515 folding, and localization: an improved \widehat{R} for assessing convergence of MCMC.
516 *Bayesian Anal.*

517 Wells, G.P. (1944). The water relations of snails and slugs: III. Factors determining activity in *Helix*
518 *pomatia* L. *J. Exp. Biol.* **20**, 79–87.

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

521 Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A.,
522 Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J.,
523 Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K. & Yutani, H.
524 (2019). Welcome to the Tidyverse. *J. Open Source Softw.* **4**, 1686.

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Shell width

Shell height

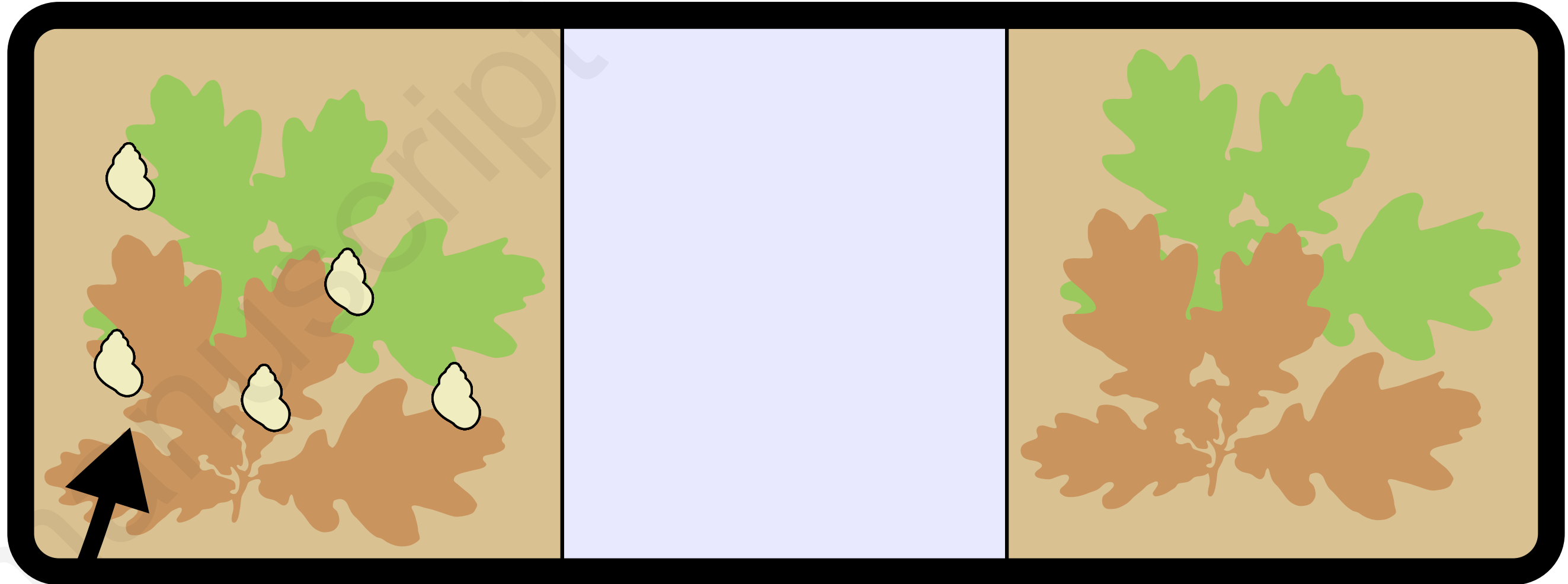
Aperture height

1 mm

B

release patch

arrival patch



inter-patch matrix

5 cm

