

Spatiotemporal analysis of parasitic nematodes preserved in land snail shells

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Short Communication

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Abstract

Understanding how parasite abundance changes over time is inherently challenging, as trematodes, nematodes and cestodes degrade quickly and are poorly preserved. Here, I propose a novel approach for investigating the spatiotemporal dynamics of parasitic nematode infection by exploiting a key component of the snail immune system – the ability to trap and encapsulate these parasites within their shell. By utilising museum and modern collections, I was able to understand how nematode populations fluctuated in two species of snails (*Cepaea nemoralis* and *C. hortensis*) from three locations (Point of Ayr in Wales, Formby in England and Strathy beach in Scotland) from 1962 to 2024. I show that *in vivo* parasite populations collected from Point of Ayr in 1962 were initially low, with 8% of shells infected, but this dramatically increased to 60% in 2016 and fell to 10% in 2024. The number of *C. nemoralis* shells infected from Formby in 2016 was 18% but increased to 31% in 2024, and 27% of *C. hortensis* shells from Strathy beach in 2016 were infected by nematodes but plummeted to 3% in 2024. Thus, dramatic spatiotemporal changes in nematode abundance can be seen over several decades. By combining preserved snails in conchology collections with collections of modern specimens, empirical evidence of how parasite numbers change over time can be quantified.

Introduction

As global climate change, pollution, habitat conversion, and invasive species accumulate, it is unknown whether parasite abundance will decrease or increase (Wood and Vanhove 2023). We need more tools to systematically evaluate long-term changes in parasite burden (Wood et al. 2023a), as it is inherently difficult to track, as the soft bodies of nematodes, cestodes, and trematodes rapidly degrade, many are microscopic, and their remains contain insufficient amounts of DNA for analysis (Littlewood and Donovan 2003). However, museum collections of preserved specimens (and their associated parasites) have recently been proposed to monitor whether parasite abundance increases or decreases over time (Wood et al. 2023a). Indeed, Wood et al. (2023b), dissected parasites from eight fish species from 1880 to 2019 and found 10.9% decline in the abundance of parasites with three or more host species in their life cycle, which translates to a 38% decline with every 1°C increase in sea surface temperature in Pudget Sound, U.S. Undoubtedly, this is a novel discovery that has ramifications for conservation and fish management but how do parasites numbers fluctuate over time in terrestrial environments? One way to understand this is to examine parasites of terrestrial gastropods (slugs and snails), which are important intermediate hosts of a wide variety of nematodes of medical, veterinary, and ecological importance (Grewal et al. 2003). For example, the zoonotic rat lungworm *Angiostrongylus cantonensis*, the causative agent of human eosinophilic meningitis (Barratt et al. 2016), the feline lungworm *Aelurostrongylus abstrusus* (Elsheikha et al. 2016), and the canine and fox lungworm *Crenosoma vulpis* and *Trogostrongylus brevior*, all of which can cause respiratory diseases in domestic and wild carnivores (Crisi et al. 2018). As well as the slug parasitic nematode *Phasmarhabditis hermaphrodita* – a biocontrol agent formulated and commercialised to control slugs and snails in the U.K. and northern Europe (Rae et al. 2023) and the genetic model nematode *Caenorhabditis elegans* (Schulenburg and Félix 2017). Gastropods use behavioural adaptations to avoid nematode infection (Rae 2023; Wilson et al. 1999), but they also mount an understudied innate immune response including antimicrobial molecules such as reactive oxygen species, C-type lectins, and lysozymes (Davison and Neiman 2021). Furthermore, research has shown that upon nematode infection, swarms of haemocyte-like cells fix to the cuticle of invading nematodes and fuse it to the inner shell (Rae 2017). This encapsulation response has been observed in many species across the phylogeny of the Stylommatophora (slugs and snails), and is not just specific to nematodes (Falkingham and Rae 2021; Rae 2017; 2018; Rae et al. 2008; Williams and Rae 2015, 2016), as trematodes (Gérard et al. 2023), and maybe even mites (Dahirel et al. 2022) have been observed fixed inside the shell and killed. Indeed, it has been shown that land snails in conchology collections harbour encapsulated nematodes that are decades, even hundreds and thousands of years old (Rae 2017; 2018). However, there is no information about how nematode dynamics infecting snails fluctuate over time collected from

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one specific location. Understanding temporal variation in nematode abundance within terrestrial gastropods is important because changes in parasite prevalence and intensity directly influence transmission risk to humans, domestic animals and wildlife. Long-term monitoring can reveal how environmental change, including shifts in climate, habitat quality and host community composition, affects parasite dynamics and may identify periods of elevated disease risk (Hudson et al. 2006). Such information is essential for understanding parasite ecology, predicting future changes in transmission and informing surveillance of emerging gastropod-borne diseases (Poulin 2021). Hence, the main aim of this study was to utilise conchology collections and modern collections to understand how nematode dynamics change over time and how this differs with host and location.

Materials and methods

Museum and modern collections of *C. nemoralis* and *C. hortensis* shells

Three locations were chosen based on results of a previous study by Rae (2017), which highlighted areas of wild *C. nemoralis* or *C. hortensis* populations with high numbers of nematodes encased in their shells: Point of Ayr, Wales (SJ120853), Formby, England (SD280080) and Strathy beach, Scotland (NC835650). These two snail species were chosen as they are highly abundant in coastal sand dunes around the U.K., are regularly infected with nematodes (see Rae 2017), and were collected extensively around the U.K. by Arthur Cain et al. in the 1960s (e.g. Cain 1968), providing a substantial collection to monitor nematode abundance in the shells over time and at different locations. *C. nemoralis* and *C. hortensis* were collected at two time points (2016 and 2024) from Formby and Strathy beach, respectively. *C. nemoralis* from Formby and Point of Ayr were collected in 2016 by technicians and are stored at LJMU (outlined in Rae, 2017) and were re-examined for nematode encapsulation. Three time points were chosen to examine *C. nemoralis* shells from Point of Ayr (1962, 2016, and 2024). In 1962, *C. nemoralis* shells were collected from Point of Ayr by A. Cain and P.M. Sheppard (see Cook and Pettitt, 1998 for further info) and their analysis was published by Cain (1968). I accessed these *C. nemoralis* shells collected by Cain and Sheppard in 1962, which are housed at Manchester Museum as part of the Arthur Cain *C. nemoralis* collection, and quantified the number of nematodes in each shell (Figure 1A–C). It should be noted that, as well as nematodes found in the inner aperture of the shell, foreign objects, debris, and small roots can be easily recorded as nematodes but are not (see Supplementary Figure 1 for more guidance).

In 2024, *C. nemoralis* were collected from Point of Ayr and Formby sand dunes, and *C. hortensis* was collected from Strathy beach. In each case, sand dunes were explored for any dead *C. nemoralis* or *C. hortensis* shells for ~2 hours, then transported back the lab in clear, resealable bags, gently washed in warm water to remove sand and vegetation and left for dry for 48 hours before examination of the inner lip of each shell for nematodes using a dissecting microscope at magnification using $\times 40$ and the numbers encapsulated was quantified. Only the shells of dead snails were collected. To understand whether the size of *C. nemoralis* shells affected nematode encapsulation (i.e. larger shells harbour more parasites), shells from Formby (2016 and 2024) and Point of Ayr (2016 and 2024) were individually weighed (g) (this was not possible for *C. hortensis* or for *C. nemoralis* from 1962). It should be noted that *C. nemoralis* is a polychromatic snail with several

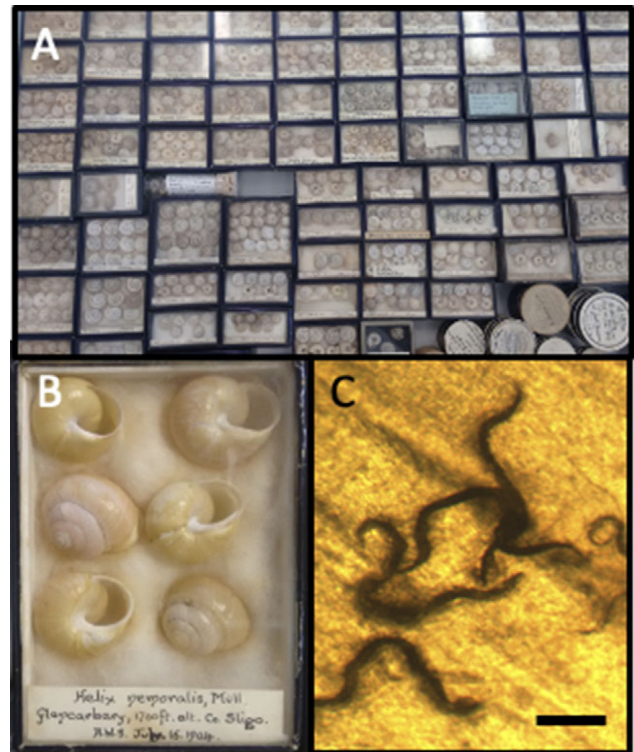


Figure 1. Museum conchology collections hold a plethora of molluscs from all over the world (A) that are hundreds, if not thousands, of years old, e.g. *C. nemoralis* from 1904 (B). Nematodes can be found encased and preserved in the inner part of the whorl of *C. nemoralis* (C). Scale bar represents 0.5 cm.

different colour and banding morphs, and this was not considered, as most shells collected were 3–5 banded yellow shells (>60%), and there were not enough morphs of the other varieties to allow comparisons.

Statistical analysis

The numbers of nematodes encapsulated in *C. nemoralis* or *C. hortensis* shells (as well as the weight of shells) collected in 2016 vs. 2024 were compared using a Student's t-test. A One-Way Analysis of Variance with Tukey's post hoc test was used to compare the numbers of nematodes encased in *C. nemoralis* shells collected in 1962 vs. 2016 vs. 2024. Chi-squared tests were used to analyse the proportion of snails with and without nematodes in their shells from each year of collection. A negative binomial generalized linear model (GLM), with shell weight, sampling time, and their interaction included as explanatory variables, was used to understand whether larger shells harboured more nematodes from *C. nemoralis* from Formby (2016 and 2024). Data analysis was carried out using Python3 (Version 3.14) using scipy.stats and statsmodels libraries.

Results and discussion

The proportion of *C. nemoralis* shells from Point of Ayr that had nematodes present increased significantly from 1962 (8.1%) to 2016 (59.7%) ($X^2 = 127.18$; $df = 1$, $p < 0.001$), then significantly decreased to 10% in 2024 ($X^2 = 45.41$; $df = 1$, $p < 0.001$). The

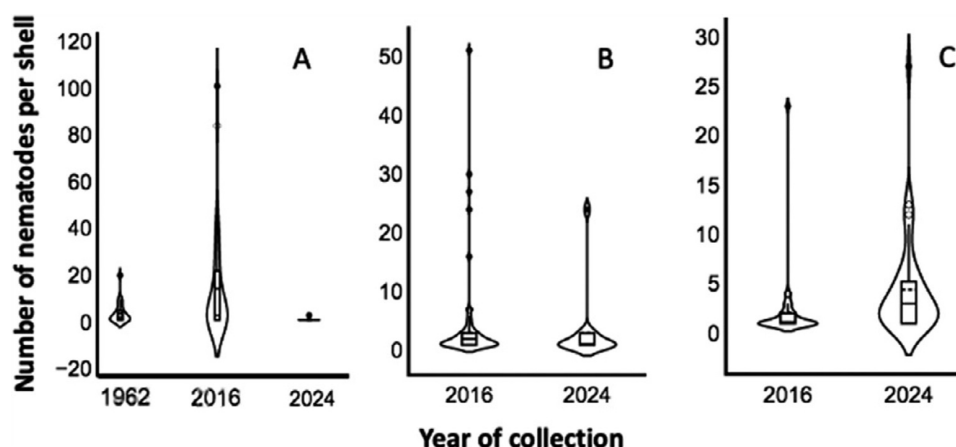


Figure 2. Violin plots illustrate the distribution of the number of nematodes encased in *C. nemoralis* shells from Point of Ayr collected in 1962, 2016, and 2024 (A), *C. hortensis* collected from Strathy beach in 2016 and 2024 (B) and Formby in 2016 and 2024 (C). The inner box represents the interquartile range (IQR), and the horizontal line denotes the median. Violin width indicates the density of observations.

numbers of nematodes in shells from 1962 ($n = 41$ shells, mean = 3.7 nematodes per shell ± 0.6 ; range 1 to 20), 2016 ($n = 40$ shells, mean = 14.1 nematodes per shell ± 3.5 ; range 1 to 101) and 2024 ($n = 9$ shells, mean = 1.2 nematodes per shell ± 0.2 ; range 1 to 3), differed significantly ($F = 5.98$; $df = 2,86$, $p = 0.004$), with the numbers of nematodes encased in shells from 1962 and 2016 increasing significantly ($p < 0.05$) (Figure 2A).

The proportion of *C. hortensis* shells from Strathy beach with nematodes (compared to without nematodes) decreased significantly from 2016 (26.7%) to 2024 (3.1%) ($X^2 = 72.52$; $df = 1$, $p < 0.001$). There was no significant difference between the numbers of nematodes found in *C. hortensis* shells collected from Strathy in 2016 ($n = 128$ shells, mean = 3.1 nematodes per shell ± 0.5 ; range 1 to 51) and 2024 ($n = 14$ shells, mean = 3.1 nematodes per shell ± 1.6 ; range 1 to 24) ($t = 0.09$; $df = 140$; $p > 0.05$) (Figure 2B). There was no significant difference in shell weight of *C. nemoralis* collected in Point of Ayr in 2016 (0.67 ± 0.02 g; $n = 55$) and those collected in 2024 (0.58 ± 0.06 g; $n = 18$) ($t(71) = 1.57$, $p = 0.121$).

In Formby, the proportion of *C. nemoralis* shells with nematodes (compared to without nematodes) increased significantly in 2016 from 17.6% to 31.3% in 2024 ($X^2 = 8.35$; $df = 1$, $p = 0.039$). The numbers of nematodes found in *C. nemoralis* shells collected from Formby in 2016 ($n = 36$ shells, mean = 2.1 nematodes per shell ± 0.6 ; range 1 to 23) and 2024 ($n = 41$ shells, mean = 4.4 nematodes per shell ± 0.8 ; range 1 to 27) increased significantly ($t = -2.54$; $df = 76$; $p < 0.05$) (Figure 2C). Shells collected in Formby 2024 were significantly heavier (1.05 ± 0.04 g; $n = 82$) than those collected in 2016 (0.6 ± 0.03 g; $n = 68$) ($t(148) = -9.52$, $p < 0.001$). A negative binomial regression was used to assess the effects of shell weight and sampling year on parasite abundance at this site. Sampling year significantly affected parasite numbers, with higher parasite burdens recorded in 2024 compared with 2016 ($\beta = 0.76$, $z = 2.75$, $p = 0.006$). Shell weight did not significantly predict parasite abundance ($\beta = 0.41$, $z = 1.20$, $p = 0.232$), suggesting that parasite load was not strongly related to host size at this location.

The value of historic collections to understand parasite abundance and diversity cannot be overstated (Wood et al. 2023a) and has only recently been explored to track parasite infection abundance through time (albeit in marine environments). For example, Welicky et al. (2021) dissected parasites from museum specimens

of English sole (*Parophrys vetulus*) collected over a 90-year period (1930–2019) and found that out of the 12 taxa, 9 did not change in abundance (e.g. nematodes, trematodes, and leeches), 2 increased (an acanthocephalan and a trematode), and another trematode species decreased. Also, by examining museum specimens, Howard et al. (2019) detailed an 8-fold increase in the nematode *Clavinema mariae* (a parasite of English Sole) in Puget Sound from 1930 to 2017. These studies have undoubtedly provided important insights into parasite dynamics in marine environments. By utilising conchology and field collections of snails, I have been able to detail parasite burden of terrestrial environments and show nematode infection of land snails is a dynamic process that differs substantially over time, between locations and host species. For example, 8% of *C. nemoralis* shells collected in Point of Ayr in 1962 had encased nematodes, and this increased substantially to 60% in 2016, and decreased to 10% in 2024. There was also a reduction in the number of nematodes encased in *C. hortensis* shells from Strathy beach from 27% infected in 2016 to 3% in 2024. This is not the trend for all locations. Indeed, the opposite was found in *C. nemoralis* shells from Formby, with the proportion of shells with encased nematodes increasing from 18% in 2016 to 31% in 2024. However, two important points about these data need to be considered. First, it should be noted that it is unclear whether encapsulated nematodes in the snails' shells represent the actual burden of the nematodes in a snail host population, as I did not dissect live snails. Encapsulation could therefore reflect infection, snail immune response, or any other process influencing the number of worms that get encased. Second, it is unclear whether the data is capturing long-term variability or short-term ebbs and flows of parasite population abundances. Other studies have reported similar results in parasites of crabs (*Hemigrapsus oregonensis* and *H. nudus*) from historical and contemporary time points where the abundance of parasitic isopods (*Portunium conformis*) varied around a stable mean for 50 years; there was no change in larval acanthocephalans, and the prevalence of microphallid trematodes increased over 50 years (Quinn et al., 2021). Only further validation studies examining the parasite burden of live snails, the mechanics of the encapsulation and immune response, and at regular intervals will be able to help answer these questions.

It is difficult to understand why nematode numbers decrease, even increase over time; perhaps urbanisation, climate change, and environmental pollution could have an effect, which has been shown in other studies. For example, Díaz-Morales et al. (2026) found the abundance of the myxozoan parasite *Myxobolus* infecting *Carpodius velifer* gills decreased by 86% from 1963 to 2005, due to increasing temperature and higher metal concentrations. In contrast, Mastick et al. (2024) discovered an increase in the numbers of *Anisakis* nematodes in tinned chum and pink salmon over 42 years, potentially due to increases in numbers of marine mammal hosts.

In terms of identifying what nematode species are encapsulated in these shells, DNA and morphological analysis identified *Phasmarhabditis californica*, and a species of mermithid infecting *C. nemoralis* (Rae 2017). This approach has been more successful in other snail species; for example, recently, Fuster-Calvo et al. (2026) managed to identify 147 nematode operational taxonomic units (OTUs) representing 3 classes and 14 orders of nematodes infecting *Naesiotus* snails from the Galápagos Islands. Also, in *Cornu aspersum*, nematodes such as *C. elegans* were found encased in shells, but the efficacy of PCR can be hindered by different factors in the shell, such as calcium content, which is a known inhibitor of PCR (Cowlishaw et al. 2019), and requires further research to optimise conditions.

In summary, conchological collections could represent a valuable resource for understanding parasite abundance, as they comprise extensive assemblages of shells from diverse species, geographic regions and at different time periods. For example, Manchester Museum holds the fourth largest mollusc collection in the U.K., with approximately 166,000 lots and 400,000 specimens (McGhie 2008). Such collections may therefore be used to investigate temporal patterns in shell-associated parasites, including nematodes, trematodes, and mites, across extended timescales.

Supplementary material. The supplementary material for this article can be found at <http://doi.org/10.1017/S0022149X26102041>.

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Competing interests. The author declares none.

References

Barratt J, Chan D, Sandaradura I, Malik R, Spielman D, Lee R, Marriott D, Harkness J, Ellis J and Stark D (2016) *Angiostrongylus cantonensis*: A review of its distribution, molecular biology and clinical significance as a human pathogen. *Parasitology* **143**, 1087–1118. doi:10.1017/S00331182016000652.

Cain AJ (1968) Studies on *Cepaea* V. Sand dune populations of *Cepaea nemoralis*. *Philosophical Transactions of the Royal Society B: Biological Sciences* **253**, 499–517.

Cool LM and Pettitt CWA (1998) Morph frequencies in the snail *Cepaea nemoralis*: Changes with time and their interpretation. *Biological Journal of the Linnean Society* **64**, 137–150.

Cowlishaw RM, Andrus P and Rae R (2019) An investigation into nematodes encapsulated in shells of wild, farmed and museum specimens of *Cornu aspersum* and *Helix pomatia*. *Journal of Conchology* **43**, 385–392.

Crisi PE, Di Cesare A and Boari A (2018) Feline troglstrongylosis: Current epizootiology, clinical features, and therapeutic options. *Frontiers in Veterinary Science* **5**. doi:10.3389/fvets.2018.00126.

Dahirel M, Proux M, Gérard C and Ansart A (2022) Morph-dependent nematode infection and its association with host movement in the land snail *Cepaea nemoralis* (Mollusca, Gastropoda). *Journal of Zoology* **318**, 181–192.

Davison A and Neiman M (2021) Mobilizing molluscan models and genomes in biology. *Philosophical Transactions of the Royal Society B: Biological Sciences* **376**. doi:10.1098/rstb.2020.0163.

Díaz-Morales DM, Atkinson SD, Boyd D, Comisso G, Christner SR, Jones I, Leslie KL, Thirtyacre J, Whalen CJ, Kuris A, Mann J, Bart HL and Wood CL (2026) Stressor interactions affect myxozoan abundance in a 42-year dataset from the Pearl River, Louisiana, USA. *Parasitology* **25**, 1–13.

Elsheikha HM, Schnyder M, Traversa D, Di Cesare A, Wright I and Lacher DW (2016) Updates on feline aelurostrongylosis and research priorities for the next decade. *Parasites Vectors* **9**, 389. doi:10.1186/s13071-016-1671-6.

Falkingham PL and Rae R (2021) 3D morphology of nematode encapsulation in snail shells, revealed by micro-CT imaging. *Scientific Reports* **11**. doi:10.1038/s41598-021-82106-6.

Fuster-Calvo A, Oiler I, MacDonald A, Parent C, Massol F, Burin G, Phillips JG, Rae R and Gravel D (2026) Shell-bound archives: Uncovering nematode encapsulations in the Galapagos' largest radiation. *American Naturalist*, in press. Available at <https://www.biorxiv.org/content/biorxiv/early/2025/11/05/2025.11.03.686299.full.pdf>.

Gérard C, De Tombeur Y, Dahirel M and Ansart A (2023) Land snails can trap trematode cercariae in their shell: Encapsulation as a general response against parasites? *Parasite* **30**. doi:10.1051/parasite/2023001.

Grewal PS, Grewal SK, Tan L and Adams BJ (2003) Parasitism of molluscs by nematodes: Types of associations and evolutionary trends. *Journal of Nematology* **35**, 146–156.

Howard I, Davis E, Lippert G, Quinn TP and Wood CL (2019) Abundance of an economically important nematode parasite increased in Puget Sound between 1930 and 2016: Evidence from museum specimens confirms historical data. *Journal of Applied Ecology* **56**, 190–200.

Hudson PJ, Cattadori IM, Boag B and Dobson AP (2006) Climate disruption and parasite–host dynamics: Patterns and processes associated with warming and the frequency of extreme climatic events. *Journal of Helminthology* **80**, 175–182. doi:10.1079/JOH2006357.

Littlewood DTJ and Donovan SK (2003) Fossil parasites: A case of identity. *Geology Today* **19**, 136–142.

Mastick NC, Welicky RL, Katla A, Odegaard B, Ng V and Wood CL (2024) Opening a can of worms: Archived canned fish fillets reveal 40 years of change in parasite burden for four Alaskan salmon species. *Ecology and Evolution* **14**, e11043.

McGhie HA (2008) Catalogue of type specimens of molluscs in the collection of The Manchester Museum, The University of Manchester, U.K. *ZooKeys* **4**, 1–46. doi:10.3897/zookeys.4.32.

Poulin R (2021) The rise of ecological parasitology: Twelve landmark advances that changed its history. *International Journal for Parasitology* **51**, 1073–1084. doi:10.1016/j.ijpara.2021.07001.

Quinn J, Lee S, Greeley D, Gehman A, Kuris AM, Wood CL (2021) Long-term change in the parasite burden of shore crabs (*Hemigrapsus oregonensis* and *Hemigrapsus nudus*) on the northwestern Pacific coast of North America. *Proceedings of the Royal Society B* **228**, 20203036. doi:10.1098/rspb.2020.3036.

Rae R (2017) The gastropod shell has been co-opted to kill parasitic nematodes. *Scientific Reports* **7**, 4745.

Rae R (2018) Shell encapsulation of parasitic nematodes by *Arianta arbustorum* (Linnaeus, 1758) in the laboratory and in field collections. *Journal of Molluscan Studies* **84**, 92–95.

Rae R (2023) Avoidance and attraction behaviour of slugs exposed to parasitic nematodes. *Journal of Invertebrate Pathology* **197**, 107896. doi:10.1016/j.jip.2023.107896.

Rae R, Robertson JF and Wilson MJ (2008) Susceptibility and immune response of *Deroceras reticulatum*, *Milax gagates* and *Limax pseudoflavus* exposed to the slug parasitic nematode *Phasmarhabditis hermaphrodita*. *Journal of Invertebrate Pathology* **97**, 61–69.

Rae R, Sheehy L and McDonald-Howard K (2023) Thirty years of slug control using the parasitic nematode *Phasmarhabditis hermaphrodita* and beyond. *Pest Management Science* **79**, 3408–3424. doi:10.1002/ps.7636.

Schulenburg H and Félix M-A (2017) The natural biotic environment of *Caenorhabditis elegans*. *Genetics* **206**, 55–86. doi:10.1534/genetics.116.195511.

Welicky RL, Preisser WC, Leslie KL, Mastick N, Fiorenza E, Maslenikov KP, Tornabene L, Kinsella JM and Wood CL (2021) Parasites of the past:

- 90 years of change in parasitism for English sole. *Frontiers in Ecology and the Environment* **19**, 470–477. doi:10.1002/fee.2379.
- Williams A and Rae R** (2015) Susceptibility of the Giant African snail (*Achatina fulica*) exposed to the gastropod parasitic nematode *Phasmarhabditis hermaphrodita*. *Journal of Invertebrate Pathology* **127**, 122–126.
- Williams A and Rae R** (2016) *Cepaea nemoralis* (Linnaeus, 1758) uses its shell as a defence mechanism to trap and kill parasitic nematodes. *Journal of Molluscan Studies* **82**, 349–350.
- Wilson MJ, Hughes LA, Jefferies D and Glen DM** (1999) Slugs (*Deroceras reticulatum* and *Arion ater* agg.) avoid soil treated with the rhabditid nematode *Phasmarhabditis hermaphrodita*. *Biological Control* **16**(2), 170–176. doi: 10.1006/bcon.1999.0757.
- Wood CL, Leslie KL, Claar D, Mastick N, Preisser W, Vanhove MPM and Welicky R** (2023a) How to use natural history collections to resurrect information on historical parasite abundances. *Journal of Helminthology* **97**, 1–13. doi:10.1017/S0022149X2200075X.
- Wood CL and Vanhove MPM** (2023) Is the world wormier than it used to be? We'll never know without natural history collections. *Journal of Animal Ecology* **97**, 1–13.
- Wood CL, Welicky RL, Preisser WC, Leslie KL, Mastick N, Greene C, Maslenikov KP, Tornabene L, Kinsella JM and Essington TE** (2023b) A reconstruction of parasite burden reveals one century of climate-associated parasite decline. *Proceedings of the National Academy of Sciences* **120**, e2211903120.