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Host–parasite relations and seasonal occurrence of *Paragordius tricuspidatus* and *Spinochordodes tellinii* (Nematomorpha) in Southern France

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Abstract

Paragordius tricuspidatus (Dufour, 1828) and *Spinochordodes tellinii* (Camerano, 1888) are two sympatric species of horsehair worms in southern France. *Paragordius tricuspidatus* was found in only one host species, *Nemobius sylvestris* (Bosc, 1792), while *Spinochordodes tellinii* was found in nine different hosts belonging to Orthoptera Caelifera. Size of nematomorphs varied strongly, but is additionally influenced by host size (in *Spinochordodes tellinii*) or number of parasites per host (in *Paragordius tricuspidatus*). Both species have a clear seasonality with *Paragordius tricuspidatus* occurring from June to early August and *Spinochordodes tellinii* occurring in August and September.

Keywords: Nematophora; Host species; Host-parasite relationships; Seasonal occurrence

1. Introduction

Horsehair worms (Nematomorpha) typically develop in arthropods (mainly terrestrial species) until they are ready to exit the host (Schmidt-Rhaesa 2001). Because nematomorphs are usually found when they have emerged from their host and started the aquatic free-living phase of their life cycle, numerous aspects of their biology remain poorly documented (but see Hanelt and Janovy 1999, 2003, 2004). Recently, the two hairworm species *Paragordius tricuspidatus* (Dufour, 1828) and *Spinochordodes telinii* (Camerano, 1888) from Southern France have proven to be valuable model systems to examine whether (and potentially how, see Thomas et al. 2003) hairworms manipulate their host behaviour to increase their probability of reaching a suitable aquatic place for reproduction (Thomas et al. 2002). Indeed, insects harbouring these hairworms display a behaviour originally not present in the host's repertoire: they seek water and jump into it (Thomas et al. 2002). The adult worms then emerge from their host and actively leave it by swimming away, beginning the search for a sexual partner.

The parasitic phase of nematomorphs remains enigmatic, because hardly any systematical approach has been performed on larger numbers of specimens to reveal their host specificity, numbers of parasites per

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host and the influence of host size or parasite number for the development of the parasite. Based on collections in Avènes les Bains in Southern France, where *Paragordius tricuspidatus* and *S. tellinii* occur sympatrically, we provide such data.

2. Material and methods

All specimens were captured around a private swimming pool in Avènes les Bains (Southern France, 70 km north of Montpellier). Capture took place mostly between 10 p.m. and 1 a.m. The swimming pool is located between a forest and a small stream in which free adult nematomorphs can be found (see also Thomas et al. 2002, 2003 for description of the location). Hosts were observed to jump into water (the swimming pool) or were set in a container with water, so that parasites and hosts could be assigned to each other. In some cases, hosts were dissected. Hosts and parasites were fixed in ethanol (70%). Length measurements were made with a ruler, diameter measurements with a caliper ruler. Determination of species was based on intensive preliminary investigations including scanning electron microscopy which confirmed that only two species were present in the location investigated. Both species are easy to distinguish from each other under the dissecting microscope due to different shapes of the anterior and posterior end.

3. Results

3.1. Host species

In all cases where *Paragordius tricuspidatus* has been found in association with its host ($n > 400$), the host was the small cricket *Nemobius sylvestris* (Bosc, 1792) (Gryllidae) (Fig. 1B). Infected *N. sylvestris* can be observed in the field and in laboratory experiments (see Thomas et al. 2002) to approach water and enter this by jumping into it. *Paragordius tricuspidatus* starts to emerge from the posterior region of the crickets with its head first very soon after the contact of the host with water. Emergence takes about 1 min and is aided, especially towards the last phase, by undulating movements by the worm. The crickets survive the parazitation and emergence, if they are able to escape from the water, but no long-term investigations according to the fitness of parasitized hosts were performed.

In contrast to *Paragordius tricuspidatus*, *S. tellinii* was found in a total of nine different hosts (see Table 1; Fig. 1D–F). Most worms were found in adult hosts (one exception is a larva of probably *Eupholidoptera chabrieri* (Charpentier, 1825)). With more than 100 cases, *Meconema thalassinum* (de Geer, 1773) is the most abundant host (Fig. 1D), followed by 11 cases, in which *Pholidoptera griseoptera* (de Geer, 1773) was host, while the remaining species were found in few or single cases.

In three cases, a specimen of *S. tellinii* was found in a swimming pool in Avignon, France, close to a potential host. These were a praying mantis (*Mantis religiosa* Linnaeus, 1758), a large locust (*Tettigonia viridissima* Linnaeus, 1758) and a scorpion (*Euscorpius flavicaudis* de Geer, 1778) (Fig. 2A–C). The emergence was not observed in these cases. All three specimens of *S. tellinii* were large females with measurements of (*Mantis*/*Tettigonia*/*Euscorpius*): 280, 305 and 345 mm in length and 1, 0.9 and 1 mm in diameter.

3.2. Measurements of free-living and parasitic nematomorphs

In *Paragordius tricuspidatus*, the length of free-living females ($n = 51$) ranges from 60 to 135 mm (mean 92.35 ± 16.41 mm), with diameters between 0.5 and 0.8 mm (mean 0.61 ± 0.08 mm). Males ($n = 47$) measure between 65 and 145 mm in length (mean 82.57 ± 16.25 mm) (50 and 60 mm are two further, exceptional measurements from two males together with two further specimens in one host specimen), their diameter ranges between 0.4 and 0.6 mm (mean 0.46 ± 0.06 mm) (see Fig. 1C for two males of different sizes and, additionally, different colouration patterns). Therefore, females are generally larger than males (Fig. 1A).

In free-living *S. tellinii*, females ($n = 60$) measure between 110 and 305 mm in length (mean 141.67 ± 39.85 mm), and between 0.5 and 1.2 mm in diameter (mean 0.73 ± 0.16 mm). Males ($n = 74$) range from 75 to 245 mm in length (mean 116.55 ± 43.59 mm), and from 0.4 to 0.7 mm in diameter (mean 0.48 ± 0.09 mm).

In 65 cases, measurements of the parasite stages within hosts were taken (Table 2). In 57 cases, *N. sylvestris* was parasitized by a single nematomorph, while in eight cases, multiple infections occurred. In six cases, two specimens of *Paragordius tricuspidatus* were found in one host, while one time three (two males and one female) and another time four (three males and one female) *Paragordius tricuspidatus* were found in one cricket. In the cases of two specimens within one host, both specimens were males in one occasion, while in all seven other cases a male and a female occurred together.

In the single infections (one nematomorph per host), males (mean 82.8 mm) are slightly shorter than females (mean 88.3 mm) (see Table 2). In cases with two or three parasite specimens in one host specimen, all measurements were within the range of single infections (length: 70–90 mm in females and in males; diameter: 0.5–0.6 mm in females, 0.4–0.5 mm in males; Table 2), but mean values of cases with two parasites were lower than in