

1 **Urban *Cepaea nemoralis* snails are less likely to have** 2 **nematodes trapped within their shells**

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10 **Abstract**

11 Urbanisation is a major human-induced environmental change which can impact not only
12 individual species, but also the way these species interact with each other. As a group,
13 terrestrial molluscs interact frequently with a wide diversity of parasites, yet the way these
14 interactions vary across space and in response to environmental pressures is poorly
15 documented. In this study we leveraged a recently discovered defence mechanism, by which
16 snails trap parasitic nematodes in their shells, to explore how snail-nematodes interactions may
17 vary in response to city life. We examined shells from the generalist snail *Cepaea nemoralis*
18 sampled in three urban areas in Belgium for trapped nematodes, and attempted to link this to
19 urbanisation and shell phenotypic traits. We found that even a small degree of urbanisation led
20 to large decreases in the rates of shell encapsulation, and that larger snails were more likely to
21 contain trapped nematodes. However, we found no evidence that shell colour, which had been
22 previously linked to immune function, was correlated to encapsulation rates. We discuss how
23 between-population variation in encapsulation rates can result from urbanisation-induced
24 changes on the nematodes side, the snail side, or both, and suggest potential tests for future
25 studies aiming to disentangle these mechanisms.

26 **Key words:** Biotic interactions, Gastropoda, immunity, parasites.

27

28 Introduction

29 Urbanisation is a major and all-encompassing human-induced environmental change, leading to
30 changes in land use, local climate, soil imperviousness, light and chemical pollution... (Parris,
31 2016). The (often negative) impacts of these multivariate changes on biodiversity are
32 increasingly well-documented: many species decline in cities, while some become successful
33 “urban adapters”, leading to major restructuring of biological communities along urbanisation
34 gradients (e.g. McKinney, 2008; Piano et al., 2020; Fenoglio et al., 2020; Liang et al., 2023). In
35 parallel, urbanisation can also cause within-species phenotypic and genetic changes (Alberti et
36 al., 2017; Szulkin et al., 2020; Diamond & Martin, 2021). Urbanisation may also have second-
37 order impacts by reshaping ecological interactions, if tightly connected species respond to
38 environmental change in different ways (Theodorou, 2022). Such urbanisation-induced changes
39 in ecological interactions, in both positive and negative directions, have been recorded for
40 plant-pollinator interactions (Liang et al., 2023), plant-herbivore and prey-predator interactions
41 (Eötvös et al., 2018; Valdés-Correcher et al., 2022; Gámez et al., 2022; Korányi et al., 2022), as
42 well as host-parasite interactions (Murray et al., 2019; Korányi et al., 2022).

43 Terrestrial molluscs (snails and slugs) are potentially valuable models in urban ecology and
44 evolution, in part because of their limited movement abilities, which means they often cannot
45 move to escape environmental changes. Like in many other taxa, urbanisation can reshape
46 molluscan communities (Lososová et al., 2011; Horsák et al., 2013; Barbato et al., 2017; Hodges
47 & McKinney, 2018), and drive evolutionary responses in urban populations (Kerstes et al., 2019).
48 Interestingly, in a comparative cross-taxon study of urbanisation impacts, snail species richness
49 seemed less negatively affected, compared to other more mobile groups (Piano et al., 2020).
50 This may be because their locally high abundances and small home ranges allow their
51 persistence in even small habitat fragments. Land molluscs are hosts to a diverse array of
52 metazoan parasites, including nematodes, flies, mites or trematodes (Barker, 2004; Segade et
53 al., 2013; Żbikowska et al., 2020). How urbanisation reshapes these interactions remains
54 understudied, despite some of these parasites being of increasing veterinary interest (Aziz et al.,
55 2016; Giannelli et al., 2016).

56 Snails and slugs can defend themselves against metazoan parasites through a variety of
57 behavioural (Wilson et al., 1999; Wynne et al., 2016; Rae, 2023) or immune responses (Furuta &
58 Yamaguchi, 2001; Scheil et al., 2014; Coaglio et al., 2018). Among the latter, it has been
59 discovered that land molluscs can use their shells to trap parasitic nematodes, killing them and
60 fusing them to the inner shell surface (Rae et al., 2008; Williams & Rae, 2015; Rae, 2017). This
61 ability seems phylogenetically widespread, even present in slugs with vestigial shells (Rae et al.,
62 2008; Rae, 2017), and could therefore provide a relatively easy to access record of ecological
63 interactions. Following anecdotal records of mites and trematodes encapsulated in shells, it has
64 further been suggested that this shell encapsulation might extend to other metazoan parasites
65 (Dahirel et al., 2022; Gérard et al., 2023). However, given how rare these non-nematode records
66 are, they may be merely by-products of a defence mechanism targeted towards nematodes,
67 rather than evidence of a more generalized defence response (Gérard et al., 2023). The few
68 snail species in which this phenomenon has been studied across multiple populations show that
69 the prevalence of individuals trapping nematodes can vary widely between sites (Rae, 2017;

70 Rae, 2018; Cowlshaw et al., 2019), but there has been no attempt, to our knowledge, to assess
71 whether this variation could be non-random with respect to environmental context.

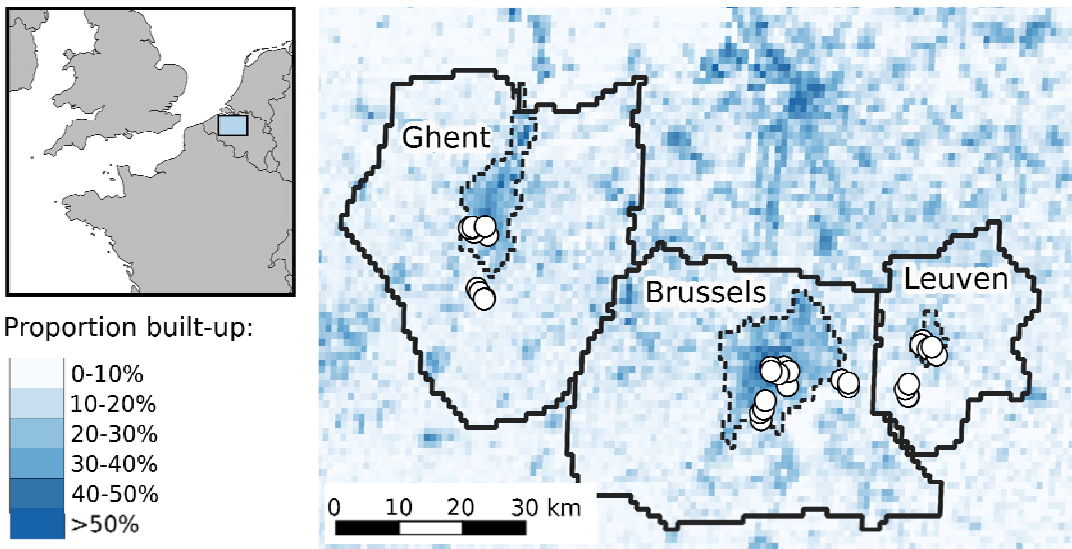
72 To that end, we combine here publicly available and standardized urbanisation metrics with
73 observations of field-collected snails across three cities in Belgium, using the grove snail *Cepaea*
74 *nemoralis* (Gastropoda, family Helicidae) as a model. Like other helicids, *C. nemoralis* can
75 encapsulate and trap parasitic nematodes in its shell (Williams & Rae, 2016; Rae, 2017; Dahirel
76 et al., 2022; Gérard et al., 2023). This snail is also common both outside and within cities
77 (Kerstes et al., 2019), and therefore a very suitable model to study variation in encapsulation
78 rates, whether it is due to urbanisation or to spatial (between-cities) differences. Furthermore,
79 the shell colour variation that made *Cepaea* species iconic models in evolutionary biology (Jones
80 et al., 1977; Ożgo, 2009) may also influence their immune response, with some evidence that
81 darker morphs mount better defences against nematodes (Dahirel et al., 2022; but see Scheil et
82 al., 2014). On the other hand, this morph variation in resistance might not translate to shell
83 encapsulation (Williams & Rae, 2016; Dahirel et al., 2022). However, existing comparisons were
84 either limited to one type of colour variation (banding pattern only, Dahirel et al., 2022), or
85 analysed experimental infections by one model nematode (Williams & Rae, 2016); we here test
86 whether this remains true when analysing naturally occurring snail-nematode interactions and
87 accounting for more dimensions of shell colour variation.

88 **Methods**

89 **Site selection and sampling**

90 We searched for *Cepaea nemoralis* snails from early October to mid-November 2022 in and
91 around the urban areas of Brussels, Ghent and Leuven in Belgium (**Fig. 1**). Potential sites were
92 selected based on pre-existing online crowdsourced records (iNaturalist contributors &
93 iNaturalist, 2024) combined with personal observations and virtual fieldwork using Google
94 StreetView to identify suitable habitats (based on Falkner et al., 2001). We visited 36 sites
95 chosen to be roughly balanced between the three cities (including their surrounding areas;
96 Brussels: 13 sites, Ghent: 13 sites, Leuven: 10 sites). In each site, we sampled living snails by
97 hand during visual search, in a radius of up to 50 m around a designated site centroid (though
98 search was *de facto* mostly concentrated within a 20 m radius). Individuals were mainly
99 searched in known favourable micro-habitats, i.e. on tall herbs and shrubs, under piled wood
100 and cardboard or loose rocks, or on fences, walls, and tree trunks (Falkner et al., 2001). Field
101 identification of *Cepaea nemoralis* snails is easy based on shell shape, size and colour (Cameron,
102 2008). We only collected adults, which can easily be separated from subadults by the presence
103 of a reflected shell lip marking the end of shell growth (Cameron, 2008). Each site was visited by
104 1 to 3 people (mean: 2.03) for a duration of 5 to 30 person-minutes (mean: 15). We collected a
105 total of 298 snails from 28 of the 36 sites visited (Brussels: 9 sites, Ghent: 10 sites, Leuven: 9
106 sites). However, 2 shells were lost before examination for parasites due to handling errors, and
107 another shell was accidentally broken for parasite examination before photographs or size
108 measurements could be done; this led to a final dataset of 295 snails still in 28 sites. For each of
109 these 28 sites, the nearest neighbouring site with snails found was between 153 and 1516 m
110 away (mean: 768 m), which is in any case farther than the maximal dispersal distances

111 (Kramarenko, 2014), indicating that even nearby sites could be considered separate
112 populations.



113
114 **Figure 1.** Location of study sites within western Europe and central Belgium. The Functional Urban Areas
115 (roughly corresponding to commuter zones, Schiavina et al., 2019; Moreno-Monroy et al., 2021)
116 that were used to link each site to a city are also displayed as solid black lines, while the corresponding core
117 urban areas (based on Florczyk et al., 2019) are displayed with dashed lines.

118 **Urbanisation metrics**

119 It is well-known that urban environmental changes are complex and multivariate (e.g. Parris,
120 2016); however, given our relatively low number of sites, and the risk of collinearity between
121 urban metrics, we decided to use simple overarching metrics focused on building presence and
122 human population density. We assessed urbanisation at each site using raster layers from the
123 Global Human Settlement Layer project for the year 2020 (<https://ghsl.jrc.ec.europa.eu/>, Joint
124 Research Centre (European Commission), 2023). We first used built-up surface (GHS-BUILT-S)
125 and population density (GHS-POP) at 100 m and 1000 m resolutions (Pesaresi & Politis, 2023;
126 Schiavina, Freire, et al., 2023). The former spatial scale matches the scale of maximal dispersal
127 movements over timespans of up to a couple years in helicid snails, while the latter is closer to
128 the scale of longer term (over several decades) population spread (Kramarenko, 2014). As an
129 additional categorical metric, we also used the Degree of Urbanisation as recorded in the
130 Settlement Model layer (GHS-SMOD, available only at 1000 m resolution, Eurostat (European
131 Commission), 2021; Schiavina, Melchiorri, et al., 2023). At the highest level of classification, the
132 standardized Degree of Urbanisation methodology mainly uses population density and
133 contiguity rules to classify grid cells as either part of a continuous high-density Urban Centre, as
134 low-density rural cells or as intermediate peri-urban/suburban cells. For each site and
135 urbanisation metric, we recorded the value of the corresponding grid cell. Interestingly, Degree
136 of Urbanisation classes, which are primarily based on population density, divide our sites in
137 almost the same non-linear way as another, independent, three-level classification based on

138 built-up surfaces used in previous urban ecology studies in the study region (e.g. Piano et al.,
139 2020) (**Supplementary Material S1**).

140 **Snail shell analysis**

141 Snail size was measured using a caliper as the shell greatest diameter (to the nearest 0.1 mm).
142 Snail shell colour morphs were scored following e.g. Cain (1988) for background colour (from
143 lighter to darker: yellow, pink or brown), number of dark bands (0 to 5 bands) and on the
144 presence or absence of band fusions (which increase the proportion of the shell covered by dark
145 bands). Snails were killed by first inducing dormancy at 6°C, then by freezing at -20°C. We
146 removed bodies from shells with forceps and lightly cleaned shells with water (bodies were
147 stored in ethanol for separately planned studies). We then broke each shell into fragments using
148 forceps, examined fragments under a binocular microscope, and recorded all animals found
149 encapsulated within the shell as in e.g. Gérard et al. (2023). A total of 606 nematodes were
150 found in 104 shells; no other metazoan parasites were recorded. As this method is destructive,
151 we took standardised photographs of the shells beforehand (dorsal and apertural views
152 following Callomon, 2019) for archival and potential future studies.

153 **Statistical analysis**

154 All analyses were done in R version 4.3.2 (R Core Team, 2023), with the help of the *tidyverse*
155 (Wickham et al., 2019) and *sf* (Pebesma, 2018) packages for data processing, as well as
156 additional packages detailed below for model fitting and exploration.

157 We analysed the probability a shell contained nematodes as a binary yes/no response at the
158 individual level, using Generalized Linear Mixed Models (GLMMs) (binomial family, logit link).
159 We ran six models; the first five all included shell size, shell morph traits (background colour,
160 band number and fusion), urbanisation and city identity (Brussels, Ghent or Leuven) as fixed
161 effects, only differing by which urbanisation metric they used (among the five described above
162 in **Urbanisation metrics**). Numeric predictors were centred and scaled to unit 1 SD. Sampling
163 site was included as a random intercept. The sixth model was a “null” model, identical to the
164 other ones except that it did not include an urbanisation metric. We ran our models using the
165 *glmmTMB* package (Brooks et al., 2017), and then used AICc to compare them. As one model
166 largely outperformed the others (see **Results**), we did all further analyses on that best model.

167 We checked for residual spatial autocorrelation using a spline correlogram (*ncf* package,
168 Bjornstad, 2022), and found no evidence of spatial structure in the best model. We then used
169 the *car* (Fox & Weisberg, 2019) and *emmeans* (Lenth, 2023) packages to test for overall effects
170 of our variables in the best model and to run (Tukey-corrected) pairwise comparisons,
171 respectively. Finally, we estimated the marginal and conditional R^2 (Nakagawa & Schielzeth,
172 2013) as measures of the proportion of variation explained by fixed effects (R_m^2) and both fixed
173 and random effects (R_c^2) respectively (using the delta method, Nakagawa et al., 2017).

174 **Results**

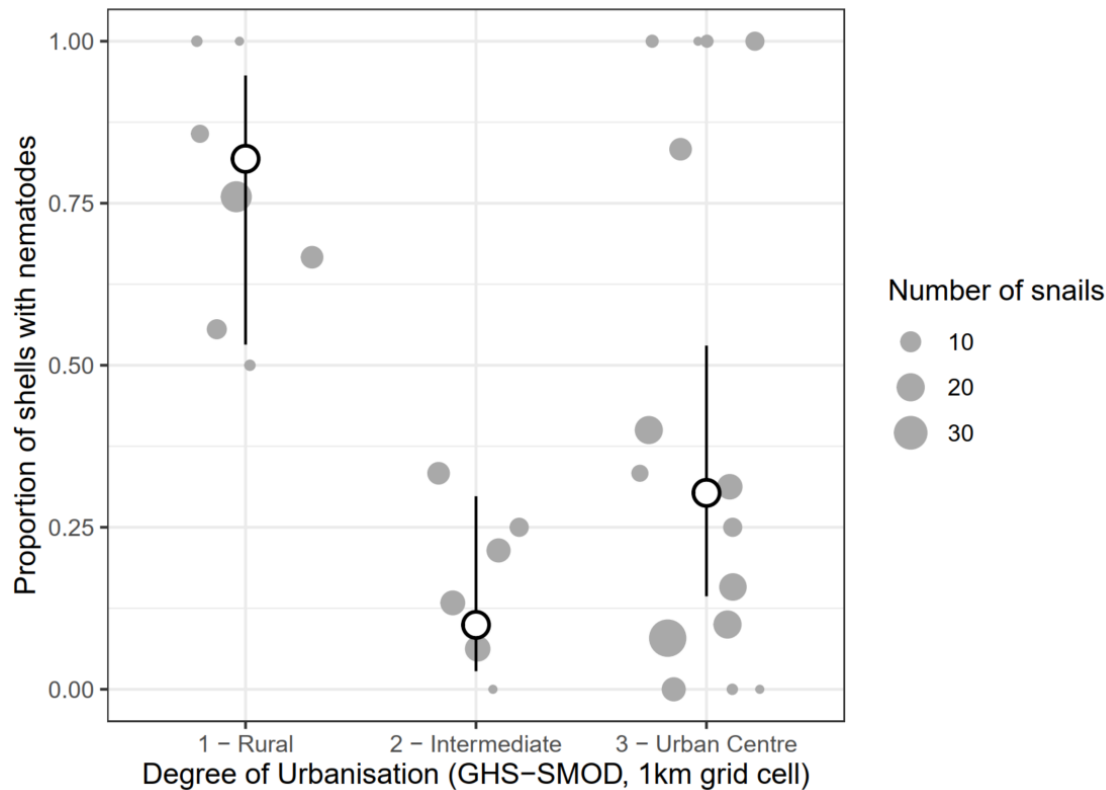
175 The model using the categorical Degree of Urbanisation (GHS-SMOD) as an urbanisation metric
176 outperformed all other models based on AICc (**Table 1**). Fixed effects and random effects

177 explained similar amounts of variance ($R_m^2 = 0.19$; $R_c^2 = 0.38$). The probability that a shell had
178 trapped nematodes was dependent on urbanisation level ($\chi^2 = 15.97$, $df = 2$, $p = 3.40 \times$
179 10^{-4}) but did not vary significantly between cities ($\chi^2 = 3.89$, $df = 2$, $p = 0.14$). Snails from
180 rural sites were more likely to contain nematodes than snails from intermediate and Urban
181 Centre populations (**Fig. 2**; rural - intermediate difference on the logit scale \pm SE: 3.71 ± 0.95 ;
182 rural - Urban Centre difference: 2.34 ± 0.77). Larger shells were more likely to contain
183 nematodes ($\chi^2 = 4.17$, $df = 1$, $p = 0.04$; standardised coefficient $\beta = 0.35 \pm 0.17$). There was
184 no clear evidence that any of the shell colour traits affected encapsulation rates (background
185 colour: $\chi^2 = 2.17$, $df = 2$, $p = 0.34$; band number: $\chi^2 = 1.90$, $df = 1$, $p = 0.17$; fusion:
186 $\chi^2 = 0.17$, $df = 1$, $p = 0.68$).

187

188 **Table 1.** Model selection table for the effect of urbanisation on shell encapsulation rates. All models
 189 otherwise include effects of city identity, shell size and shell morph (background colour, number of
 190 bands and band fusion).

Urbanisation variable in model	df	log-likelihood	AICc		AICc weight
Degree of Urbanisation categories (SMOD, 1000 m resolution grid)	11	-149.5	322.0	0.00	0.95
None ("null" model)	9	-155.9	330.4	8.43	0.01
Population density (1000 m resolution grid)	10	-155.2	331.1	9.11	0.01
Built-up surface (1000 m resolution grid)	10	-155.4	331.5	9.49	0.01
Population density (100 m resolution grid)	10	-155.4	331.6	9.61	0.01
Built-up surface (100 m resolution grid)	10	-155.6	331.9	9.91	0.01



191
 192 **Figure 2.** Effect of the Degree of Urbanisation in 1000 m grid cells on the probability a snail shell
 193 contained encapsulated nematodes. Grey dots are observed proportions per population, with the size of
 194 the dot proportional to the number of snails; white dots (and error bars) are estimated marginal means
 195 from the best model (and their 95% confidence intervals), with the effects of the other predictors
 196 averaged out.

197 Discussion

198 We found that population differences in the prevalence of *Cepaea nemoralis* snails
199 encapsulating nematodes in their shell as a defence mechanism were partly driven by
200 environmental conditions, with trapping rates decreasing with increasing urbanisation (**Fig. 2**).
201 This effect was better explained by a categorical classification of the Degree of Urbanisation,
202 rather than by linear effects of continuous urbanisation variables. This indicates that the
203 response to urbanisation is here non-linear, as the increases in population density/built-up rates
204 needed to go from a rural to an intermediate area are much smaller than those needed to go
205 from intermediate to Urban Centre, and most of the variation in density/built-up is within Urban
206 Centres rather than between categories (**Supplementary Material S1**).

207 A difficulty for interpreting our results is that nematodes trapped in shells will accumulate with
208 time (Williams & Rae, 2015; Rae, 2017), meaning that as they may have endured more
209 infections, older snails may be more likely to have them. If urbanisation reduces snail survival
210 rates, a plausible proposal because snail survival is strongly temperature-dependent (e.g.
211 Wolda, 1967) and cities are generally hotter environments (Manoli et al., 2019), then our urban-
212 rural differences in nematodes trapped might merely reflect differences in average snail
213 age/survival. Age estimation in shelled gastropods, especially in terrestrial snails with
214 determinate growth like *Cepaea*, is notoriously challenging. There are documented proxies of
215 time to maturity, such as the number of dormancy-induced growth stops visible on the shell, or
216 of adult age, such as shell wear or shell layers in cross-sections (Pollard et al., 1977; Williamson,
217 1979). However, they are imprecise, and we may expect them to vary in response to
218 urbanisation, as spatial variation in local climate can lead for instance to spatial variation in
219 dormancy regimes (Staikou et al., 2024), and so potentially in the relationship between age and
220 growth stops. This could make these proxies useless to compare age between populations, as
221 would be needed here, unless thorough calibration studies are undertaken. We note though,
222 reassuringly, that the number of nematodes found in infected shells does not seem to decrease
223 in more urbanised sites (**Supplementary Material S2**). This is contrary to what we would expect
224 if variation in shell encapsulation was primarily explained by variation in age/time available to
225 accumulate nematodes and urban snails were on average younger.

226 If we assume that our results reflect differences in snail-nematodes interactions between urban
227 and non-urban areas, several mutually non-exclusive mechanisms may explain why urban
228 *Cepaea nemoralis* shells are less likely to trap nematodes. Each of these mechanisms directly
229 suggests potential tests for future studies:

- 230 • First, snail parasitic nematodes infecting *C. nemoralis* may be less abundant in cities.
231 Many of the nematodes known to infect land snails have at least one free-living life stage
232 in the soil, and some are facultative parasites (Morand et al., 2004; Pieterse et al., 2017).
233 Increasingly impervious substrates in cities (Parris, 2016) may deprive these of habitat
234 critical for their life cycle. Where habitat is available, soil nematode communities are
235 profoundly altered by urbanisation, like other taxa (Li et al., 2022; Gong et al., 2024).
236 However, this does not lead to overarching declines in nematode abundance; rather,
237 some trophic groups decline while others thrive (Li et al., 2022; Gong et al., 2024).

238 Unfortunately, detailed information on nematodes parasitizing animals is typically
239 lacking from these analyses; soil sampling specifically targeting parasitic nematodes
240 (Jaffuel et al., 2019) would here be particularly useful.

241 • Second, individual differences in behaviour, especially space-related behaviour, may lead
242 to differences in the risk of encountering and then being infected by parasites (Barber &
243 Dingemans, 2010). In chipmunks (*Tamias sibiricus*), some individuals are consistently
244 more explorative than others, which affects their risk of encountering ticks (Boyer et al.,
245 2010). A similar result was also found in firebugs (*Pyrrhocoris apterus*) (Gyuris et al.,
246 2016). Habitat loss and fragmentation associated with urbanisation are expected to
247 exert strong selection pressures on movement and space use (Cote et al., 2017). If this
248 results in lower movement in urban snail populations, this might then reduce their
249 encounter rates with parasites. In the snail *Cornu aspersum*, another related species
250 commonly found in cities, urbanisation does not seem to lead to reduced boundary-
251 crossing behaviour in that species however (Dahirel et al., 2016), although that is only
252 one component of mobility. Urbanisation-induced increases in temperature may also
253 alter the frequency at which snails hide into shelters or climb above the substrate (Rosin
254 et al., 2018), and potentially again the risk of encountering parasites. The picture is
255 however complicated by behaviour-parasite feedbacks, where while host behaviour
256 shapes infection risk, infection can then alter host behaviour in turn (Ezenwa et al.,
257 2016). In *Cepaea nemoralis*, nematode infection itself might lead to reduced movement
258 propensity, but only in some morphs (Dahirel et al., 2022). More studies of movement
259 behaviour across urbanisation gradients are here needed.

260 • Third, shell encapsulation rates are not direct records of snail-nematode interactions,
261 but rather informative on the host's ability to mount a defence in such interactions. This
262 defence is not always effective, as demonstrated by cases where field-caught snails
263 showed active infections but zero shell-trapped nematodes (see e.g. data in Dahirel et
264 al., 2022). If immune response in general and the pathways involved with shell
265 encapsulation specifically decline with urbanisation, then this alone could explain our
266 results even in the absence of changes in nematode communities. In vertebrates,
267 available evidence suggests that urban living can lead to both depressed or stimulated
268 immune function, depending on taxon and context, especially food availability (Murray
269 et al., 2019; Minias, 2023). In terrestrial molluscs, chemical pollutants seem to negatively
270 impact many, but not all, physiological components of immune defence (Radwan et al.,
271 2020). In the freshwater snail *Lymnaea stagnalis*, higher temperatures led to declines in
272 immune function (Leicht et al., 2017). The exact physiological pathways involved in shell
273 encapsulation in land molluscs remain however unstudied, to the best of our knowledge.

274 On the phenotype side, larger shells were more likely to contain trapped nematodes. This could
275 be the result of survivor bias alone, if larger snails are more likely to survive infection. Although
276 we cannot exclude that other nematodes have larger effects, experimental nematode infections
277 by *Phasmarhabditis* are almost never lethal in adult *Cepaea nemoralis*, contrary to other snail
278 species (Wilson et al., 2000; Williams & Rae, 2016). Other potential explanations for this result

279 can be sorted along three non-exclusive lines, similar to the mechanisms suggested above to
280 explain the effect of urbanisation:

281 • Larger snails might harbour larger parasite infections (e.g. Daniels et al., 2013), which
282 would increase the likelihood that some nematodes are trapped. However, there is no
283 link between nematode abundance in active infections and snail size in *C. nemoralis*
284 (Dahirel et al., 2022). Furthermore, although our sample size is small, we find no clear
285 effect of body size on the number of nematodes trapped in the present study
286 (**Supplementary Material S2**).

287 • If large and small snails differ in their space use, they might also differ in their parasite
288 exposure risk. On the one hand, while only one dimension of space use was tested, there
289 was no link between short-term movement and size in adult *C. nemoralis* (Dahirel et al.,
290 2022). On the other hand, there is a positive correlation between adult size and
291 emigration propensity (Oosterhoff, 1977).

292 • Finally, small and large snails may differ in their immune defence abilities. Comparative
293 studies suggest that large and small snail species and subspecies differ in their immune
294 strategies at the physiological level (Russo & Madec, 2011, 2013). However, the range of
295 body size and life history variation is much larger in these scenarios than among adults
296 of *C. nemoralis*, limiting the transferability of these results. Larger adults might also be
297 larger because they were able to access more or better resources during development,
298 which may make them able to defend against parasites more easily. However, the link
299 between resource quality or access and adult size (as opposed to growth rate or adult
300 mass) is actually ambiguous in helcid snails (Wacker & Baur, 2004; Nicolai et al., 2012).
301 More physiological studies focused on within-, rather than among-species variation may
302 help understand better this link between body size and encapsulation rates.

303 In contrast to shell size, we found no relationship between any of the shell colour traits and
304 nematode trapping rate. This confirms experimental results from Williams & Rae (2016) using
305 infections by *Phasmarhabditis elegans*. However, colour morphs do differ in active infection
306 rates or other aspects of immune response in *C. nemoralis* (Dahirel et al., 2022) and other
307 polymorphic snails (Scheil et al., 2013, 2014). This discrepancy may indicate that shell
308 encapsulation is driven by different physiological pathways than other components of snail
309 immune defence.

310 Beyond the effects of phenotype or environment, how to relate the prevalence of nematodes
311 trapped in shells with rates of active parasite infections remains an open and complex question.
312 We were not able to compare the two here as snail bodies were reserved for other
313 investigations. Nematodes trapped in shells reflect the cumulative history of infection, which
314 may or may not be meaningfully correlated with active infection at a given time. For instance, if
315 variation in snail-nematode interactions is driven by e.g. variation in nematode density in the
316 environment, we may expect a positive correlation, as higher nematode densities should drive
317 up rates of both shell encapsulation (Rae, 2018) and active infection (although if encapsulation
318 is highly effective, it may end up suppressing dose-dependent effects on active infection,
319 Williams & Rae, 2015). On the other hand, if variation is mostly driven by snail immune

320 response, we may expect a negative correlation instead: nematode density being equal, snails
321 with more effective immune systems may be more likely to successfully trap nematodes in
322 shells while being less likely to harbour active infections. Additionally, we do not know much
323 about whether some nematode species are more likely than others to end up trapped in shells
324 (identification by sequencing of encapsulated nematodes may be promising here, Cowlshaw et
325 al., 2019). While this would need to be validated, the strength and direction of between- and
326 within-sites correlation between active infections and shell-trapped nematodes may provide
327 useful indicators of the main drivers of snail-nematodes interactions in response to city life.

328 We acknowledge that the relatively small size of our sample does not allow us to draw firm
329 causal conclusions. Nonetheless, we hope our results may encourage larger studies regarding
330 host-parasite interactions in land molluscs in the context of environmental change. As new
331 technical developments such as micro-CT imaging allow non-destructive analyses of snail shells
332 (Falkingham & Rae, 2021), these may extend to using museum and other natural history
333 collections to understand how interactions vary in space and time (Cowlshaw et al., 2019),
334 reaffirming their value for urban ecology and evolution (Shultz et al., 2020).

335 **Author contributions**

336 Initial study idea: MD, DB. Site selection and fieldwork: MD, HR, KDW. Shell data collection: HR,
337 after initial training by MD. Data analysis: MD, after preliminary analyses by HR. Initial
338 manuscript draft: MD. All authors contributed critically to edits and gave final approval for
339 publication.

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345 **Conflict of interest disclosure**

346 The authors declare they have no financial conflict of interest in relation with the content of this
347 article. DB is a recommender for PCI Ecology and PCI Evolutionary Biology.

348 **Data availability**

349 Data and R scripts to reproduce all analyses presented in this article, as well as a copy of the
350 Supplementary Materials, are available on Github (https://github.com/mdahirel/HELICITY-2022_shell-nematodes)
351 and archived in Zenodo (DOI:
352 <https://doi.org/10.5281/zenodo.10794928>).

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