New records of host-parasite relationships between *Coenagrion scitulum* (Rambur, 1842) (Odonata) and water mite larvae (Hydrachnidia) in core and edge host populations

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Abstract

The relationships between water mite larvae parasitizing *Coenagrion scitulum* in core and edge populations were described. A total of 636 larvae of 7 water mite species were found on 143 *C. scitulum* adults (82 females and 61 males). *C. scitulum* was recorded for the first time as a host species for *Arrenurus cuspidator*, *A. bruzelii*, *A. bicuspidator*, *A. tricuspikator*, *A. claviger* and *Hydryphantes octoporus*. The degree of infestation by particular parasite species was typical for these species. In contrast, the parasites' preferences for host body parts were not typical, as they preferred abdominal segments 2–4, which in earlier studies had been avoided by water mite larvae. No differences were found in degree of infestation of *Coenagrion scitulum* individuals between core and edge populations, with the exception of *Hydryphantes octoporus*, which parasitized damselflies only in core populations.

Keywords

Arrenurus, *Hydryphantes octoporus*, damselfly, ectoparasitism, infestation

Introduction

Water mites (Hydrachnidia) belong to the Parasitengona because their larvae parasitize aquatic insects. This strategy allows water mites to disperse and colonize new water bodies (Bilton *et al.* 2001; Zawal 2003a, 2003b; Bohonak *et al.* 2004; Martin 2008). There are two means of infestation: one group of mites parasitizes insects permanently abiding in water and leaving this environment only periodically, i.e. beetles and true bugs (Cichocka 1995; Zawal 2002, 2003c; Fairn *et al.* 2008; Incekara and Erman 2008; Zawal *et al.* 2013; Abe *et al.* 2015), and the other group parasitizes insects whose larvae live in the water, while the adults permanently abide outside of the water (Davids 2004; Zawal 2004a, 2004b, 2006a, 2006b; Buczyńska *et al.* 2015; Stryjecki *et al.* 2015). The larvae of *Arrenurus*, parasitizing damselflies, belong to the latter group (Zawal, 2004a; 2004b, 2006a, 2006b; Baker *et al.* 2006, 2007, 2008; Zawal and Jaskuła 2008; Radhakrishnan *et al.* 2010; Kulijer *et al.* 2012; Kulijer *et al.* 2013; Kaunisto *et al.* 2015; Młynarek *et al.* 2015).

Two mechanisms may cause differentiation in the degree of parasitism between core and edge populations of the host species. Firstly, metapopulation theory predicts that infestation of the host population by parasites is enhanced by close proximity to patches with extant host populations (Boyett *et al.* 2000; Hanski 1999). Kaunisto *et al.* (2015) showed that the number of water mite larvae infesting *Coenagrion hastulatum* decreases from core to edge populations in Finland. Secondly, stressful conditions at range edges have been linked to poorer body condition (Pitt *et al.* 2008; Busch *et al.* 2011) and this may impair investment in immune function making individuals more susceptible to parasites at the range margins (Briers 2003). In contrast, in the specific case of moving range margins, a higher investment in immune function at the leading range edge has been documented (Therry *et al.* 2014a) which has the potential to decrease parasite susceptibility at edge populations. Theoretical (e.g., Travis and Dytham 2002) and empirical studies (reviewed in Hill *et al.* 2011) indicated the evolution of increased dispersal abilities during range expansion.

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Dispersers are often larger (Anholt 1990; Michiels and Dhondt 1991) or in better body condition than residents (Sundström 1995). Given that immune function is often positively correlated with individual condition (Yang *et al.* 2007), one may also expect a higher immune function at the leading range edge. Furthermore, selection for a high investment in immune function to lower parasite load may be enhanced through the negative effect of high parasite load on dispersal ability (e.g. Nagel *et al.* 2010).

There is no information available about the host-parasite relationships in core and edge populations of range expanding damselflies. Therefore, the key objective of this paper was to investigate differences in water mite infestation between core and edge populations of the poleward moving damselfly *C. scitulum* (Swaegers *et al.* 2013). In addition, we investigate new water mite associations with *C. scitulum* to extend the knowledge on water mite parasitism in this host species.

Materials and Methods

One hundred and forty-three adults of *C. scitulum* (82 females and 61 males) were captured in 2010 and 2011 in small water bodies in France (C1 – Le Bouchet 46°43'13.99"N 1°10'20.19"E, C2 – Vauville 49°37'10.11"N 1°50'24.21"W, C3 – Roussent 50°21'50.35"N 1°47'09.58"E, C4 – Merlimont 50°26'17.26"N 1°35'17.67"E), Germany (E1 – Abweiler

49°12'54.48"N 7°11'38.37"E, E2 – Webenheim 49°14'52.96"N 7°16'18.91"E, E3 – Zülrich 50°41'54.25"N 6°38'59.33"E), Belgium (E4 – De Panne 51°06'06.16"N 2°36'31.64"E, E5 – Knokke 51°21'30.81"N 3°20'33.02"E) and The Netherlands (E6 – Cadzand 51°22'50.19"N 3°23' 58.61"E) (Fig. 1). Up to the 1990 s the northern range limit of *C. scitulum* was situated in Northern France, where after a north-eastward range expansion occurred (Swaegers *et al.* 2013). The populations of *C. scitulum* in France were located within the historical distribution of the species and were defined as core populations (Swaegers *et al.* 2013). The populations in Germany, Belgium and The Netherlands were situated at the expansion front and founded less than five years before sampling and were defined as edge populations (Therry *et al.* 2014b).

Water mite larvae were removed with tweezers. The body length of the larvae was measured from the frontal part of the gnathosoma to the end of the idiosoma. The larvae were identified using a key by Zawal (2008).

Intensity of infestation (number parasites per individual of host) relative to hosts, sexes of hosts, parts of host body and hosts from particular populations were analysed.

Statistical significance between intensity of infestation was determined by the Kruskal-Wallis and Mann-Whitney tests in Statistica v. 12.5 software. The effect of population status (core vs edge) was analysed on log-transformed mite scores using mixed models (SAS v. 9.3) with replicated populations status as random effect.

Fig. 1. Locations of the *C. scitulum* study populations and the European historical species' range (shaded area based on Dijkstra 2006). Core populations are indicated with circles and edge populations are indicated by triangles

Table I. Overview table of the water mite species on the damselfly *C. scitulum* with characteristics of the infestation patterns. nh – number of host individuals, np – number of parasite individuals

Parasite species	Females				males			
	nh	np	range	average $\pm$ STD	nh	np	range	average $\pm$ STDd
<i>A. bicuspidator</i>	12	24	1–8	1.9 $\pm$ 1.98	5	15	1–8	3.0 $\pm$ 2.53
<i>A. bruzelii</i>	45	208	1–22	4.6 $\pm$ 4.30	42	202	1–22	4.8 $\pm$ 4.23
<i>A. claviger</i>	1	2	2–28	15.0 $\pm$ 13.00	1	2	2	2.0
<i>A. cuspidator</i>	76	344	1–30	4.5 $\pm$ 5.08	32	110	1–15	3.3 $\pm$ 2.96
<i>A. maculator</i>	1	25	25	25.0	1	25	25	25.0
<i>A. tricuspidator</i>	1	4	4	4.0	1	4	4	4.0
<i>H. octoporus</i>	7	29	1–11	3.9 $\pm$ 3.66				
TOTAL	143	636	1–30	4.6 $\pm$ 5.22	82	358	1–25	4.3 $\pm$ 4.35

Results

A total of 636 water mite larvae were recorded on the sampled *C. scitulum* individuals. These belonged to six species of water mites from the subgenus *Arrenurus* s. str. and one from the genus *Hydryphantes* (Table I). The Kruskal-Wallis test revealed no significant differences between the degree of infestation of all water mite species ($H(6, N = 147) = 11.88, p = 0.065$), but showed statistically significant differences between degree of infestation for the most numerous species (*A. bicuspidator* (Berl.), *A. bruzelii* (Koen.), *A. cuspidator* (Müll.), *A. maculator* (Müll.) and *Hydryphantes octoporus*

(Koen.); ($H(3, N = 143) = 7.945869, p = 0.0471$). The intensity of infestation of all species tested did not differ between males (4.4 mean with 4.46 SE) and females (4.1 mean with 5.60 SE) (Kruskal-Wallis test, $N = 19, H_1 = 2.15, p = 0.14$), but statistically significant differences between the intensity of infestation of host sexes for *A. bruzelii* and *A. cuspidator* (Mann-Whitney U test: $Z = -1.3657, p = 0.0172$ and $Z = -1.1679, p = 0.0243$). *Arrenurus bruzelii* infested females much more often and in greater numbers, while *A. cuspidator* infested males and females with equal frequency, but the intensity of infestation of males was markedly higher (Table I). The intensity of infestation (Fig. 2) did not differ between

Fig. 2. The occurrence of water mites on the different body parts of the damselfly host *C. scitulum*

Fig. 3. Body size of water mite larvae

Fig. 4. Average number of parasites on one host in particular hosts' populations

Fig. 5. Body size of parasites in core and edge hosts' populations

body parts of the hosts (Kruskal-Wallis test: $H(3, N = 42) = 2.66, p = 0.4462$).

The body size of water mite larvae varied from 180 to 1668 µm. The widest range of values was noted for *H. octoporus*. This species was also distinguished by the largest larvae, but *A. cuspidator* had the largest mean body size (Fig. 3). The differences are statistically significant (Kruskal-Wallis test: $H(6, N = 520) = 181.50, p < 0.001$).

total of seven water mite species were observed, with the number of species per population ranging from one to four (Fig. 4). Two species, *A. tricuspidator* (Müll.) and *A. claviger* (Koen.), were each found in only one edge population and one species, *A. maculator* was only found in one core population. Another species, *H. octoporus*, was found in only two core populations (Fig. 4). Core (4.6 mean with 5.45 SE) and edge (3.3 mean with 2.19 SE) populations did not differ in the number of attached water mites per adult damselfly ($F_{1,6.72} = 0.54, p = 0.488$), but high variation was noted among populations with the same population status (core vs edge) (random effect population nested in population status: Wald $Z = 26.1, df = 1, p < 0.001$).

Statistically significant differences were observed between the body size of water mite larvae in core and edge populations both for all species of parasites together (Kruskal-Wallis test: $H(6, N = 520) = 181.50, p < 0.001$) and for the most numerous species (*A. cuspidator*) (Fig. 5) (Mann-Whitney U test $Z = -2.38, p = 0.0175$).

Discussion

C. scitulum is a damselfly species on which parasitizing larvae of only two water mite species (*A. maculator* and *A. radiatus*) had previously been recorded (Davids 1997). The present study adds another six species to this list of parasites (Table I). The species of the genus *Arrenurus* noted here are widely distributed opportunists in terms of host species, previously recorded on numerous odonate species (Zawal 2004a, 2006a, 2006b; Ilvonen *et al.* 2016). In contrast, *H. octoporus* is an exception in the family Hydryphantidae, parasitizing Odonata (Zawal and Dyatlova 2008; Kulijer *et al.* 2013) while the all other species of the family parasitize Heteroptera and Diptera (Smith and Olivier 1986).

The intensity of infestation of *C. scitulum* does not vary between individual parasite species and the intensity of infestation is similar as observed in other Odonata species (Zawal 2004a, 2006a, 2006b).

A general rule in Coenagrionidae is that adult males spend more time near a water body while the adult females disperse in the vicinity and return to the water to breed (Dijkstra 2006). This also applies to *C. scitulum*, with the females characterized by substantially greater dispersion (Angelibert and Giani 2003). Ilvonen *et al.* (2016) found no differences in infestation by water mites between the two sexes of damselflies, which conflicts with the data presented by Rob and Forbes (2005), who observed a higher infestation by water mites for females

of *Lestes disjunctus*. The case described in the present study is interesting, with different strategies adopted by two parasite species, *A. bruzelii* and *A. cuspidator*. *A. bruzelii* is a species associated with small water bodies, occurring frequently but generally not abundantly (Gerecke *et al.* 2016), which in the light of the results obtained here may result from its parasitism strategy involving a preference for female damselflies. *A. cuspidator*, on the other hand, is a very common and abundant species, which may be linked to the frequent infestation of both sexes of damselflies as well as the higher infestation rate of males. This is confirmed by earlier data for other host species of the family Coenagrionidae (Baker *et al.* 2008; Zawal and Buczyński 2013).

The number of attached parasites did not differ between body parts which is not typical for damselflies, as previous literature (Zawal 2004a, 2006a, 2006b). Abdominal segments 1–3 are passed over by water mite larvae, probably due to their connection with reproduction (Baker *et al.* 2007).

The body size of the parasites noted here was markedly different from that of newly hatched larvae (Zawal 2006c, 2006d, 2006e; Tuzovskij 2007), indicating that they had been parasitizing the hosts for a long time, which is consistent with the sampling time. Previous studies indicate spring and early summer as the period when most *Arrenurus* larvae hatch (Daszkiewicz and Zawal 2004; Włodarczyk and Zawal 2004; Dzierzgowska *et al.* 2011; Kłosowska *et al.* 2011; Bańkowska *et al.* 2016).

The theory of metapopulations suggests a decrease in the abundance of species towards the boundaries of their range, and to a large extent this applies to parasites as well (Price 1980). Kaunisto *et al.* (2015) demonstrated a pronounced reduction in water mite larva of the genus *Arrenurus* parasitizing *Coenagrion hastulatum* in Finland. In this case it was linked to the climatic zone, which caused the abundance of both hosts and parasites to decrease as latitude increased. The present study did not confirm previous results, as the ranges of parasite (water mite) species were considerably wider than the host range (*C. scitulum*). In consequence the edge host populations were attacked by core populations of parasites. Interestingly, *C. scitulum* individuals from edge populations have a higher immune function than core individuals when reared at common garden conditions (Therry *et al.* 2014a), yet this did not translate into higher immune function in the wild (Therry *et al.* 2014b) nor into lower mite parasitism in edge populations. *H. octoporus* was noted only in core populations, which is in line with previous studies whereby the species has been recorded as a parasite of odonates exclusively in the south of Europe (Zawal and Dyatlova 2008; Kulijer *et al.* 2013). *H. octoporus* as an adult was found in almost whole Europe (Di Sabatino *et al.* 2010), but up to now nothing is known about its parasitizing in North Europe. The differences noted between core and edge populations in the body size of the parasites are likely due to climate differences, as higher temperatures lead to faster development of parasites in the core populations located further south.

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