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# Larval aquatic and terrestrial mites infesting parthenogenetic *Ischnura hastata* (Odonata: Coenagrionidae) from the Azores islands

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**Abstract** We report here the prevalence of parasitism by water mites (*Arrenurus* sp.) and terrestrial mites (*Leptus killingtoni*) on parthenogenetic *Ischnura hastata* (Odonata: Coenagrionidae) from the Azores islands. *Leptus killingtoni* was only found on the island of Pico, and the prevalence of infestation was highly variable among the different ponds studied, ranging from 0 to 41%. *Leptus killingtoni* was observed on three of the four odonate species from the archipelago: *I. hastata*, *I. pumilio,* and *Sympetrum fonscolombii*, all of them new hosts for this species. Aquatic mites have been found parasitizing *I. hastata* females on the island of São Miguel. The prevalence of mite parasitism by *Arrenurus* sp. on *I. hastata* was very low, ranging from 12% (2003) to 1% (2008), and in most of the studied ponds, no mites were found attached to females. Although *I. hastata* coexists with a sexual congener species in the Azores (*I. pumilio*), they are syntopic in only a small fraction of ponds. Therefore, a comparison between *I. hastata* and *I. pumilio* was insufficient to test the predictions of the Red Queen Hypothesis, and further research on

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parasitism rates in both species needs to be done. In any case, the low prevalence of mite parasitism found in the Azores, coupled with the fact that most of the populations in the archipelago are almost free from competitors and predators, could explain the persistence of these *I. hastata* parthenogenetic populations, despite their low levels of genetic variation.

**Keywords** Odonata · *Ischnura hastata* · Mite ectoparasitism · *Arrenurus* · *Leptus killingtoni* · Parthenogenesis

## Introduction

Aquatic mites belonging to the genera *Arrenurus* (Arrenuridae), *Hydryphantes* (Hydryphantidae) and *Limnochares* (Limnocharidae) (Acari: Hydrachnida), are among the most prevalent ectoparasites affecting adult dragonflies and damselflies (Corbet 1999; Zawal and Dyatlova 2008). The aquatic, hexapod larvae of water mites attach phoretically to the last-instar odonate larvae, and during the emergence of the adult, the mites move to the thorax or abdomen of the dragonfly, where they remain attached feeding on the host's body fluids throughout their parasitic phase. After engorgement, the mite larvae drop from their host and start the aquatic phase of their life cycle (Corbet 1999). In addition to water mites, terrestrial mites belonging to the genera *Charletonia* and *Leptus* (Acari: Parasitengona) have also been recorded as parasites of odonates (Turk 1945; Southcott 1966, 1999; Haitlinger 1987; Zheng 1996; Grant and Samways 2007). In this case, the terrestrial mite larvae actively seek out and crawl onto adult Odonata when they are perched on the vegetation.

Parasite loads can be very high in some odonate populations, with large numbers of mites found on a single individual. For instance, Andrés and Cordero (1998) found that 98% of teneral individuals in a population of the damselfly *Ceriagrion tenellum* (Villers, 1789) were parasitized and the average load was 55 mites per individual. Ectoparasitic mites are known to negatively affect host population dynamics, through reductions in survivorship (Robinson 1983; Braune and Rolff 2001), mating success (Andrés and Cordero 1998), and alteration of host's activity patterns such as dispersal (Reindhart 1996; Conrad et al. 2002). Thus, they constitute important selective forces for odonates.

The interaction between hosts and parasites is currently considered a major force underlying the persistence of sexual reproduction. In accordance with the Red Queen Hypothesis (Van Valen 1973; Bell 1982; Ridley 1995) which suggests that organisms are constantly under selection from an ever-changing environment, it has been suggested that sexually reproducing organisms are better able to respond to parasites through the creation of new genotypes. Thus, asexuals would be expected to show higher parasitism rates than sexually reproducing organisms, due to their lower levels of genetic diversity and inability to create novel genotypes through recombination (Hamilton et al. 1990). Testing the predictions of the Red Queen Hypothesis is difficult, because the ideal model for such research is a comparison of parasitism in related forms reproducing sexually and asexually. The tests made until now generally supported the idea that asexuality is disadvantageous when parasites constitute strong selective forces (Lively et al. 1990; Moritz et al. 2010; reviewed for plants by Clay and Kover 1996), but in some cases the evidence is contrary to this idea (Hanley et al. 1995). A recent review of the assumptions of this hypothesis has argued that new experimental data and an increased theoretical effort are still needed (Salathé et al. 2008).

*Ischnura hastata* (Say, 1839) (Odonata, Coenagrionidae) is a New World damselfly species, widely distributed from Canada to South America (Westfall and May 1996). It has also colonized the Azores archipelago in the Atlantic Ocean, where it reproduces exclusively through parthenogenesis (Cordero Rivera et al. 2005; Lorenzo-Carballa and Cordero-Rivera 2009). The genetic analyses of the parthenogenetic populations from the islands have shown a very low clonal diversity (Lorenzo-Carballa et al. submitted), which makes *I. hastata* a good model to test the predictions of the Red Queen Hypothesis.

With this initial aim, we sampled several localities at different islands within the Azores archipelago, to study the prevalence (number of infected hosts/number of host examined) of mite parasitism in *I. hastata* females and compare this with rates of parasitism in *I. pumilio* (Charpentier, 1825), the other coenagrionid species found in the archipelago.

We found larvae of water mites (*Arrenurus* sp.) and terrestrial mites [*Leptus killingtoni* (Turk, 1945)] infesting odonates in the Azores islands. Here, we provide detailed morphological data on these mite species, together with details on the new hosts and locality records. Although the prevalence of mite parasitism was not high enough to test the predictions of the Red Queen Hypothesis, we provide data on ectoparasitism rates in *I. hastata*, and we address the potential implications of parasitism in this species, given its unique reproductive strategy among the Odonata.

## Materials and methods

### Patterns of mite parasitism in *Ischnura hastata*

In July 2003, we observed ectoparasitic mites on *I. hastata* females at the pond Lagoa do Landroal, in the island of Pico. In July–August 2008 we visited this and several other ponds in this island, to study the prevalence of mite parasitism on *I. hastata* and to compare it with infestation rates on *I. pumilio*, the other coenagrionid species found in the archipelago, which reproduces sexually (see Table 1 for a list of sampled locations). Infestation rates were assessed visually, and the number of mites on each individual was recorded with the aid of a hand lens. Following examination, some parasitized damselflies were preserved in absolute ethanol for subsequent mite identification and photography. Some of the specimens were prepared for Scanning Electron Microscopy (SEM).

Prevalence of mite parasitism was also studied in a population in São Miguel island over 15 different days between 27 July and 24 August 2008, during the course of a mark-recapture experiment (Lorenzo-Carballa et al. 2009). Each female captured during the study was examined for mites, and the number of mites on each individual was determined with the aid of a hand lens. As with the populations from Pico, some parasitized hosts were preserved in absolute ethanol for later mite identification and photography, and some specimens were also prepared for SEM.

Additional data on mite parasitism within parthenogenetic populations of *I. hastata* were obtained by counting the mites on females collected at several ponds in the islands of Flores, Faial, Pico, Terceira, Sao Miguel, Corvo and Santa Maria during the course of our expeditions to the Azores in the years 2003 and 2008 (see Table 2 for a list of sampled locations). These females were collected with the aid of a hand net, sweeping the vegetation close to the shore of the ponds, where they were mostly encountered. After sweeping, females were preserved in absolute ethanol, and the number of mites was later recorded in the laboratory under a binocular microscope. For a comparison with sexual populations, we assessed the rate of mite parasitism in samples of *I. hastata* previously collected from several populations in Colombia, Cuba, Mexico and the US (see Table 4 for a list of sampled locations).

### *Mite species description*

Before slide preparation, mite larvae were removed from their hosts using forceps. Single mites, as well as the host body parts with the mites attached, were prepared for SEM.

For SEM, samples were subjected to increasing concentrations of ethanol as follows: 30, 50, 70, 80, 90 for 30 min each; and then placed in absolute ethanol for 30 min for two changes. After dehydration, ethanol samples were placed in a series of amyl-acetate:ethanol dilutions as follows: 1:3, 1:1; 3:1 for 30 min each; and then placed in 100% amyl-acetate for 30 min for two changes. Finally, samples were subjected to critical point drying to complete the dehydration process. In order to view specimens, they were first attached with double-sided carbon tape to aluminum stubs so that they could be coated with gold in a sputter-coating apparatus (Emitech K550X). The surface topography of mites was viewed at 10 kV in a Philips XL 30 scanning electron microscope.

Mite larvae found on *I. hastata* from Pico Island were identified by Ryszard Haitlinger as *Leptus killingtoni*. Diagnosis for this species was given by Southcott (1992) (Fig. 1). The species was first described by Turk (1945) without many important details. Later, Southcott (1992) made a new description of the species, including some figures. Unfortunately, metric data were based only on a single specimen from Great Britain. Further metric data from this species in North–West Spain were given by Haitlinger (2006). Thus,

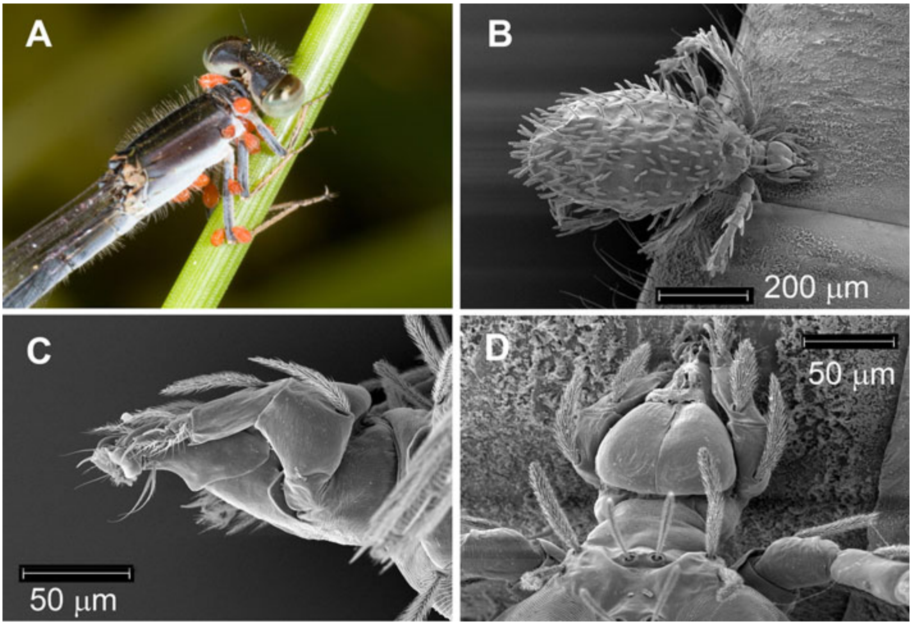

**Fig. 1** **a** Adult female *Ischnura hastata* from Lagoa do Landroal (Pico), July 2008. This specimen had at least 13 larvae of *Leptus killingtoni*, some of which are not engorged. **b** Dorsal view of a *L. killingtoni* larva (Scanning Electron Microscopy, SEM). **c** Lateral view of the head and mouth of a *Leptus* larva (SEM). **d** Detail of the head and the attachment to the cuticle of the damselfly (SEM)

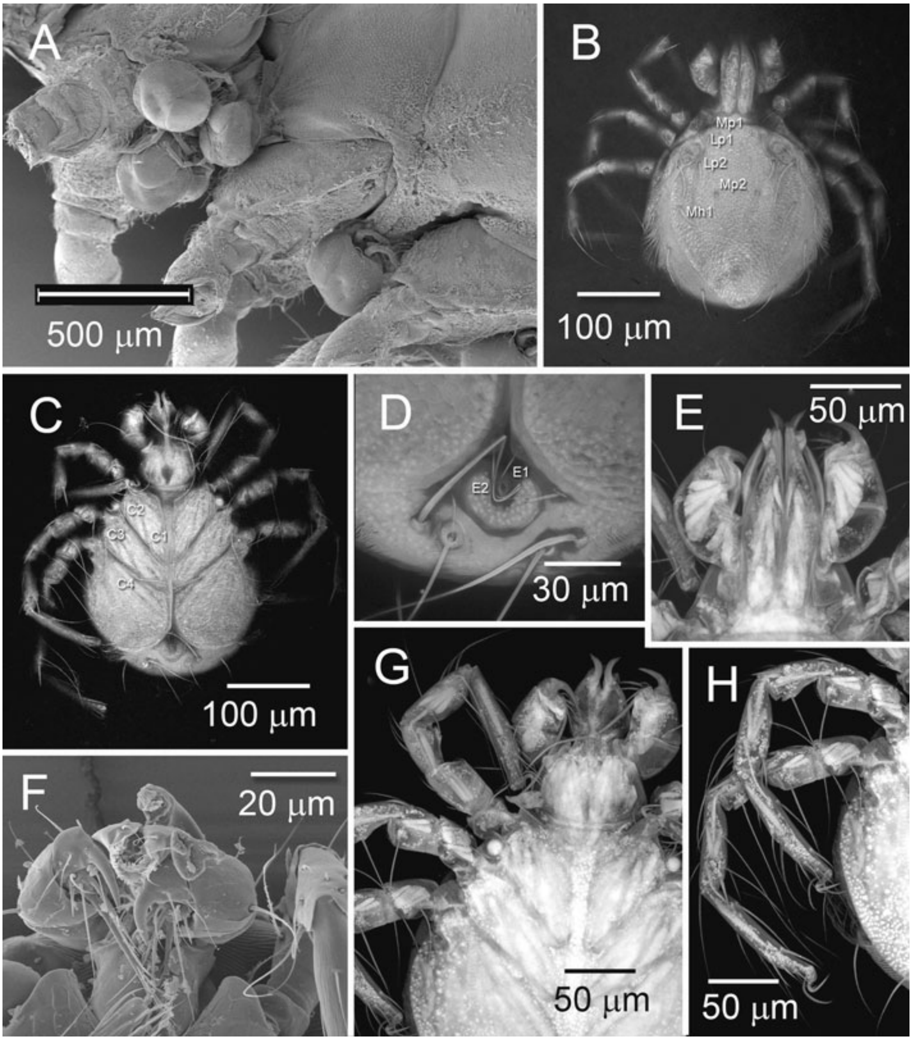

**Fig. 2** **a** Two larvae of *Arrenurus* sp. on the coxae of *Ischnura hastata* (Scanning Electron Microscopy, SEM). **b** Dorsal view of a non-engorged larva of *Arrenurus* sp. (Laser Scanning Confocal Microscopy, LSCM, maximum intensity projection, MIP). **c** Ventral view of a non engorged larva of *Arrenurus* sp. (LSCM, MIP). **d** Detail of Excretory plate (LSCM, alpha blended of two sets of MIP images). **e** Chelicerae (LSCM, MIP). **f** Pedipals last segments (SEM). **g** First leg (LSCM, MIP). **h** Second and third leg (LSCM, MIP)

our data from *L. killingtoni* collected in the Azores complement the morphological description of this species.

Ten mite larvae were mounted on slides using Berlese's medium. Each specimen was observed under a Jenaval microscope (Carl Zeiss) using an objective 40 × 0.6500/0.17-A, and a measuring ocular GF-Pw 10× was used to take measurements of the relevant taxonomic structures of these larvae. Terminology, abbreviations and standard data are based on the system described by Southcott (1992) and Haitlinger (2006).

**Table 1** Prevalence of parasitism by *Leptus killingtoni* on *Ischnura hastata* and *I. pumilio* at different ponds sampled in Pico island in 2008. Listed are: pond name, number of individuals examined (*n*), prevalence of parasitism (P) and range in mite load (I)

| Date | Pond | *n* | | P[a] | | I |
|---|---|---|---|---|---|---|
| | | Males | Females | Males | Females | |
| *Ischnura hastata* | | | | | | |
| July | Cabeço da Lagoinha | n.a | 83 | n.a. | 0.17 | 1–3 |
| | Lagoa do Landroal | n.a | 134 | n.a. | 0.41 | 1–12 |
| | Lagoa do Caiado | n.a | 4 | n.a. | 0 | – |
| | Large pond East Lagoa do Peixinho | n.a | 27 | n.a. | 0.04 | 1 |
| | Small pond E Lagoa do Peixinho | n.a | 32 | n.a. | 0.06 | 1 |
| | Unnamed pond | n.a | 63 | n.a. | 0 | – |
| August | Cabeço do Caveiro | n.a | 423 | n.a. | 0.01 | 1 |
| | Lagoa do Gato | n.a | 619 | n.a. | 0.04 | 1–2 |
| *Ischnura pumilio* | | | | | | |
| July | Cabeço da Lagoinha | 0 | 0 | – | – | – |
| | Lagoa do Landroal | 26 | 69 | 0.23 | 0.35 | 1–4 |
| | Lagoa do Caiado | 26 | 52 | 0.13 | 0.15 | 1–4 |
| | Large pond East Lagoa do Peixinho | 24 | 44 | 0 | 0.04 | 1 |
| | Small pond E Lagoa do Peixinho | 5 | 11 | 0.09 | 0 | 1 |
| | Unnamed pond | 1 | 0 | 0 | – | – |
| August | Cabeço do Caveiro | 0 | 1 | – | 0 | – |
| | Lagoa do Gato | 17 | 10 | 0 | 0 | – |

[a] Prevalence is presented here as a proportion

Mite larvae found on *I. hastata* from São Miguel island were initially identified by Antonio G. Valdecasas as belonging to the clade Hydrachnidia (water mites), which is known to parasitize aquatic insects when the mites are in the larval stage. Although there has been a considerable increase in our knowledge of water mite larval taxonomy (Martin 2006; Zawal 2008a; Smith et al. 2009 and references therein) even today a larva of an unknown female cannot be confidently identified to species. Three water mite larvae were transferred to temporary glycerin slides. Each specimen was placed on a special aluminum slide with an open circle in the middle. A Thermo Shandon 24 × 40 #1.5 coverslip was added to the aluminum slide as a base, and a Zeiss/Scott 18 × 18 #1.5 coverslip with a declared thickness of 0.170 ± 0.001 mm was used as a cover to minimize light aberrations. This particular preparation procedure allows Laser Scanning Confocal Microscopy (LSCM) acquisition in both the dorsal and ventral views. LCSM acquisition was carried out using a Leica TCS SPE at 10× 0.30 N.A., 20× 0.70 N.A., 40× dry 0.75 N.A. and 63× gli 1.30 N.A. at an excitation wavelength of 488 nm, and a wide emission wavelength range between 500 and 590 nm was used to collect as much fluorescence as possible. The acquisition resolution ranged between 1,024 × 1,024 and 2,048 × 2,048 pixel. Image stacks were processed using FIJI (available at http://www.pacific.mpi-cbg.de/wiki/index.php/Fiji) and Mipav (available at http://www.mipav.cit.nih.gov/). Alpha blended and maximum intensity projections (MIP) final images were checked for gamma correction and contrast with Photoshop CS3. No other manipulation of the images was carried out.

**Table 2** Prevalence of parasitism by *Arrenurus* sp. in parthenogenetic *Ischnura hastata* populations. Listed are: year of sample collection, island, pond name, number of females examined (*n*), prevalence of parasitism (P) and range in mite load (I)

| Year | Island | Pond | *n* | P[a] | I |
|---|---|---|---|---|---|
| 2003 | Flores | Caldeira da Lomba | 11 | 0 | – |
| | Pico | Lagoa do Landroal | 10 | 0 | – |
| | Faial | Caldeira | 25 | 0 | – |
| | Terceira | Lagoa do Ginjal | 32 | 0 | – |
| | | Lagoa do Negro | 20 | 0 | – |
| | Sao Miguel | Lagoa do Carvão | 17 | 0.12 | 2 |
| | | Furnas | 1 | 0 | – |
| | Corvo | Caldeira | 3 | 0 | – |
| 2008 | Santa Maria | Ribeira do Sancho | 2 | 0 | – |
| | Pico | Lagoa do Landroal | 18 | 0 | – |
| | Sao Miguel | Lagoa do Carvão | 35 | 0 | – |
| | | Lagoa do Fogo | 3 | 0 | – |
| | | Lagoa do Pico da Lagoa | 83 | 0 | – |
| | | Lagoa do Pau Pique | 207 | 0 | – |
| | | Lagoa do Areeiro | 2,781 | 0.01 | 1–5 |

[a] Prevalence is presented here as a proportion

Nomenclature and measurements used here follow Zawal in his extensive studies of *Arrenurus* larvae (see Zawal 2008b and references therein). Voucher specimens are deposited in the water mite collection of the MNCN (Madrid).

## Results

### Mite species infesting *Ischnura hastata* at the Azores

Morphological data for *L. killingtoni* collected in Pico are shown in Appendix—Table 6. These specimens from the Azores (Fig. 1) differ from specimens previously collected in Spain in that they show a greater range variability of some measurements, mainly W (width of scutum), AW (distance between scutalae AL), PsGd (length of dorsal palpfemoral seta) and leg segments (Appendix—Table 7).

Mite larvae found parasitizing *I. hastata* from Lagoa do Areeiro in São Miguel Island have been identified as belonging to the genus *Arrenurus* (Acari, Hydrachnidia). Below, we describe the morphology of these mite larvae and identify them to the lowest taxonomic level possible; we also make some additional comments on these specimens.

#### *Arrenurus (Arrenurus) sp. (Fig. 2)*

Body shape from nearly round to elliptical depending on the engorgement state of the larvae (Fig. 2a, b). In the non-engorged specimens, the gnathosoma projects beyond the anterior end of the dorsal plate (Fig. 2b, c). Dorsal plate shield shaped, similar to *A. affinis* (Koenike, 1887), with anterior margin almost straight and covering nearly all of the idiosoma in the non-engorged specimen. Dorsal plate (Fig. 2b) with scale-like reticulation and with five pair of setae: Lp1 tripartite, the other four apparently smooth. Mp1–Mp1 distance longer than Mp2–Mp2. Ratio dorsal plate width/Mp1–Mp1 <3.2 (Zawal 2008a).

There is a pair of small eyes, clearly identifiable from their pigment, below the anterior part of the dorsal plate. In one specimen, the eye pigment extended beyond the eye plaque. Another pair of eyes is located laterally to the dorsal plate on eyes capsule, which have a small process in its posterior part.

Coxal plates I, II and III separated from one another by four pairs of setae (Fig. 2c) on each side and medially. The length of the median margin of the coxal plate II is the shortest. Distance between C1–Cp1 median margin about ½ the distance between C4–Cp4 median margin. Excretory plate almost rounded with two pairs of setae, width slightly greater than length (Fig. 2d). Excretory pore closer to the anterior end of the excretory plate and slightly anterior to E2 setae.

Pedipalps five-segmentated and typical for *Arrenurus* species (Fig. 2f). PIII1 seta bi-pectinate, PV7 pectinated. Chelicerae bisegmentated (Fig. 2e). Legs with five movable segments (Fig. 2g, h). Total length of legs similar to the *A. affinis* (Koenike, 1887), *A.neumani* (Piersig, 1895), and *A. vietsi* (Koenike, 1911) species complex (Zawal 2008b). Metric values of the different morphological characters are shown in Appendix—Tables 7 and 8.

### *Prevalence and intensity of infestation*

Prevalence of infestation by *L. killingtoni* was highly variable among the different ponds studied in Pico Island, ranging from 0 to 41% on *I. hastata*, and from 0 to 35% on *I. pumilio*. Parasite load was 1–12 mites per female in the case of *I. hastata*, and 1–4 mites

**Table 3** Attachment sites of *Leptus killingtoni* and *Arrenurus* sp. upon *Ischnura hastata*. Data shown in the table correspond to 2008. For *L. killingtoni*, only data from the populations of Lagoa do Gato and Lagoa do Cabeço do Caveiro are shown

| Mite species | Host site | Observed no. of mites |
|---|---|---|
| *Leptus killingtoni* | | |
| | Legs | 5 |
| | Abdomen segment I (SI) | 3 |
| | Abdomen SII | 1 |
| | Abdomen SIII | 3 |
| | Abdomen SIV | 3 |
| | Abdomen SV | 1 |
| | Abdomen SVI | 1 |
| | Abdomen SVII | 1 |
| | Abdomen SVIII | 2 |
| | Tip of abdomen | 2 |
| | Thorax | 5 |
| | Total | 27 |
| *Arrenurus* sp. | | |
| | Ventral side of thorax, between legs | 65 |
| | Space between thorax and abdomen | 2 |
| | Mouth | 4 |
| | Legs | 1 |
| | Total | 72 |

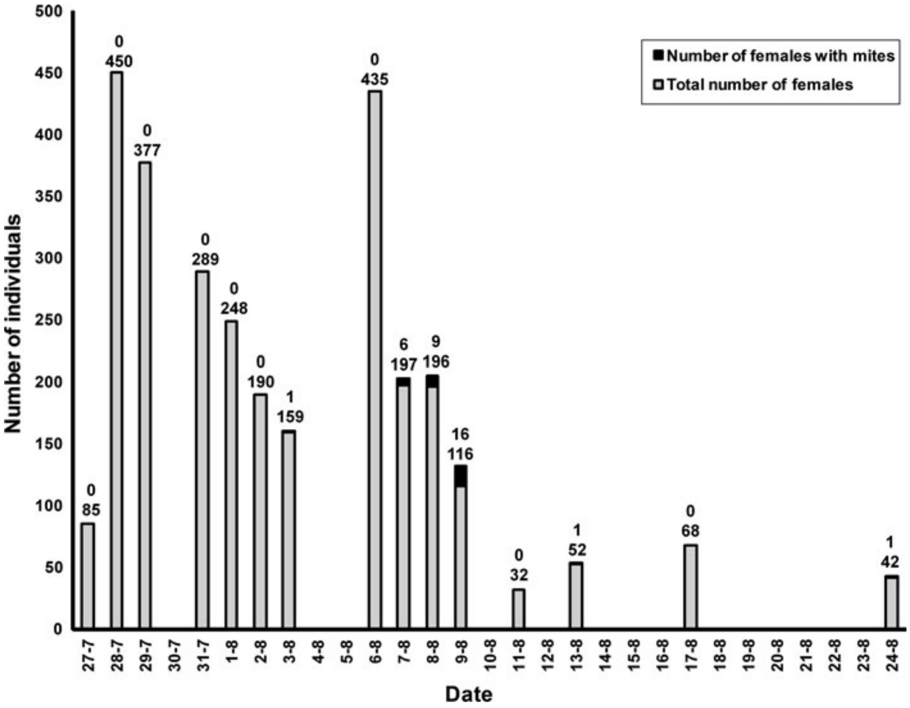

**Fig. 3** Variation in the proportion of female *Ischnura hastata* parasitized by *Arrenurus* sp. at Lagoa do Areeiro, São Miguel, between 27 July and 24 August 2008. Numbers on bars indicate the number of infested females (*above*) and the total number of females captured each day (*below*)

in the case of *I. pumilio* (Table 1). In *I. hastata* females, *L. killingtoni* larvae attached predominantly to the abdominal segments (17 out of 27, Table 3), although some attached also to the thorax and legs (Table 3; Fig. 1). In one case a mite was found attached to the eye of a female *I. hastata*.

The prevalence of mite parasitism by *Arrenurus* sp. on *I. hastata* was very low. With the exception of one population in the island of São Miguel (Lagoa do Carvão), where 12% of the collected females ($n = 17$, Table 2) were parasitized, no mites were found in any of the 119 females collected in the Azores in 2003. Parasite load was two mites per individual in the samples collected in 2003 (Table 2). In 2008 we found a similar pattern, but in this year the females collected at Lagoa do Carvão ($n = 35$, Table 2) were not parasitized at all. Prevalence of mite parasitism in the population of Lagoa do Areeiro (São Miguel) was 1%, considering both the females included in the mark-recapture study and the females previously collected and preserved in ethanol ($n = 2{,}781$, Table 2). Variation in the prevalence of parasitism was found in this population during the study period, ranging from 0.6% when the first parasitized females were observed to 2.4% at the end of the study, with a maximum of 13.8% (Fig. 3). Parasite load across the period was 1–5 mites per female (Table 2). *Arrenurus* sp. seems to select the ventral surface of the thorax, between the legs, as the main site of attachment (65 out of 72, Table 3, Fig. 2a), although two females had mites attached to the mouth and a female had one attached to a leg (Table 3).

Mites found on samples of sexual *I. hastata* collected in America had the typical morphology of Hydrachnidia, and were found attached also to the ventral surface of the

**Table 4** Prevalence of mite parasitism in sexual *Ischnura hastata* collected at different localities in America. Listed are: year of sample collection, locality, pond name, number of both males and females analyzed (*n*), prevalence of parasitism (P) and range in mite load (I)

| Year | Locality | Pond | Males | | Females | | I |
|---|---|---|---|---|---|---|---|
| | | | *n* | $P^a$ | *n* | $P^1$ | |
| 2003 | Vero Beach (Florida) | Baptist church pond | 3 | 0.33 | 38 | 0.08 | 1–4 |
| | | Unitarian universalist fellowship pond | 16 | 0 | 8 | 0.13 | 1 |
| | | West airport pond | 2 | 0 | 13 | 0.08 | 1 |
| 2004 | Vicam (México) | Unnamed pond | 7 | 0 | 24 | 0 | |
| 2007 | Santiago de Cuba | Unnamed pond | | | 22 | 0 | |
| 2010 | Santiago de Cuba | Unnamed pond | | | 8 | 0 | |
| | Santiago de Cuba | Mola | 18 | 0 | 17 | 0 | |
| | Santiago de Cuba | La Redonda | 13 | 0 | 22 | 0 | |
| | Bucaramanga (Colombia) | Humedal El Pantano | 16 | 0 | 32 | 0.06 | 1–2 |

[a] Prevalence is presented here as a proportion

thorax of their hosts. As for the parthenogens, prevalence of parasitism in the sexual populations examined was low. In the samples collected in Colombia, prevalence of parasitism was 6% for females ($n = 32$, Table 4), whereas no mites were found on males ($n = 16$, Table 4). Mite load in this population was 1–2 mites per female. In the three populations from Florida examined, prevalence of parasitism for females varied between 8 and 13% (Table 4). In two of these populations no mites were found on males, and in one population one out of three males (Table 4) was infested. Mite load in these populations ranged from 1 to 4 mites per individual. No mites were found on the individuals collected in Mexico and Cuba (Table 4).

## Discussion

Two very different mites parasitize parthenogenetic *I. hastata* at the Azores. The most prevalent is *L. killingtoni*, a terrestrial mite already known from Pico Island, where it was found on the caterpillar *Pseudaletia* (=*Mythimna) unipuncta* (Haworth, 1809) (McNeill and Treat 1992). Larvae of this mite species have been previously reported as parasites of Odonata, with the following species reported as hosts in Great Britain (Turk 1945): *Pyrrhosoma nymphula* (Sulzer, 1776), *Enallagma cyathigerum* (Charpentier, 1840), *Coenagrion puella* (Linnaeus, 1758), *Ceriagrion tenellum*, *Lestes sponsa* (Hansemann, 1823), *Cordulegaster boltonii* (Donovan, 1807), *Anax imperator* Leach, 1815, and *Orthetrum coerulescens* (Fabricius, 1798). Herein we reported the prevalence of this mite on *I. hastata* and *I. pumilio* from Pico, but we have also observed these mites on *Sympetrum fonscolombii* (Selys, 1840) at the same island. The latter three species are new hosts for *L. killingtoni*.

The greatest number of *L. killingtoni* larvae that we recorded on an *I. hastata* individual was 12 (Table 1), although one female with a higher parasite load was observed (Fig. 1a). A similar number of mites (eight) has been previously recorded in odonates from the UK (Turk 1945), which suggests that the effect of this terrestrial mite on odonates should be less intense than the effect of water mites, whose loads can be in some cases much higher than 100 (Anderson and Anderson 1998; Table 5).

The second type of mite found associated with *I. hastata* were water mites found at the island of São Miguel. Only two genera of water mites have been mentioned for the Azores: *Sperchon* and *Arrenurus* (Viets 1978; Raposeiro et al. personal communication). The specimens found on *I. hastata* conform to the morphological characteristics of the larvae of *Arrenurus* as described by Zawal (2008a) in his monograph on *Arrenurus* larvae, but they do not conform to any of the previously described larvae, and thus our description is given as reference. To be certain of the specific identity of a water mite larva it is necessary to associate the adult female with the hatched eggs. This has not been possible with the mites found on *I. hastata*, and thus the larvae have been identified to the lowest category possible. These specimens have the diagnostic characteristics that identify them as belonging to the subgenus *Arrenurus* (*Arrenurus*). Although approximately 170 species of *Arrenurus* were described from Europe and about 400 from the world, the larval stage of no more than 70 are known. In the Azores, only *A. chavesi* has been recorded, but this species is presently considered *incertae sedis* (Viets 1987). From the general morphology of the dorsal and ventral shields, our specimens from São Miguel are closest to the *A. affinis*, *A. neumani* and *A. vietsi* group, whose larvae are indistinguishable (Zawal 2008b). Thus, to identify these larval mites at the specific level we must wait for the finding of some adult specimens.

The prevalence of mite parasitism in adult Odonata varies between years, populations, and individuals within populations (Corbet 1999). Factors such as differences in host exposure, immunity, phenology and spatial constraints also influence field variation in parasitism by water mites (Lajeunesse et al. 2004; Lajeunesse 2007). In the present study, the prevalence of infestation of parthenogenetic *I. hastata* by *Arrenurus* sp. was low, but comparable to what we have observed in the samples from sexual populations examined from the Americas (see Table 4). Published records of mite parasitism for different Coenagrionidae species are shown in Table 5. These data reveal that the prevalence of parasitism on *I. hastata* is in general lower than that observed in other damselfly species. Our estimates of parasitism in the samples of *I. hastata* from sexual populations are similar to previously published estimates for this species (Lajeunesse 2007; see Tables 4 and 5).

With respect to the attachment sites, we have found a tendency of aquatic mite larvae to attach to the ventral surface of the thorax, a pattern that has previously been reported for *Arrenurus* larvae (Smith 1988). In the case of *L. killingtoni*, most larvae were found attached to the host's abdomen, although sometimes to the thorax, legs and even head and eyes, suggesting that *L. killingtoni* does not show a clear preference when attaching to their hosts, an observation already reported for this genus (Baker 1982).

The low prevalence of parasitism found in the sexual *I. hastata* populations may be due to the habitat characteristics of this species, or simply to the lack of temporal and spatial co-occurrence of *I. hastata* with the mite larvae. In order to better assess the impact of mite parasitism in this species, it would be necessary to compare the prevalence of parasitism in different habitat types from the same locations. In the case of the parthenogenetic populations, we have found that the prevalence of mite parasitism is also very low, and at most of the studied ponds, no mites were found attached to odonates. The data collected at Lagoa do Areeiro (São Miguel) suggest differences in phenology between *I. hastata* and *Arrenurus* sp., since the maximum prevalence of parasitism in this population was observed at the end of the study period, when the number of *I. hastata* females in the population had diminished. Alternatively, the low prevalence of parasitism found in the Azores could simply be explained by the scarcity of parasites in the archipelago.

**Table 5** Bibliographic records of parasitism by water mites in several odonate species belonging to the family Coenagrionidae. Listed are: species name, number of individuals analyzed (*n*), prevalence (P, presented as a proportion) and range in mite load (I)

| Species | *n* | P | I | Males | | | Females | | | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *n* | P | I | *n* | P | I | |
| *Argia vivida* (Hagen in Selys, 1865)[a] | 57 | | 20–360 | | | | | | | Anderson and Anderson (1998) |
| *A. vivida*[b] | 86 | | 20–160 | | | | | | | Anderson and Anderson (1998) |
| *Cercion hieroglyphicum* (Brauer, 1865)[c] | 1,312 | 0.42 | 1–152 | | | | | | | Mitchell (1968) |
| *C. hieroglyphicum*[d] | 1,312 | 0.98 | 5–57 | | | | | | | Mitchell (1968) |
| *Ceriagrion tenellum*[e] | 2,233 | 0.93 | 1–135 | 1,308 | 0.92 | 1–120 | 925 | 0.96 | 1–135 | Andrés and Cordero (1998) |
| *C. tenellum*[f] | 1,725 | 0.24 | 1–70 | 1,068 | 0.21 | 1–55 | 657 | 0.28 | 1–70 | Andrés and Cordero (1998) |
| *Coenagrion puella* (Villers, 1789) | 200 | 0.74 | 1–100 | | | | | | | Bonn et al. (1996) |
| *C. puella* | 327 | 0.54 | – | 288 | 0.51 | – | 39 | 0.72 | – | Conrad et al. (2002) |
| *C. pulchellum* (Vander Linden, 1825) | 148 | 0.21 | 1–42 | 111 | 0.25 | 1–30 | 37 | 0.08 | 4–12 | Zawal (2006) |
| *Enallagma cyathigerum* (Charpentier, 1840) | 468 | 0.28 | 1–164 | 394 | 0.25 | 1–79 | 74 | 0.43 | 1–164 | Zawal (2006) |
| *E. ebrium* (Hagen, 1861)[g] | 406 | 0.29 | 1–12 | 181 | 0.30 | 1–12 | 225 | 0.29 | 1–12 | Léonard et al. (1999) |
| *Erythromma najas* (Hansemann, 1823) | 84 | 0.33 | 1–195 | 70 | 0.34 | 1–97 | 14 | 0.29 | 1–195 | Zawal (2006) |
| *Ischnura elegans* | 204 | 0.19 | 1–144 | 137 | 0.13 | 1–10 | 67 | 0.3 | 1–144 | Zawal (2006) |
| *I. elegans* | 236 | 0.08 | 1–6 | 160 | 0.11 | 1–6 | 96 | 0.01 | 1–6 | Zawal and Dyatlova (2006) |
| *I. hastata* | 114 | 0.12 | 1–22 | | | | | | | Lajeunesse (2007) |
| *I. posita* (Hagen, 1861) | 2,215 | 0.5 | – | 1,135 | 0.55 | – | 1,080 | 0.44 | – | Robinson (1983) |
| *Nehalennia gracilis* (Morse, 1895) | 16 | 0.13 | 1–9 | | | | | | | Lajeunesse (2007) |
| *N. speciosa* (Charpentier, 1840) | 124 | 0.6 | 1–8 | 83 | 0.58 | 1–7 | 41 | 0.63 | 1–8 | Reinhardt (1996) |
| *Platycnemis pennipes* (Pallas, 1771) | 116 | 0.27 | 1–63 | 76 | 0.26 | 1–40 | 40 | 0.28 | 1–63 | Zawal (2006) |
| *Pyrrhosoma nymphula* (Sulzer, 1776) | 4 | 0.25 | 0–4 | 1 | 1.00 | 4 | 3 | 0 | – | Zawal (2006) |

[a] Newly emerged damselflies

[b] Damselflies with engorged mites

[c] Mite species: *Arrenurus mitoensis,* Imamura and Mitchell (1967)

[d] Mite species: *A. agrionicolus* Uchida, 1937

[e] Individuals marked as tenerals

[f] Individuals marked as adults

[g] Mite species: *Limnochares americana* (Lundblad, 1941)

In the light of the Red Queen Hypothesis (Van Valen 1973; Bell 1982; Ridley 1995), we would predict that *I. hastata* in the Azores, with its asexual reproduction and very low genetic diversity (Lorenzo-Carballa et al., submitted), would be less able to evolve resistance to parasites, and would thus host higher parasite loads than sexual populations (Bell 1982; Ridley 1995). However, we did not find this pattern, though this could be due to the overall lower abundances of parasites in the Azores, rather than a heightened resistance to mite parasitism in these asexual populations One possible solution to this problem is to compare parasitism rates in parthenogenetic *I. hastata* with those of sexual *I. pumilio*, which are also found in the Azores. Unfortunately these two species were rarely found coexisting in large numbers, and the data available for this comparison (see Table 1), although suggestive, do not allow us to test the predictions of the Red Queen Hypothesis. Besides, using adult damselflies to estimate mite infection intensity might not be meaningful. For example, it has been proved that underwater oviposition, a common behavior in *I. hastata* at the Azores (Lorenzo-Carballa et al. 2009), favors detachment of water mites in damselflies (Rolff 1997). Further studies should concentrate on detecting mites in immature females. In the case of *L. killingtoni*, we have observed that the mites easily detached from their hosts when captured in the net (Lorenzo-Carballa and Cordero-Rivera, personal observations). All these facts suggest that our estimates of prevalence of mite parasitism are likely to be underestimates, and thus the comparative analysis of mite parasitism could be an unsuitable system to study questions related to parasites and the evolution of sex. In this respect, a comparative investigation of the distribution and virulence of endoparasites might be revealing. For example, gregarines have been reported as parasites of seven different families of Odonata, and larvae of the mermithid *Linstowimermis* (=*Amphimermis*) *tinyi* (Nickle, 1972) have been described as parasites of *I. hastata* nymphs (Corbet 1999). Future research should be directed towards a comparative analysis of parasitism rates between both species in several ponds at the Azores. Thus, the parthenogenetic populations of *I. hastata* in the Azores may still lead to new findings concerning the Red Queen Hypothesis in the future.

In conclusion, the low prevalence of mite parasitism found in the Azores, coupled with the fact that most of the populations in the archipelago are almost free from competitors and predators (Lorenzo-Carballa et al. 2009) could explain the persistence of the *I. hastata* parthenogenetic populations, despite their low levels of genetic variation. This example adds new evidence to the idea of the islands as suitable habitats for the persistence of parthenogenetic reproduction (Whittaker and Fernández-Palacios 2007).

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## Appendix

See Tables 6, 7 and 8.

**Table 6** Metric data of *Leptus killingtoni* larvae from: Great Britain (Southcott 1992), Spain (Haitlinger 2006) and Azores (this work). Abbreviations used here are explained in Southcott (1992) and Haitlinger (2006). All measurements are given in micrometers

| | G. Britain ($n = 1$) | Spain ($n = 10$) | Azores ($n = 10$) | | G. Britain ($n = 1$) | Spain ($n = 10$) | Azores ($n = 10$) |
|---|---|---|---|---|---|---|---|
| IL | | 362–806 | 406–756 | TiI | 145 | 134–148 | 138–160 |
| IW | | 202–571 | 305–540 | GeI | 114 | 100–108 | 92–116 |
| L | | 90–104 | 80–102 | TfI | | 66–70 | 62–72 |
| W | 114 | 96–102 | 96–114 | BfI | | 72–84 | 70–92 |
| AW | 78 | 72–78 | 74–88 | TrI | | 44–50 | 42–54 |
| PW | 103 | 86–90 | 88–102 | CxI | | 58–70 | 62–72 |
| AA | 15 | 10–12 | 8–12 | TaII | 113 | 114–124 | 104–122 |
| SB | 20 | 14–16 | 12–20 | TiII | 136 | 120–130 | 110–134 |
| AL. | 57 | 70–84 | 68–76 | GeII | 100 | 84–90 | 84–100 |
| PL | 64 | 66–76 | 64–80 | TfII | | 62–80 | 58–72 |
| AM | 46 | 40–50 | 40–54 | BfII | | 60–78 | 62–78 |
| S | 64 | 62–72 | 60–84 | TrII | | 42–54 | 42–50 |
| AP | 18 | 12–18 | 12–18 | CxII | | 80–90 | 80–92 |
| ISD | 49 | 50–56 | 52–60 | TaIII | 129 | 110–122 | 110–128 |
| GL | | 156–172 | 154–178 | TiIII | 182 | 164–176 | 158–180 |
| Ds. | 46–60 | 38–62 | 38–60 | GeIII | 109 | 92–106 | 92–106 |
| 1a | | 48–58 | 48–60 | TfIII | | 72–78 | 68–80 |
| 2a | | 42–60 | 48–64 | BfIII | | 76–90 | 72–90 |
| 1b | | 66–82 | 70–82 | TrIII | | 52–54 | 46–54 |
| 2b | | 38–44 | 34–42 | CxIII | | 72–84 | 80–92 |
| 3b | | 50–58 | 48–58 | leg I | | | 604–682 |
| PsFd | | 54–78 | 58–74 | leg II | | | 554–634 |
| PsGd | | 42–54 | 46–62 | Leg III | | | 642–712 |
| TaI | 120 | 114–126 | 112–132 | Ip | | | 1,800–2,028 |

**Table 7** *Arrenurus* sp. larvae. Lengths of body parts ($n = 3$). Nomenclature and measurements used follow Zawal (2008b): *Cp* coxal plate, *Exp* excretory pore, *Expp* excretory pore plate, PI–PV segments on pedipal; for setae Mp1, Lp1, Lp2, Mh1 and C1–C4 see Fig. 2. All measurements are given in micrometers

| | N1 | N2 | N3 |
|---|---|---|---|
| Body length | 240 | 414 | 311 |
| Body width | 219 | 370 | 266 |
| Dorsal plate length | 224 | 208 | 231 |
| Dorsal plate width | 165 | 166* | 166 |
| CpI medial margin length | 76 | 78 | 76** |
| CpII medial margin length | 30 | 38 | 34** |
| CpIII medial margin length | 41 | 48 | 38** |
| Distance: Mp1–Mp1 | 59 | 59 | 59 |
| Distance: Lp1–Lp1 | 65 | 69 | 70 |
| Distance: Lp2–Lp2 | 90 | 98 | 96 |

**Table 7** continued

| | N1 | N2 | N3 |
|---|---|---|---|
| Distance: Mp2–Mp2 | 52 | 58 | 53 |
| Distance: Mh1–Mp2 | 48 | 48 | 45 |
| Distance: Mp1–Lp1 | 10 | 7* | 13 |
| Distance: Mp1–Lp2 | 44 | 38* | 48 |
| Distance: Mp1–Mp2 | 80 | 62* | 80 |
| Distance between C1 and CpI median margin | 22 | 23 | 21 |
| Distance between C4 and CpIII median margin | 40 | 44 | 46 |
| Distance between C1 and C2 | 57 | 57 | 57 |
| Excretory pore plate length | 27 | 28 | 25 |
| Excretory pore plate width | 29 | 30 | 28 |
| Distance between Exp and Expp posterior margin | 17 | 17 | 15 |
| Distance between E1 setae and Expp anterior margin | 4 | 5 | 4 |
| Distance between E2 setae and Expp posterior margin | 10 | 10 | 11 |
| PI length | 8 | 12 | |
| PII length | 33 | 38 | |
| PIII length | 31 | 32 | |
| Length of PIV claw | 28 | | |
| Length of cheliceral segment I | 112 | | |

* Figures underestimate real length due to curvature of the structure

** Limits of these measurements are somewhat arbitrary, especially in CpIII

**Table 8** *Arrenurus* sp. larvae. Lengths of body parts ($n = 3$). Nomenclature and measurements used here follow Zawal (2008b). All measurements are given in micrometers

| | | Trochanter | Femur | Genu | Tibia | Tarsus |
|---|---|---|---|---|---|---|
| N1 | Leg 1 | 30 | 40 | 44 | 61 | 95 |
| | Leg2 | 40 | 46 | 48 | 65 | 97 |
| | Leg 3 | 48 | 48 | 46 | 70 | 97 |
| N2 | Leg1 | 40 | 42 | 46 | 63 | 91 |
| | Leg2 | 36 | 42 | 46 | 65 | 99 |
| | Leg3 | 44 | 40 | 46 | 68 | 97 |
| N3 | Leg 1 | 34 | 38 | 40 | 61 | 95 |
| | Leg 2 | 32 | 40 | 48 | 63 | 97 |
| | Leg 3 | 38 | 34 | 42 | 66 | 95 |

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