**Harrison’s rule explains intraspecific variation in the body size of an endoparasite**

~~Does Harrison’s rule explain intraspecific variation in endoparasite body sizes?: The body size of~~ *~~Skrjabingylus nasicola~~* ~~depends on the skull size of the host~~

~~Does Harrison’s rule explain intraspecific variation in pendoarasite body sizes?: Body size variation of~~ *~~Skrjabingylus nasicola~~* ~~as a function of host skull size~~

~~Harrison’s rule as an explanation for intraspecific variation in endoparasite body sizes: body size variation of~~ *~~Skrjabingylus nasicola~~* ~~as a function of host skull size~~

~~Harrison’s rule as an explanation for intraspecific variation in endoparasite body sizes: the body size of~~ *~~Skrjabingylus nasicola~~* ~~depends on the skull size of the host~~

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Parasitic organisms display considerable variation in body size, with differences observed between species, populations, and even individuals within the same population (Poulin 1996). This variability is significant because body size is an important life-history trait for many parasites, influencing their transmission efficiency (Kelehear et al. 2012), host specificity (Bush & Clayton 2006) and, notably, their overall reproductive capacity. Larger parasites are generally associated with increased lifetime fecundity and shorter maturation times within hosts (Morand 1996, Trouvé et al. 1998, Harnos et al. 2016; Skorping et al. 1991, Morand & Sorci 1998). Larger body size can amplify parasite virulence due to heightened fecundity (Poulin 2007). However, the underlying reasons for variations in parasite body size are complex and not yet fully understood.

Host body size is often cited as a key factor explaining interspecific size variations in higher parasite taxa. Harrison (1915) discovered the first evidence of a positive association between parasite and host body sizes across species, known as Harrison's rule. This relationship has been documented for many parasite/host associations (Leung 2022) involving endoparasites like nematodes and nematomorpha (Morand & Sorci 1998, Morand et al. 1995, Ni et al. 2021) as well as ectoparasites such as lice, fleas and rhizocephalan barnacles (Harvey & Keymer 1991, Harnos et al. 2016, Nagler et al. 2017, Maestri et al 2020). Several proposed causal mechanisms include larger hosts providing additional resources, influencing parasite size and increasing lifetime fecundity (Poulin 2007), mechanical or physical constraints associated with parasitism (Morand et al. 2000), and the simultaneous influence of environmental factors on the body sizes of hosts and parasites (Maestri et al. 2020).

The influence of host size on intraspecific parasite body size has received relatively limited attention. Previous studies have primarily focused on specific species of ectoparasites, including parasitic isopods (Wenner & Windsor 1997, Tsai et al. 2001, Welicky et al. 2019), copepods (Van Damme et al. 1993), monogeneans (Cone & Burt 1985, Thoney 1988) and rhizocephalan barnacles (Nagler et al. 2017), revealing a positive relationship between host and parasite sizes. However, conflicting results (Baker et al. 2005, Welicky et al. 2019) and observations limited to one sex of the parasite (Tsai et al. 2001) have also been documented. In contrast to ectoparasites, there is a lack of empirical tests exploring the relationship between the intraspecific sizes of endoparasites and their hosts in the existing literature (but see Poulin & Latham 2002).

It is better established that infection intensity can have a significant role in shaping intraspecific size variation in endoparasites. Within large infrapopulations, parasites can exhibit a phenomenon known as the "crowding effect," where the average size of the parasite decreases as the number of parasites per host increases (Read, 1951). Density-dependent growth has been particularly well-documented in cestodes (e.g., Read, 1951; Heins et al., 2002; Sistermans et al., 2023), but has also been observed in other helminth endoparasites such as nematodes (Poulin 1999, Mohamed et al. 2020), nematomorphs (Hanelt 2008) and trematodes (Saldanha et al. 2009). Several factors contribute to this phenomenon, including competition for host resources, host immune responses and direct interactions between parasites (Quinell et al. 1990, Bush & Lotz 2000). However, conflicting results have also been reported. Some studies examining the relationship between helminth size and worm burden in humans, for instance, did not find a significant correlation (Quinell et al. 1990, Walker et al. 2009).

Host size and infection intensity can thus both influence intraspecific size variation in endoparasites, either independently or through interaction. Poulin & Latham (2002) demonstrated a correlation between total worm length and host size in a mermithid nematode infecting an amphipod species. They also found that worm length increased with higher infection intensity, which may be specific to their study system as the size of the host increased with increasing parasite load. To the best of our knowledge, no study has compared the relative contributions of these factors in helminths parasitic in vertebrates. It is possible that limited size variation in the host or the infected organ makes it difficult to assess the influence of host size on parasite size. Also, larger individuals of the same host species often have a higher parasite load (e.g. Zelmer & Arai 1998, Poulin 2000, Horn et al. 2023). In other words, host size and parasite load tend to be confounded, making it challenging to disentangle the effects of host size and density dependence on parasite body size.

*Skrjabingylus nasicola* is a parasitic nematode belonging to the family Metastrongyloidae. It has a widespread distribution across the Palearctic, specialising in parasitising the nasal and frontal sinus cavities of multiple species of mustelids (Anderson 2000). First stage larvae migrate from the final host’s sinuses to the back of its throat, are being swallowed and expelled with the host's faeces. The infective forms of the parasite then develop in terrestrial gastropods, while small rodents, shrews, amphibians, or reptiles can act as paratenic hosts (Anderson, 2000). In Europe, the parasite is known to occur in the stoat (*Mustela erminea*), the least weasel (*Mustela nivalis*), the European polecat (*Mustela putorius*) and the American mink (*Neogale* *vison*) (Hansson 1968, King 1977, Heddergott et al. 2016). *S. nasicola* has the potential to cause significant damage to the cranial bone structure of its hosts. The impact in least weasels and stoats can be especially serious, resulting in perforations of the bones that can converge and expose the frontal sinus and nasal cavity (Hansson 1968, King 1977, Frantz et al. 2022).

According to Hansson (1968), *S. nasicola* mainly occurs in the conchae, also known as nasal turbinates, within the lateral nasal parts. In arctoid carnivores, the total turbinal surface area scales isometrically with skull length (Green et al. 2012). The skulls of the different European host species of *S. nasicola* vary in size and exhibit pronounced sexual dimorphism. The smallest skulls (based on condylobasal length) are found in the least weasel, while the largest are found in polecats. Additionally, females in all four host species have significantly smaller skulls compared to males (Reichstein 1993, Stubbe 1993, Wolsan 1993, Abramov & Baryshnikov 2000). Hosts with larger skulls, as well as males, are thus likely to provide more physical space for the growth and proliferation of the nematodes *S. nasicola*. The variation in skull size, which can be easily measured, may have an influence on worm size. Additionally, infestation intensity has been observed to differ between individual hosts (Müller & Heddergott 2009, Frantz et al. 2022). This host-parasite system thus presents a valuable opportunity to investigate the factors driving endoparasite body size.

Here, our main objective was to disentangle the drivers of endoparasite body size, using *S. nasicola* as a model system. We first employed genetic barcoding to confirm the presence of a single species of *S. nasicola* across all four host species. We then aimed to determine whether Harrison's rule or infection intensity played a more significant role in driving the body size of *S. nasicola*. Additionally, we sought to investigate the nature of the interaction between these two factors. To achieve this, we test the following three scenarios: (i) worm size is solely determined by the skull size of the host, with larger hosts have larger worms, (ii) worm size depends solely on infection intensity, with individual worms becoming smaller when the size of the infrapopulation increases, (iii) both host size and infection intensity influence worm size: Worms tend to be larger in the skulls of the larger hosts or in the skulls of males compared to females of the same species. However, the size of the worms decreases with increasing infection intensity. Finally, we also considered the number of nematodes as a dependent variable to gain a better understanding of the factors influencing infection intensity.

Methods

Sampling of hosts and parasites

Between XXXX and YYYY, we collected fresh skulls from xxxxxx European polecats that had a complete body and were sufficiently well-preserved to allow to test for the presence of cranial helminth parasites (Fig. 2).

Talk about skull sites in the hosts

Analysis of genetic data

In order to confirm the species identity of *Skrjabingylus* nematodes, we amplified a 661-base-pair-(bp)- long fragment of the cytochrome c oxidase I (COI) subunit, using primers NemF2\_t1 and NemR2\_t1 (Prosser et al. 2013), following the methods outlined in Heddergott et al. (2015). According to Heddergott et al. (2015) the COI marker can be used to differentiate between different species of *Skrjabingylus*. We barcoded a set of 16 worms recovered from European polecats, 13 worms from least weasels, seven worms from American minks and four sampled from stoats. Each worm was collected from a different individual. For comparative purposes, a single *S. petrowi* specimen sampled from a pine marten (*Martes martes*) was also barcoded. We re-sequenced the individual that gave rise to *S. petrowi* haplotype 2 (GenBank accession no. KP724693) as well as the two individuals that give rise to *S. nasicola* haplotypes 1 and 2 (GenBank accession nos. KP724695/ KP724696) in order to increase the length of the sequence (Figure or Table with information on sampling locations).

Sequence alignment was performed using the MUSCLE procedure (Edgar 2004) imbedded in MEGA v.X (Tamura et al. 2011). Sequences were collapsed to haplotypes using software COLLAPSE V1.2 (D. Posada; unpublished software). A median-joining haplotype network was generated using popart (Leigh and Bryant 2015). The identity of the host species was plotted on the haplotype network as traits. DNASP v.6.12.03 (Rozas et al. [2017](https://link.springer.com/article/10.1007/s10531-022-02371-3#ref-CR64)) was used to calculate haplotype diversity (*H*d) and nucleotide diversity (π)

Statistical analysis

Statistical analyses were performed in program R v.4.2.0 (R Core Team 2022), and all the generalised linear mixed effects models (GLMMs) were generated with the glmmTMB package (Brooks et al. 2017). We systematically calculated the variation inflation factors (VIFs) with the full GLMMs without interactions to check for multicollinearity. We considered that there was no substantial correlation when VIF values were <5 (James et al. 2013). We only included two-way interactions to avoid convergence and fitting issues, and to ease interpretation. We considered the identity of each host individual as random effects (random intercepts) to account for inter-individual stochasticity. We evaluated whether the inclusion of random effects improved the model by comparing the Akaike information criteria (AIC) of models with and without random effects, fit with restricted maximum likelihood (Zuur et al. 2009).

To calculate AIC for all potential models fit with non-restricted maximum likelihood, we used the dredge() function in the MuMInv.1.46.0 R package (Bartoń 2022). We then selected the models whose AIC values were within 2 of the model with the lowest AIC. We selected the most parsimonious model (lowest number of degrees of freedom) within that subset of models. Finally, we conducted model averaging using the model.avg() function of the MuMIn package. Model averaging helped us evaluate the importance of each predictor when multiple models were of similar performance according to AIC. In addition to model averaging, we counted how many times each predictor was present in models within the subset. Because ‘condylobasal length of host’ and ‘host species’ were highly correlated, we ran our procedure excluding one and then the other.

We first sought to identify the most important predictors to explain the length of worms using a Gaussian GLMM. They included the numbers of worms (to test for a potential density-dependent effect on size), the sex of the worm (to characterize sexual dimorphism), the sex of host (to evaluate sex-dependent disease dynamics), which side of the skull was infested (to evaluate asymmetry in skull or infection), the condylobasal length and the species identity (to test Harrison’s rule). Then, we modelled the length of worms within species to see if the interspecific relationship between condylobasal length and length of worms held within species. For this analysis, we kept the same model formula as in the best model obtained with the complete dataset. Finally, we modelled the number of worms using a Poisson GLMM with the same predictors and length of worms. We tested for overdispersion in the Poisson models (Gelman and Hill 2006).

Results

Genetic data

We obtained 603 bp of clean COI sequence for each of the 41 *Skrjabingylus* worms. Among these sequences, we identified 31 different haplotypes (GenBank accession nos. XXXXXXXX-XXXXXXXX) that differed at 94 variable sites. Excluding the *S. petrowi* specimen, the remaining 30 haplotypes differed at 40 variable sites. The haplotype network showed that the *S. petrowi* sequence was strongly differentiated and differed at 72 variable sites (11.9%) from the closest empirical sequence (Fig. X, Fig. SX). The network suggested that all other sequences originated from the same species, i.e. *S. nasicola*. There was no clustering of haplotypes according to host species. Rather, the haplotypes obtained from the four host species were distributed throughout the network. While unique singletons accounted for 48.4% of the 31 haplotypes, five haplotypes were observed more than once. Four of these were observed in at least two different host species and each host species shared at least one worm haplotype with another host species. *S*. *nasicola* haplotype diversity of was very high (*H*d± SD: 0.973 ± 0.016) and nucleotide diversity low (π ± SD: 0.0071 ± 0.0164).

Statistical analysis

Since VIF values were <2.05 in all full GLMMs (without interactions) throughout the study, our models did not have multicollinearity issues (show in Table?). When trying to identify predictors for nematode length and including ‘condylobasal length of host’ as a predictor (instead of ‘host species’), our model selection procedure resulted in XX equivalent models based on AIC ([Table S3](https://www.sciencedirect.com/science/article/pii/S2213224422000591#appsec1)). According to the most parsimonious model, females *S*. *nasicola* were significantly larger than males and hosts with larger skulls harboured significantly larger worms (Table X). Additionally, a significant interaction was observed between the sex of the nematodes and the skull size of the host, with the size difference between sexes being significantly higher in hosts with larger skulls (Fig. X). Infection intensity did not have a significant effect on the length of *S*. *nasicola*. The very large marginal R2 of 0.961 indicates that our model had a very high power to predict accurately the length of *S*. *nasicola* nematodes based on our fixed effects predictors.

When including ‘host species’ as a predictor instead of ‘condylobasal length of host’, the most parsimonious model (among XX equivalent models based on AIC; Table SXX) found that the size of the nematodes differed between host species (Table SCC), with larger host significantly more likely to harbour larger worms (Fig. 2). Again, females *S*. *nasicola* were significantly larger than males and there were significant interactions between the host species and the sex of the nematode, with the difference in sizes between the two sexes being significantly more pronounced in the larger host species. Again, infection intensity did not significantly affect the length of *S*. *nasicola*. The present model also had a very large marginal R2 of 0.962.

When modelling the length of the nematodes worms within species, the significant predictors differed between species. Specifically, in the case of the two larger species (European polecat and the American mink), hosts with larger skulls were significantly more likely to harbour larger worms (table xx) and we identified significant interactions between the host species and the sex of the nematode. These interactions resulted in a more pronounced difference in sizes between the two sexes in larger hosts (Graph?? I presume it’s the same as above). Both models had very large marginal R2 values (polecat: mR2 = 0.957; mink: mR2 = 0.957). In contrast, in the two smaller species (stoat, the least weasel), we found no evidence either for condylobasal length affecting worm length, or for an interaction between condylobasal length and sex of the worms. The marginal R2 values for these two model were still high (stoat: mR2 = 0.817; least weasel: mR2 = 0.737), although slightly lower than the values observed for the models relating to the two host larger species.

When identifying predictors for infection intensity and including ‘condylobasal length’ as a predictor (instead of ‘host species’), our model selection procedure resulted in XX equivalent models based on AIC (XXTable S3). According to the most parsimonious model, female *S*. *nasicola* were significantly more abundant than males and female hosts were significantly more likely to exhibit a higher infection intensity than males. Moreover, *S*. *nasicola* were found to be significantly more abundant on the right side of the skull compared to the left. There was no observed effect of skull size or worm length on infection intensity. The marginal R2 of 0.708 indicates that our model had a reasonably high predictive power for estimating infection intensity based on our fixed-effect predictors.

Interaction with T. acutum? High predictive power of our model

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