



Peer Community In Ecology

Urbanisation linked to a decline in the proportion of snails with trapped nematodes in their shell

Alison Duncan based on peer reviews by **Robbie Rae** and 1 anonymous reviewer

Maxime Dahirel, Hannah Reyné, Katrien De Wolf, Dries Bonte (2024) Urban *Cepaea nemoralis* snails are less likely to have nematodes trapped within their shells. bioRxiv, ver. 4, peer-reviewed and recommended by Peer Community in Ecology.

<https://doi.org/10.1101/2024.03.07.583959>

Submitted: 11 March 2024, Recommended: 26 August 2024

Cite this recommendation as:

Duncan, A. (2024) Urbanisation linked to a decline in the proportion of snails with trapped nematodes in their shell. *Peer Community in Ecology*, 100687. [10.24072/pci.ecology.100687](https://doi.org/10.24072/pci.ecology.100687)

Published: 26 August 2024

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Urbanisation modifies species' habitats affecting their density, distribution, fitness, and behaviour with knock-on effects for their parasites' abundance and transmission (Bradley & Altizer 2007). A meta-analysis found that changes in resource provisioning due to anthropogenic change can have both positive and negative effects on parasite infection in wildlife populations, but that feeding on urban waste had an effect of reducing infection, especially for helminths and protozoa (Becker, Streicker & Altizer 2015). Another study found that urbanisation reduced ectoparasite load in birds, but had no effect on endoparasites or avian flu (Reid et al. 2024). These changes may be due to novel diets reducing transmission via predation upon trophic hosts (Becker, Streicker & Altizer 2015) or behavioural, leading to more time available to preen (Reid et al. 2024). Less is known about how urbanisation affects invertebrates (but see Lewthwaite et al., 2024) and their parasites. This is important considering that invertebrates are often intermediate hosts of, and/or vector other parasites.

Recent work has found that snails and slugs can trap nematodes in their shells to prevent infection (Rae 2017). This newly discovered resistance mechanism reveals that the shell serves an immune defence function. It also provides a record of nematode exposure and documents incidences of resistance to infection as the trapped nematode becomes fixed onto the shell surface (Rae 2017). Dahirel and co-authors exploit this to investigate whether snail-nematode interactions change in response to increasing levels of urbanisation (Dahirel et al. 2024).

They explore whether the proportion of *Cepaea nemoralis* snails with trapped nematodes in their shell changes across an urbanisation gradient. They also explore whether different phenotypic snail traits, notably shell size, colour, band number and fusion explain the likelihood of having trapped nematodes in their shells.

An increase in urbanisation was associated with a decrease in the proportion of snails with trapped nematodes in their shells. At the same time larger shells were more likely to have trapped nematodes, but this effect did not change across the urbanisation gradient.

The authors discuss that reduced nematode encapsulation in urban environments may be due to lower encounter rate due to either fewer nematodes in urban environments, changes in snail behaviour reducing exposure, or alternatively that urban snails were less resistant to nematode infection.

It will be interesting to investigate how this resistance mechanism is related to other forms of snail immunity and whether high rates of nematode encapsulation are an indicator of high resistance or high exposure. This will enable nematode trapping to be used as a marker to indicate environments and/or snail populations harbouring high levels of parasitism and further exploitation of museum collections to understand host-parasite interactions in the past (Rae 2017).

References:

Becker, D.J., Streicker, D.G. & Altizer, S. (2015) Linking anthropogenic resources to wildlife-pathogen dynamics: a review and meta-analysis. *Ecol Lett*, 18, 483-495. <https://doi.org/10.1111/ele.12428>

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Maxime Dahirel, Hannah Reyn , Katrien De Wolf, Dries Bonte (2024) Urban *Cepaea nemoralis* snails are less likely to have nematodes trapped within their shells. *bioRxiv*, ver.4 peer-reviewed and recommended by PCI Ecology <https://doi.org/10.1101/2024.03.07.583959>

Lewthwaite, J.M.M., Baiotto, T.M., Brown, B.V., Cheung, Y.Y., Baker, A.J., Lehnen, C., McGlynn, T.P., Shirey, V., Gonzalez, L., Hartop, E., Kerr, P.H., Wood, E. & Guzman, L.M. (2024) Drivers of arthropod biodiversity in an urban ecosystem. *Sci Rep*, 14, 390. <https://doi.org/10.1038/s41598-023-50675-3>

Rae, R. (2017) The gastropod shell has been co-opted to kill parasitic nematodes. *Sci Rep*, 7, 4745. <https://doi.org/10.1038/s41598-017-04695-5>

Reid, R., Capilla-Lasheras, P., Haddou, Y., Boonekamp, J. & Dominoni, D.M. (2024) The impact of urbanization on health depends on the health metric, life stage and level of urbanization: a global meta-analysis on avian species. *Proc Biol Sci*, 291, 20240617. <https://doi.org/10.1098/rspb.2024.0617>

Reviews

Evaluation round #4

DOI or URL of the preprint: <https://doi.org/10.1101/2024.03.07.583959>

Version of the preprint: 4

Authors' reply, 13 August 2024

Dear Alison,

Thank you for your swift reply regarding our latest changes to the manuscript PCI Ecology #687.

Regarding the specific request for the plain text version of all data columns:

- this was already done: see https://github.com/mdahirel/HELICITY-2022_shell-nematodes/blob/main/data/HELICITY22_sitesdata_converted_from_gpkg.csv, first uploaded five days ago for

the site-level information. The comment seems to imply that phenotypic data were also “locked” behind the geopackage format; this was never the case and phenotypic data were always in their own csv tables from the start (phenotype and sites are in their own separate data files due to our adherence to “tidy data” structuring principles).

- The analysis.qmd file has been updated as of today with an additional explanation referring to this new file, to further clarify things. (lines 87-100 of the current version of analysis.qmd)(all files are up to date in the DOI-referenced archive on Zenodo).

- Result parity between the reference analyses using the original geopackage and the alternative ones using csv input reconverted in geospatial format within the analysis code has been checked and confirmed

- In any case, geopackages are standard and widely used open-source formats for geographic data, which can be opened from any software with geospatial capacities (including Python or GIS software). In R specifically, any R installation with the sf package loaded (which is explicitly required to run the analysis code) can read them without any issue (see line 33 in analysis.qmd). Running the analysis.qmd code requires the sf package for other functions beyond loading this specific file.

We stand by our decision to have all our modelling choices stem directly from either existing literature results or upstream data analyses themselves based on the literature, rather than broad data exploration, and therefore do not make further changes to the manuscript itself in response to the remaining general comment. The preprint version number is as a result unchanged.

Best regards,

Maxime Dahirel, on behalf of all authors

Decision by Alison Duncan, posted 13 August 2024, validated 13 August 2024

Dear Maxime,

Thank you for your responses. I am absolutely fine with your replies to queries 1 and 3.

I am still though not convinced that an inclusion of an additional 3 models each with a 2-way interaction (or one model with these 2-ways interactions) is fishing. Surely the premise of the whole paper is then ‘fishing’ as there are no clear predictions as to how any of these variables would impact nematodes being trapped in snail shells. Even if overall each of these variables does not have a significant effect, it is quite possible that there may be a significant interaction with urbanisation.

Either way, if you really insist on not including it, please can you provide an easily accessible data sheet (e.g. CSV) containing the urbanisation metric and the different phenotypic measures (size, band number etc). This way people who prefer to use different statistical packages can easily access your data. For info, I cannot access or download the gpkg file with the urbanisation data or call it in R.

Kind regards, Alison

Evaluation round #3

DOI or URL of the preprint: <https://doi.org/10.1101/2024.03.07.583959>

Version of the preprint: 3

Authors’ reply, 12 August 2024

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Decision by [Alison Duncan](#), posted 30 July 2024, validated 03 August 2024

Minor revisions of preprint

Dear Maxime,

Thank you for your reply. I can now see from the revised version of the supplementary materials the models including the interaction between size and urban metrics. However, I still do not completely agree with your replies.

1. I understand that the model with the interaction term has an AICc of 323.1 which is larger than 322. However, the difference in AICc is < 2 meaning these models are equivalent. This means that you cannot say that the model without the interaction is the better model -the models with and without the interaction are comparable. In this scenario you should discuss that you can't distinguish whether there is or isn't an interaction between size and urbanisation and future work needed to uncover this.

2. I agree that you have limited power to detect all interactions. However, it would be interesting for the reader to compare models that include different 2-way interactions restricted to effects already included in the model. Please can you do this (at least) for the 'Degree of Urbanization categories (SMOD)' metric with each of the phenotypic measures. You can include fusion versus no fusion as a categorical variable. There should not be a problem for estimating the best fit model using AICc if only including these 2-way interactions.

Only including these interactions are justified based on the fact that it is interesting to see how changes in different phenotypic measures across an urbanisation gradient change encapsulation and risk of nematode infection.

This information can be included in the Supplementary materials.

3. You need to be more explicit in your discussion with regards to the 5 sites with a high proportion of nematodes. State that you cannot identify any cause of why these 5 sites have $> 75\%$ encapsulated nematodes.

Kind regards,

Alison

Reviewed by anonymous reviewer 1, 08 July 2024

Dear recommender,

I have red version 3 of the manuscript entitled "Urban *Cepaea nemoralis* snails are less likely to have nematodes trapped within their shells". The authors kindly addressed the suggestions made to the previous version of the manuscript and clarified all the raised issues. I have not further comments or suggestions.

Best!

Evaluation round #2

DOI or URL of the preprint: <https://doi.org/10.1101/2024.03.07.583959>

Version of the preprint: 2

Authors' reply, 29 June 2024

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Decision by [Alison Duncan](#), posted 27 June 2024, validated 27 June 2024

Revisions of preprint

Dear Maxime,

Thank you for the revised manuscript. I have read the replies to the recommenders and the new version of the manuscript. I like the manuscript and think it will make a really nice contribution to PCI Ecology, but I disagree with the decision not to include the analyses including shell size. The discussion is not too long and so there is space to add this information. A difference <2 in AICc between two different models means that they are equivalent. This means that the model with the size*rural describes the data as well as the model without the interaction. Another option would be to re-run the analyses correcting for shell size as suggested by Reviewer 1 and present this in the results. Even though you found no overall effect of urbanization on snail size, there could still be an interaction with different size snails in different urban environments having differing levels of trapped nematodes.

Please can you also add a sentence to the methods stating why you don't include all the interaction terms. It would make sense to include all interactions in the maximal model and then simplify based on those which are not significant. If the maximal model does not converge then why not just include all 2-way interactions.

Another point which may be interesting to explore is that Figure 3 shows that there seems to be 2 groupings among urban snails; some sites having very high nematode prevalences and the others low. Is there anything particular about the sites with high prevalence? You could re-run statistical models for only the urban group to see any of the explanatory variables are significant when only considering this group.

For information, there is only the old version of the Supplementary materials on bioRxiv and the data set made available does not include the urban metrics.

I really think these additions will add to the manuscript.

Kind regards, Alison

Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.1101/2024.03.07.583959>

Version of the preprint: 1

Authors' reply, 07 June 2024

[Download author's reply](#)

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Decision by [Alison Duncan](#), posted 19 April 2024, validated 19 April 2024

Minor revisions of preprint

Dear Maxime,

Both reviewers have read your preprint and are very positive about your study. Both provide a few recommendations, mostly for clarification. Reviewer 1 also suggests that it would be interesting to repeat your analysis including an interaction between shell size and your urban metric to see if urbanisation is a factor impacting shell size and risk of nematode infection. Please can you respond the reviewer's recommendations, make the requested changes, or respond as to why you do not consider them appropriate.

Kind regards,

Alison Duncan

Reviewed by anonymous reviewer 1, 11 April 2024

Review of the manuscript entitled “Urban *Cepaea nemoralis* snails are less likely to have nematodes trapped within their shells”.

In this manuscript the authors assessed the effect of urbanization on host-parasite interactions, in particular on encapsulation of parasitic nematodes by the land snail *Capaea nemoralis*. They compare different metrics of urbanization and additionally measure other traits that may affect this defensive mechanism. They find that urbanization decreases the chances of finding encapsulated nematodes and discuss the possible explanations for this pattern.

I find this study well conducted and, overall, the analyses seem adequate and the discussion well framed. Additionally, the manuscript is clear and reading it was interesting and pleasant.

I only have one main recommendation and a few small suggestions.

Main recommendation:

In the statistics section the authors present the main models containing several fixed factors but they opted to not include interactions among such factors. I understand that the authors are mainly interested in the effect of such factors and not on the interactions among them. Additionally, most factors have no significant effects (so interactions are probably meaningless). However, the authors do find a significant effect of shell size on the probability of finding encapsulated nematodes (line 182/183). Lacking the interaction between this factor and the urbanization metric I wonder if rural snails have overall bigger shells and if this increases the chance of having encapsulated nematodes. Is that the case? If you standardize the data according to size, do you still find that rural populations are more likely to have encapsulated nematodes? It may be interesting to do an extra model including only the best urbanization metric, shell size and their interactions, to check if these two significant effects depend on each other or not. Either way it might be an interesting point to add on the discussion.

Minor comments:

Line 48: “...cross-taxon study **of** urbanization impacts...”

Line 49: please revise the word “seemed”. Is it your interpretation of some pattern observed in the cited work? Or do the authors show a tendency and not significant effects?

Line 50: please revise “small home ranges”. Do you mean habitat requirements? It is not clear.

Line 108: please remove “still”.

Line 249: please change “another related species” to “a related species”.

Line 251: removing “in the species however” may improve the flow of the sentence.

Line 285: do you mean body size or shell size?

Reviewed by **Robbie Rae**, 28 March 2024

OK, so I would answer yes to all the questions above. I really like your paper. It's written really well, it covers all the literature and the hypothesis is great. Your results are very clear and deserve to be published (it would be good for the embryonic field of nematodes getting trapped in shells :)). A few points in no particular order:

1. Please explain more about the number of nematodes found in the shells. The data is in supplementary but I think you could make more of nematode abundance e.g. I would like to know what the range of numbers of nematodes you found in the shells is and does that differ with location? The max I found was 101 nematodes in a snail shell...

2. In the discussion please change ‘*Phasmarhabditis elegans*’ to ‘*Phasmarhabditis hermaphrodita*’.

3. In general, I think your discussion is far too long and should be edited down a lot. I think you need to consider the fact there may not be many parasitic nematodes in cities compared to rural environments. You do touch on this, but there needs to be more.

4. Did you find any trematodes or mites in the shells?

5. I find it really interesting you found no difference in the numbers of nematodes trapped in the different morphs of shells. I also found this experimentally, but there is a general increase in the number of nematodes encapsulated in shells that have 0, 1 then 3 to 5 bands, so I just wonder if there is something going with the different morphs. (Sorry nothing for you to really add to the paper there, I'm just thinking).

6. Please can you add some pictures or a picture of nematodes being trapped in the shells?

Best of luck with the paper!

RR