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ORIGINAL PAPER

Parasitism by water mites in native and exotic Corixidae: Are mites limiting the invasion of the water boatman *Trichocorixa verticalis* (Fieber, 1851)?

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Abstract The water boatman *Trichocorixa verticalis verticalis* (Fieber 1851) is originally from North America and has been introduced into the southern Iberian Peninsula, where it has become the dominant Corixidae species in saline wetlands. The reasons for its success in saline habitats, and low abundance in low salinity habitats, are poorly known. Here we explore the potential role of water mites, which are typical parasites of hemipterans, in the invasion dynamics of *T. v. verticalis*. We compared infection levels between *T. v. verticalis* and the natives *Sigara lateralis* (Leach, 1817) and *S. scripta* (Rambur, 1840). No mites were found in saline wetlands where *T. v. verticalis* is highly dominant. Larvae of two mite species were identified infecting corixids in habitats of lower salinity: *Hydrachna skorikowi* and *Eylais infundibulifera*. Total parasite prevalence and prevalence of *E. infundibulifera* were significantly higher in *T. v. verticalis* compared with *S. lateralis* and *S. scripta*. Mean abundance of total infection and of *E. infundibulifera* and *H. skorikowi* were also higher in *T. v. verticalis*. When infected with *H. skorikowi*, native species harbored only one or two parasite individuals, while the smaller *T. v. verticalis* carried up to seven mites. When infected with *E. infundibulifera*, native species harboured only one parasite individual, while *T. v. verticalis* carried up to 6. Mite size didn't differ among host species, suggesting that all are suitable for engorgement. Both mite species showed a negative correlation between prevalence and salinity. *T. v. verticalis* susceptibility to parasitic mites may explain its low abundance in low salinity habitats, and may contribute to the conservation of native corixids. The success of *T. v. verticalis* in saline wetlands may be partly explained by the absence of parasitic mites, which are less halotolerant.

Keywords *Trichocorixa verticalis verticalis* · Corixidae · Water mite · *Hydrachna skorikowi* · *Eylais infundibulifera* · Doñana

Introduction

Invasive species have become a major conservation problem in aquatic ecosystems at the global scale (Leppäkoski et al. 2002). Understanding the interactions between invasive species and the recipient community (including free-living organisms and parasites) is key to understanding the invasion process, to improve our capacity to predict the outcome of invasions and to design strategies for the conservation of native taxa.

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The introduction and spread of invasive species is a significant but insufficiently studied factor in disease emergence (Kelly et al. 2009a; Mastitsky et al. 2010). Although it is now widely recognized that the impacts of species introductions on native communities are often mediated via parasites (Prenter et al. 2004; Dunn 2009), our understanding of how such impacts occur is incomplete. Most studies have focused on the effect of the loss of coevolved parasites during the introduction process ('Enemy Release Hypothesis', Torchin et al. 2002, 2003; Keane and Crawley 2002; Colautti et al. 2004; Prenter et al. 2004), and the introduction of exotic parasites arriving with alien hosts to the recipient community ('Parasite Spillover', Dobson and Foufopoulos 2001; Power and Mitchell 2004). However, with the exception of native parasites affecting exotic plants and invertebrates of economic importance, which have been the subject of studies of biological control (Williams et al. 2003; Li et al. 2012), the acquisition of new parasites by exotic species has been largely overlooked, even though it is potentially a frequent and important process (Kelly et al. 2009b; Mastitsky et al. 2010). Depending on the mechanism and the role played by the novel parasite, the consequences for the invasion success of the alien host and the impact on the recipient community can be highly variable. Disentangling such mechanisms will improve our understanding of biological invasions and enhance our ability to predict the outcomes of ongoing and future invasions.

Trichocorixa verticalis verticalis (Hemiptera: Corixidae) is native to North America and occurs in brackish and saline wetlands (Sailer 1948). Recently it has invaded aquatic ecosystems in Africa, Oceania and Europe, where it is the only known exotic corixid (Rabitsch 2008, 2010; Guareschi et al. 2013). It is predicted to spread extensively across Europe during the course of this century (Guareschi et al. 2013). However, there are currently few data on its potential ecological impact in the introduced range. In its native North America, this omnivorous insect is important in structuring the pelagic planktonic communities of aquatic ecosystems through predation on cladocerans (Simonis 2013) and anostracans (Wurtsbaugh 1992). In Great Salt Lake (USA), during periods of low salinity, *T. v. verticalis* has been shown to affect the food web of the lake through its predation on brine shrimp *Artemia franciscana* Kellog, 1906 (Wurtsbaugh 1992). It causes a strong trophic cascade affecting microbes and phytoplankton (Wurtsbaugh 1992). Therefore, we can expect *T. v. verticalis* to have a significant impact in wetlands of the introduced range.

In its introduced range in the south of the Iberian Peninsula, *T. v. verticalis* is highly dominant and abundant in permanent saline fish ponds and salt ponds where native Corixidae are rare and may have been competitively excluded. In contrast, native corixids dominate in seasonal ponds and marshes of lower salinity within the same general area (Rodríguez-Pérez et al. 2009; Van de Meutter et al. 2010a). This strong pattern in relation to salinity remains unexplained, especially as experiments with adult corixids have shown that *T. v. verticalis* adults perform well at low salinities and are not more resistant to high salinities than some native corixids (Van de Meutter et al. 2010b; Coccia et al. 2013). Indeed, the native *Sigara selecta* (Fieber, 1848) is more halotolerant than *T. v. verticalis* (Van de Meutter et al. 2010b).

There is no previous information on the potential role of parasites in the invasion dynamics of the American corixid. Corixidae are known to be hosts to a diverse community of parasites, water mites (Hydracarina) being among the most common (Reilly and McCarthy 1991). Parasitic mites occur in almost all fresh and brackish aquatic environments, where they can reach densities of more than 2000 specimens per square meter (Smith et al. 2010). While most nymphal and adult stages are predatory and free-living in aquatic ecosystems, the larval stage is parasitic (Davids 1973). Mites can strongly impact host populations and influence biological interactions between corixid species (Smith 1977). Therefore, they have the potential to play an important role in the outcome of competition between native and invasive species. However, there are no previous studies of parasitic mites on the Corixidae of the southern Iberian Peninsula. Likewise, there is a lack of information about factors affecting host preference by water mites. The size of hosts appears to be one important factor (Blower and Roughgarden 1988) and the difference in size between *T. v. verticalis* and native species may potentially influence parasitism rates and hence the success of the invasion.

The aim of this study was to compare infestation levels of larval water mites in native (*Sigara lateralis* and *Sigara scripta*) and exotic corixids (*T. v. verticalis*) along the salinity gradient in Doñana in southwest Spain, and to consider their role in the invasion of *T. v. verticalis*. We test the following hypotheses: (1) *T. v. verticalis* is released from mite parasitism at the high salinities where it dominates; (2) parasites grow to a larger size in larger corixid species; and (3) mites attach to a wider range of body parts in *T. v. verticalis* because this species is less sclerotized than native species. The results of this study may have important implications for the conservation of native corixid fauna in Europe.

Materials and methods

Study area

The climate in the study area is Mediterranean subhumid, characterized by hot, dry summers and mild winters. Sampling of seasonal habitats where native and invasive corixids coexist was mainly conducted within the

Caracoles estate in the northern edge of Doñana National Park (Southwest Spain, see Fig. 1). This is a marshland area containing 96 experimental temporary ponds of different size and depth (see Frisch et al. 2012; Sebastián-González and Green 2014 for details). Experimental ponds are fed mainly by precipitation that occurs generally from late September to early April.

Sampling was also carried out in the Veta la Palma fish ponds (Fig. 1) where *T. v. verticalis* is the dominant corixid (Rodríguez-Pérez et al. 2009; Rodríguez-Pérez and Green 2012). Veta la Palma is an extensive fish farm composed of 37 shallow brackish ponds within Doñana Natural Park. These permanent, saline, ponds are supplied with water from the estuary of the River Guadalquivir (see Kloskowski et al. 2009; Rodríguez-Pérez and Green 2012 for details). In general, the fish ponds are much more saline on average than the seasonal marsh and temporary ponds in Doñana (Rodríguez-Pérez et al. 2009; Kloskowski et al. 2009; Van de Meutter et al. 2010a).

Details of the sampling sites, dates and sampling objectives are summarized in Table 1.

Specific sampling

On 27 June 2011 a total of 307 adult corixids (111 *T. v. verticalis*, 103 *S. lateralis* and 93 *S. scripta*) were collected specifically for the study of parasites using a D-framed pond net (500 µm mesh; 16 × 16 cm) from an individual temporary pond at the Caracoles estate (hereafter AC3). The sampling date was selected because corixids reached maximum abundance in summer, and this particular pond was chosen based on previous observations of the species coexistence [authors' personal observation]. After collection, individuals were placed inside plastic containers filled with damp aquatic vegetation and transported alive to the laboratory. Once at the laboratory, specimens were carefully separated and individually stored in 1.5 ml Eppendorf tubes filled with 70 % ethanol, until examination for parasites. This sampling was designed to minimize the probability of water mites becoming detached from the host prior to examination, in order to have an exact measure of infection rates.

General sampling in Caracoles and Veta la Palma ponds

We also studied the prevalence of infected corixids in a large collection of samples collected from 32 ponds within the Caracoles estate, which were representative of all size and depth classes and 10 points within 7 natural or semi-natural waterbodies in the immediate surroundings (Fig. 1) during May–June of 2 years (2010–2011), as part of a broader study on the invasion of *T. v. verticalis*. Water

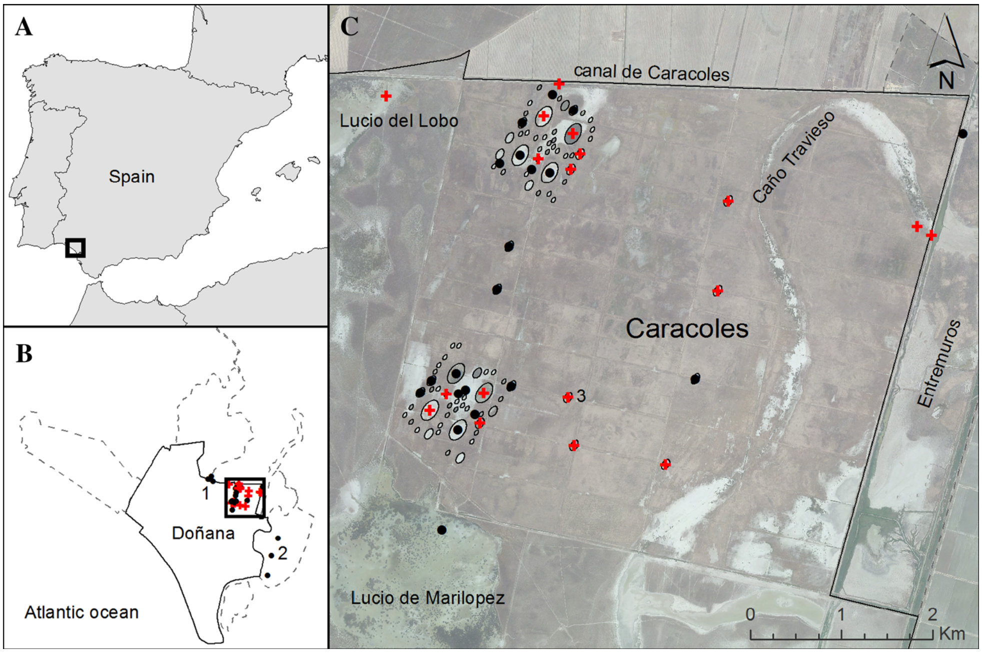

Fig. 1 Map of the study area showing the Doñana region in southern Spain (**a**). The *solid lines* indicate the boundary of Doñana National Park and the *dashed lines* indicate Doñana Natural Park (**b**). The area where we found water mites within the Caracoles estate and immediate surroundings is framed. *Red crosses* represent sites with water mites and corixids; *black dots* indicate sampled sites without water mites but with corixids. The number (*1*) indicates FAO sample sites and (*2*) indicates Veta la Palma fish ponds. Map detail **c** shows the spatial arrangement of all sites with water mites. The number (*3*) indicates the pond (AC3) of the specific sampling. See Frisch et al. (2012) for further details of the Caracoles ponds

Table 1 Summary of the location, dates and objectives of sampling

Sampling type	General sampling
Main objective	Broader study of seasonal dynamics of corixid communities; plus water mite infections
Study area/total no ponds/date	Caracoles estate and waterbodies in the immediate surroundings/42 ponds/May–June 2010–2012
	Veta la Palma fish ponds/3 ponds (Gaveta 3, A3, A7)/May–July 2011
Sampling type	Specific sampling
Main objective	Most accurate possible calculation of mite infection rates
Study area/no ponds/date	Caracoles estate/1 pond (AC3)/27 June 2011

salinities vary spatially and temporally, with a range of 2.62–37.8 ppt during the study period in the selected sites.

Details of mite infections are presented here for those sites that held both parasitic mites and at least two species of corixids. To establish the prevalence and abundance of mites in the fish ponds where *T. v. verticalis* is highly dominant, we examined 909 *T. v. verticalis* adults collected from 3 permanent ponds (G3, A3 and A7, which were representative of the salinity gradient within the pond complex) during May–July 2011 (Fig. 1). Water salinities varied from 4.3 to 25.8 ppt during the study period in the selected ponds. These samples were collected in a sweep net as before, but individuals from the same pond were stored together in 5 ml vials filled with 70 % ethanol until they were examined for the presence of parasites. Therefore we cannot exclude the possibility of some mites becoming detached from their hosts (although the attachment sites remain visible, see "Results").

Some free-living adult mites were found in four different sites during the general sampling: two temporary ponds within the Caracoles estate (AC4 and AE5); one semi-natural pond (FAO pond) within Doñana National Park; and one intermittent stream (Caño Guadiamar) within Doñana Natural Park (during March 2010, and March and May 2011). These samples were used to compare species composition with parasitic larvae and to aid larval identification. Salinity (ppt) was measured in situ using a WTW 340i multiprobe.

Using a stereomicroscope we identified each corixid species in our samples (after Jansson 1986; Nieser et al. 1994; L'Mohdi et al. 2010), determined its sex and checked for the presence of mites. Body length of corixids was measured on images taken with a digital camera (AxioCam Icc1) connected to a Zeiss microscope (Discovery V8). For the inspection of the thoracic and abdominal torsum, hemielytra and wings were lifted. We measured prevalence (proportion of individuals infected), mean abundance (number of parasites averaged for each corixid species), and mean intensity (number of parasites averaged for all infected corixids) for total mite infection and for each mite species in the different hosts (see Bush et al. 1997 for definitions of infection descriptors).

We recorded the attachment site for each individual mite and compared the susceptible surface area between different hosts using all infected individuals (from both specific and general samplings). Site of attachment was subdivided into different regions: head, pronotum, legs (pairs 1–3/right–left/femur, tibia, tarsum), abdomen (1–7 abdominal segments) and thorax. All water mites were measured on images, in the same manner as corixids, as indicators of parasite growth (Davids 1973).

Larval identification

Larvae were inspected under a Zeiss Standard bright-field microscope and a representative subset were detached, slide mounted and studied with a Leica TCS SPE Confocal Laser Scanning Microscope (see Lorenzo-Carballa et al. 2011 for detailed procedure). Serial sections were acquired and subsequently worked out with Fiji/Imagej (ver 1.48d; downloaded from http://fiji.sc/Fiji), Amira (ver 5.5.0) and Photoshop CS5 extended. Morphological diagnostic characters were used to identify *Hydrachna* (Davids 1973) and *Eylais* (Nielsen and Davids 1975).

Statistical analysis

We evaluated the significance of the differences between corixid species in prevalence with Z tests (Snedecor and Cochran 1989) and in abundance and intensity with Kruskal–Wallis and Mann–Whitney U tests. We also used Z tests to compare the prevalence between males and females of each corixid species. The size of the different host were compared with Kruskal–Wallis tests followed by pairwise multiple comparisons, and the size of water mite larvae were compared with a Mann–Whitney U-test. The effect of host species, number of parasites per host and salinity on mite size was analyzed using generalized linear models. For this particular analysis we used only data from 2011 because of the low number of infected individuals recorded in 2010.

Generalized linear models with binomial responses were used to test the effect of salinity and sampling date (categorized by months and years) on the presence of water mite larvae. Generalized linear models were bias corrected according to Firth (1993). *P* values were always adjusted for multiple comparisons through false discovery rate (Benjamini and Hochberg 1995). Statistical analyses were conducted using Statistica 12.0 (StatSoft, Inc.) and R (v 2.15.3, R Development Core Team 2008).

Results

Larvae of two water mite species infecting Corixidae (Hemiptera: Heteroptera) were identified from the Caracoles estate: *Hydrachna skorikowi* Piersig, 1900 and *Eylais infundibulifera* Koenike, 1897 (Acari: Hydrachnellae) (Figs. 2, 3, 4, 5). In addition to these two species, *Piona nodata* (Müller, 1776) (Acari: Hydrachnellae) was identified in the sample of adult mites. This species has previously been reported to have populations with females laying small eggs resulting in parasitic larvae and populations producing large eggs resulting in non-feeding larvae (Smith 1988); seasonal shifts in the lifestyle have been also observed, with a parasitic phase produced in winter and a free-living one in summer (Böttger 1962). *P. nodata* can infect other insect groups such as chironomids (Peyrusse et al. 2004).

Description of the larvae

Full descriptions of the larvae of *H. skorikowi* and *E. infundibulifera* may be found in Davids (1973) and Nielsen and Davids (1975), respectively. Our identification of specimens agrees with the general descriptions of the larvae and their diagnostic characters. A median margin of the first coxa longer than the lateral margin and a pair of strong setae in the third coxal group are characteristic of the larvae of *H. skorikowi* (Fig. 4). The larvae and protonymph of *E. infundibulifera* has a dorsal plate with converging posterior ridges and a pair of long anterior setae (Fig. 3).

Infection indexes from the specific sampling in a temporary pond

Total prevalence of water mites at pond AC3 on 27/06/2011 differed among corixid species. *T. v. verticalis* exhibited the highest values, followed by *S. lateralis* and *S. scripta* (Table 2). While the exotic *T. v. verticalis* was

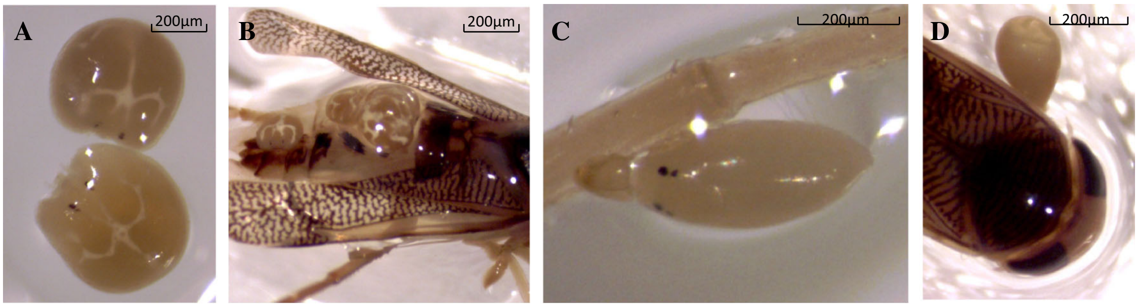

Fig. 2 Individuals of *E. infundibulifera* (**a**, **b**) and *H. skorikowi* (**c**, **d**). These individuals are discoloured by preservation in alcohol. The natural colour of the mites is *red* due to the presence of carotenoids

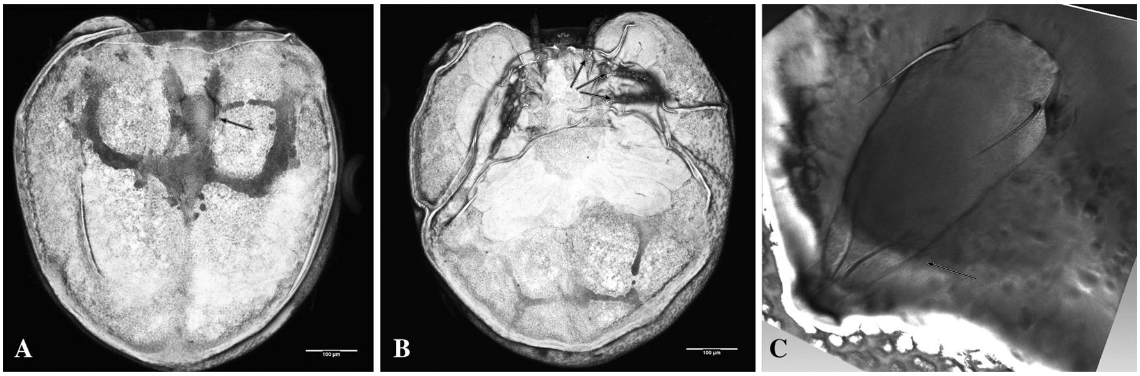

Fig. 3 Protonymph of *E. infundibulifera* Koenike, 1897. **a** Dorsal view. *Arrow* points to the dorsal plate. Maximum intensity projection. **b** Ventral view. *Arrows* point to vestiges of three pairs of legs. Maximum intensity projection. **c** Dorsal plate, 3D reconstruction (Amira). *Arrow* points to diagnostic groove of *E. infundibulifera*

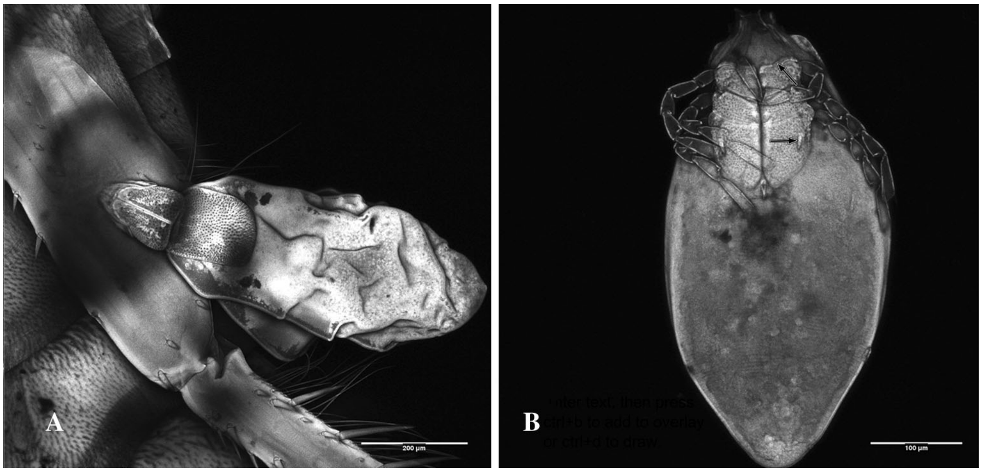

Fig. 4 *Hydrachna skorikowi* Piersig, 1900. **a** Larva attached to the femur of *Trichocorixa verticalis verticalis*. Maximum intensity projection. **b** Idiosome, ventral view. The *arrow* points to a diagnostic character of this species. Maximum intensity projection

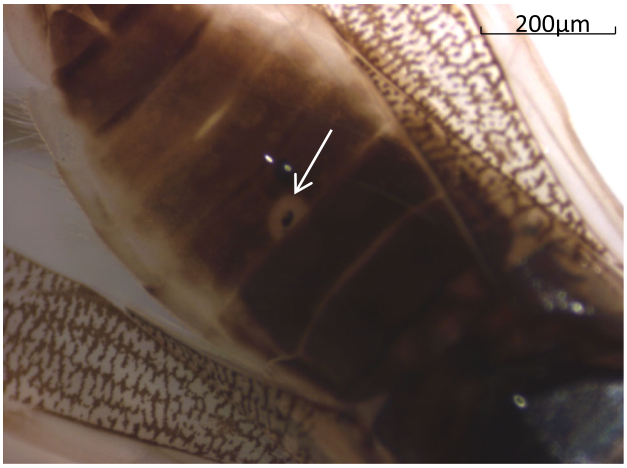

Fig. 5 *Sigara lateralis* showing a *brownish spot* which indicates the previous presence of a larval mite

infected by both mite species in this sampling, native corixid species were infected by only one species (*E. infundibulifera* for *S. lateralis* and *H. skorikowi* for *S. scripta*). Paired comparisons (Z tests) showed that differences in total prevalence were significantly higher in *T. v. verticalis* compared with both *S. lateralis* ($Z = 2.705$, $P < 0.05$) and *S. scripta* ($Z = 2.875$, $P < 0.05$). Prevalence of *E. infundibulifera* was significantly higher in *T. v. verticalis* compared with *S. scripta* ($Z = 2.643$, $P < 0.05$) but not compared with *S. lateralis*. Differences in prevalence of *H. skorikowi* among corixid species were not significant. Males and females of the different hosts did not differ in prevalence in total or for either mite species ($P > 0.05$).

Total mean abundance of mites was significantly different between corixid species (Table 2). Pairwise comparisons (Mann–Whitney U test) showed that abundance was significantly higher in *T. v. verticalis* than *S. lateralis* ($U = 5100.5$, $P < 0.005$) or *S. scripta* ($U = 4563$, $P < 0.005$), but did not differ between *S. lateralis* and *S. scripta* ($U = 4748$, $P = 0.63$). Mean abundance of *E. infundibulifera* was also significantly different between corixid species (Table 1), being significantly higher in *T. v. verticalis* than *S. lateralis* ($U = 5308$, $P < 0.05$) or *S. scripta* ($U = 4696$, $P < 0.005$), but not differing between *S. scripta* and *S. lateralis* ($U = 4696$, $P = 0.18$). Mean abundance of *H. skorikowi* was also significantly different between host species (Table 2). Abundance was significantly higher in *T. v. verticalis* than *S. lateralis* ($U = 5407.5$, $P < 0.05$), but there were no differences between *T. v. verticalis* and *S. scripta* ($U = 4937$, $P = 0.09$) or *S. lateralis* and *S. scripta* ($U = 4738$, $P = 0.297$).

Total mean intensity of mites was not significantly different between corixid species, neither were there significant differences for either mite species (Table 2, but note the small sample size for native corixids). When infected, native species harbored only one parasite individual; however water mite loads in *T. v. verticalis* ranged between 1 and 7 parasites per host (1–6 for *E. infundibulifera* and 1–3 for *H. skorikowi*).

Infection index from the general sampling in temporary ponds and permanent Veta la Palma fish ponds

Samples collected from fish ponds during May ($n = 305$), June ($n = 94$) and July 2011 ($n = 510$) revealed no evidence of mite parasitism in adult *T. v. verticalis* (Table S1).

From samples collected in May–June 2010–2011 in temporary ponds, we selected the 19 sampling events out of 123 (including ponds in Caracoles estate and natural water bodies in the surrounding area) in which mite parasites and

Table 2 Prevalence (P %), Mean Abundance (MA ± SE) and Mean Intensity (MI ± SE) of *Hydrachna* and *Eylais* water mite larvae infecting Corixidae from the Caracoles estate (pond AC3, Doñana National Park) on 27/06/2011

	SL (n = 103)	*SS* (n = 93)	*TVV* (n = 111)	H, U
Prevalence (%)				
Eylais	1.94	0.00	9.01	
Hydrachna	0.00	1.07	5.40	
Total	1.94	1.07	12.61	
Mean Abundance (MA ± SE)				
Eylais	0.02 ± 0.014	0.00 ± 0.00	0.22 ± 0.084	H = 12.58**
Hydrachna	0.00 ± 0.000	0.01 ± 0.011	0.08 ± 0.036	H = 7.87*
Total	0.02 ± 0.014	0.01 ± 0.011	0.297 ± 0.101	H = 16.89***
Mean intensity (MI ± SE)				
Eylais	1.00 ± 0.00	0.00 ± 0.00	2.40 ± 0.618	U = 6
Hydrachna	0.00 ± 0.00	1.00 ± 0.00	1.50 ± 0.342	–
Total	1.00 ± 0.00	1.00 ± 0.00	2.36 ± 0.561	U = 1.76

Compared with Kruskal–Wallis and Mann–Whitney U tests

SL = *Sigara lateralis*; SS = *Sigara scripta*; TVV = *Trichocorixa verticalis verticalis*; H = Kruskal–Wallis H statistic; U = Mann–Whitney U statistic

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.0005$

at least two corixid species were recorded. We found similar patterns of parasite infection as for AC3. *S. lateralis* was infected in 9 out of 18 samplings where this species was present (88.8 % of infected individuals with *H. skorikowi* and 20 % with *E. infundibulifera*); *S. scripta* was infected in 3 out of 13 samplings where it was present (100 % of individuals with *H. skorikowi* and 0 % with *E. infundibulifera*); *T. v. verticalis* was found to be infected in 13 out of 17 samplings where it was present (15.4 % of individuals with *H. skorikowi* and 92.3 % with *E. infundibulifera*) (Table 3). Considering all the samplings (n = 19), *T. v. verticalis* showed the highest values of total prevalence in 13 cases, and *S. lateralis* in 5 cases. The maximum values of prevalence for *H. skorikowi* were 10 % for *S. lateralis*, 40 % for *S. scripta* and 69.2 % for *T. v. verticalis*; the maximum values for *E. infundibulifera* were 1.47 % for *S. lateralis* and 100 % for *T. v. verticalis* (Table 3).

Parasite intensity across the period was 1–2 for *E. infundibulifera* and 1–7 for *H. skorikowi*. When infected with *E. infundibulifera*, *T. v. verticalis* was infected with 1–2 individuals, while *H. skorikowi* load reached up to seven individuals per host; native species were infected with only one *E. infundibulifera* per corixid, and only three *S. lateralis* were infected with more than one *H. skorikowi* (two individuals per host) (Table 3). In addition to *T. v. verticalis*, *S. lateralis* and *S. scripta*, two other infected corixid species were recorded. *Corixa affinis* Leach, 1817 which was infected in two samplings with *H. skorikowi* (prevalences of 7.14 % (n = 14) and 1.44 % (n = 69)) and *Sigara stagnalis* (Leach, 1817) which was infected in only one sampling with *H. skorikowi* but with 100 % (n = 1) prevalence.

Determinants of water mite prevalence

Generalized linear models indicated that water salinity was a significant predictor for the occurrence of both *E. infundibulifera* ($P < 0.001$) and *H. skorikowi* ($P = 0.018$) Table 4). In both cases, there was a negative partial effect, such that prevalence was lower at higher salinities when controlling for date and corixid species. The prevalence of *E. infundibulifera* was significantly lower in either of the two native corixid species than in *T. v. verticalis*. Similarly, the prevalence of *H. skorikowi* was significantly lower in *S. lateralis* than in *T. v. verticalis*. Prevalence was lower in *S. scripta* than in *T. v. verticalis*, but not significantly so (Table 4). Sampling date also significantly affected mite presence. The occurrence of *E. infundibulifera* was significantly higher in June 2011 than in June 2010 or in May 2011. For *H. skorikowi*, its presence was significantly higher in May 2011 than in May or June 2010, and significantly higher in June 2011 than in June 2010 (Table 4).

Relationship between host size and mite size

We found differences in body length of hosts among corixid species (Kruskal–Wallis test, H = 128.83, $P < 0.001$), *S. lateralis* being the biggest (4.73 ± 0.25 mm) followed by *S. scripta* (4.39 ± 0.25 mm) and *T. v. verticalis* (4.16 ± 0.32 mm). All pairwise comparisons were statistically significant ($P < 0.05$). The two water mite larvae species didn't

Table 3 Prevalence (%) of *Hydrachna skorikowi* (HS) and *Eylais infundibulifera* (EI) water mite larvae infecting Corixidae (SL = *Sigara lateralis*; SS = *Sigara scripta*; TVV = *Trichocorixa verticalis verticalis*) from temporary ponds in Doñana National Park

Pond	Date	Salinity	*SL*			*SS*			*TVV*		
			n	HS	EI	*n*	HS	EI	*n*	HS	EI
ENTREMUROS 1	11/06/2010	2.7	35	2.86	0	0			3	0	0
LUCIO DEL LOBO	11/06/2010	2.2	54	3.7	0	20	0	0	14	0	7.14
0N1GP	14/05/2011	2.3	32	6.25	0	5	0	0	1	0	0
6N2MP	14/05/2011	4	10	10	0	5	0	0	0		
AC3	15/05/2011	1.2	129	8.53	0	5	40	0	13	69.23	0
AC4	15/05/2011	1.3	25	16	0	0			0		
AE6	15/05/2011	1.5	51	3.92	0	0			2	0	0
AE8	15/05/2011	3.4	57	3.51	0	4	0	0	1	0	0
0N2GP	24/06/2011	4.4	9	0	0	4	0	0	1	0	100
3N3MP	24/06/2011	8.5	1	0	0	0			1	0	100
6N2MP	24/06/2011	20.9	2	0	0	0			10	0	20
9N3PP	24/06/2011	7.6	241	0	1.24	38	2.63	0	26	0	15.38
0S2GP	25/06/2011	8.67	46	0	0	0			30	0	10
0S4GS	23/06/2011	23.7	21	0	0	38	0	0	89	0	3.37
3S3MP	23/06/2011	21	31	0	0	7	0	0	34	0	2.94
5S1PP	23/06/2011	5.9	136	0.74	1.47	1	0	0	10	0	20
AC3	25/06/2011	15.88	43	0	0	30	0	0	53	1.89	5.66
AC4	25/06/2011	23.97	72	0	0	35	0	0	71	0	1.41
CANAL CARACOLES	26/06/2011	8.4	4	0	0	21	4.76	0	16	0	18.75

Only samples (ponds/date) where parasites and at least two corixid species were present are included here (37.8 % of the total number of samples). Data from AC3, 27/06/2011 (Table 2) are not included

Table 4 Results from a GLM with binomial error estimating *Eylais* or *Hydrachna* presence according to sample date, salinity and corixid species (SL = *S. lateralis*; SS = *S. scripta*)

Coefficients	Estimate	Std. Error	Pr(>lzl)	Odds ratio
EYLAIS				
Salinity	−0.116	0.031	<0.001*	8.873e−01
SL	−2.910	0.480	<0.001*	5.036e−02
SS	−3.553	1.399	0.011*	6.931e−09
05/10 versus 06/10	−1.217	1.608	0.449	1.469e+06
05/10 versus 05/11	−1.119	1.996	0.574	8.462e−01
05/10 versus 06/11	2.097	1.466	0.153	6.010e+07
06/10 versus 05/11	0.097	1.621	0.952	1.102
06/10 versus 06/11	3.313	0.866	<0.001*	27.486
05/11 versus 06/11	3.216	1.450	0.026*	24.944
HYDRACHNA				
Salinity	−0.284	0.146	0.018*	0.752
SL	−1.868	0.419	<0.001*	0.154
SS	−0.618	0.609	0.310	0.539
05/10 versus 06/10	0.250	1.512	0.868	1.284
05/10 versus 05/11	3.341	1.418	0.018*	28.259
05/10 versus 06/11	2.165	1.600	0.176	8.717
06/10 versus 05/11	3.091	0.601	<0.001*	22.006
06/10 versus 06/11	1.915	0.815	0.019*	6.787
05/11 versus 06/11	−1.176	0.819	0.151	0.308

Trichocorixa verticalis verticalis (TVV) was used as the reference category for the presence of water mite larvae infecting native Corixids (i.e. TVV was aliased), as no significant differences in the prevalence of mites were found between native species. Reference groups for sampling date are those on the right. Asterisks indicate statistically significant predictors differ in size (mean ± SE: 534.98 ± 23.18 µm for *E. infundibulifera* and 535.29 ± 24.40 µm for *H. skorikowi*: U = 575.5, $P = 0.985$). The size of *E. infundibulifera* was very similar between host species (mean ± SE: 573.69 ± 22.10 µm for *S. lateralis* and 566.52 ± 13.92 µm for *T. v. verticalis*). The same was true for *H. skorikowi* (549.40 ± 62.57 µm for *T. v. verticalis*; 506.88 ± 46.81 µm for *S. lateralis*; 617.68 ± 207.37 µm for *S. scripta*). Accordingly, the results of a generalized linear model of mite size indicated no significant effect of host species, salinity, nor the number of parasites infecting the host ($P > 0.194$ for *H. skorikowi* and $P > 0.181$ for *E. infundibulifera*). Nonetheless, the date of sampling (May or June) significantly affected the size of *H. skorikowi* ($F_{1, 38} = 25.498$, $P = 0.00001$) with bigger larvae in June. For *E. infundibulifera*, we didn't include the effect of date in the generalized linear model because this mite species was only present in June.

Differences in attachment sites between mite and host species

Attachment sites were highly specific for both mite species. *E. infundibulifera* invariably attached to the dorsal side of the abdomen (Fig. 2a, b); *H. skorikowi* (Fig. 2c, d) mainly selected the legs but it was also found on the hemelytra, abdomen, head and pronotum (Table 5). *E. infundibulifera* was found attached over a higher surface area when infecting *T. v. verticalis* (2–5 abdominal segments) compared to *S. lateralis* (2–3 abdominal segments) (Table 5). *H. skorikowi* attached over a higher diversity of sites when infecting *T. v. verticalis* (legs, abdomen, head, and pronotum, in order of declining frequency) followed by *S. lateralis* (legs, abdomen and hemelytra) and *S. scripta* (legs and head) (Table 5). When attached to the legs there was no significant difference between the proportions on the right and left sides.

Table 5 Attachment sites of *H. skorikowi* and *E. infundibulifera* when infecting *Sigara lateralis* (SL), *S. scripta* (SS) and *Trichocorixa verticalis verticalis* (TVV) from Doñana

Corixid species	Water mite species	Area of attachment (%)	Specific point (%)	
SL	*E. infundibulifera*	Abdomen (100)	Segment II (20)	
			Segment III (80)	
	H. skorikowi	Legs (92.8)	Leg I (7.7)	Femur (100)
			Leg II (73.1)	Femur (31.6)
				Tibia (31.6)
				Tarsum (31.6)
				Indet (5.2)
			Leg III (19.2)	Femur (80)
				Tibia (20)
		Abdomen (3.6)		
		Hemelytre (3.6)		
SS	*H. skorikowi*	Legs (75)	Leg I (33.3)	Femur (100)
			Leg II (33.3)	Femur (100)
			Leg III (33.3)	Tarsum (100)
		Head (25)		
TVV	*E. infundibulifera*	Abdomen (100)	Segment II (59.3)	
			Segment III (29.6)	
			Segment IV (7.4)	
			Segment V (3.7)	
	H. skorikowi	Legs (87.1)	Leg I (3.7)	Femur (100)
			Leg II (63.0)	Femur (70.6)
				Tibia (29.4)
			Leg III (33.3)	Femur (77.8)
				Tibia (22.2)
		Abdomen (6.5)	Segment V (50)	
			Indent (50)	
		Head (3.2)		
		Pronotum (3.2)		

Data correspond to both the "specific sampling" and "general sampling" (Table 1)

Discussion

Differential infection between native and invasive corixids

T. v. verticalis is a highly successful invader in coastal wetlands of higher salinities in the southern Iberian Peninsula (Rodríguez-Pérez et al. 2009; Van De Meutter et al. 2010b; Guareschi et al. 2013). Although information remains limited, its ability to outcompete native corixids at high salinities seems to be related to its high fecundity and a capacity to complete several generations a year. Furthermore, the eggs and nymphs of some native corixid species do not seem resistant to such high salinities (J.A. Carbonell and C. Coccia, unpublished data). The present study supports the hypothesis that the much lower relative abundance of *T. v. verticalis* in temporary wetlands of lower salinity may be caused by their susceptibility to harmful parasitic mites, which are absent in the saline wetlands. We have shown that *T. v. verticalis* was not infected by water mites in saline wetlands, where *T. v. verticalis* is often the only corixid species recorded.

It is a widespread pattern that species richness of invertebrates decreases at higher salinities in Mediterranean wetlands (e.g. Frisch et al. 2006; Waterkeyn et al. 2008), and adult *Eylais* mites cannot tolerate the high salinities in the areas where *T. v. verticalis* is found to be dominant (V. Céspedes, A.J. Green and M.I. Sánchez unpublished data). Although we cannot rule out the possibility that the absence of mites from fish ponds is also related to the permanent hydroperiod and/or the high density of fish, decapod shrimps or other predators (Kloskowski et al. 2009), our results from temporary wetlands support a strong salinity effect. In generalized linear models, a negative partial correlation between salinity and prevalence was detected for both mite species. *Hydrachna* was particularly rare at higher salinities, so *T. v. verticalis* may encounter this parasite much less than *Eylais*, which was much more prevalent at higher salinities. However, date was confounded with salinity in our dataset because the temporary wetlands dry out in summer, so that a difference in phenology between mite species may be more important than a difference in salinity tolerance.

In temporary wetlands, we recorded consistently higher levels of parasitism by larval water mites in *T. v. verticalis* compared with *S. lateralis* and *S. scripta*, both for *H. skorikowi* and for *E. infundibulifera*. There is a clear pattern of consistently higher prevalence in *T. v. verticalis* for *E. infundibulifera*. In contrast, our generalized linear model analyses suggest that the greater prevalence of *H. skorikowi* in *T. v. verticalis* is only clear for *S. lateralis*, and it would as yet be premature to conclude that this mite favours *T. v. verticalis* as a host compared to all native species.

Both mite species recorded are obligate parasites of water boatmen (Heteroptera: Corixidae) (Stevens and Greven 1999; Reilly and McCarthy 1991). *H. skorikowi* is a palearctic species, so if it generally prefers *T. v. verticalis* as a host, this would be a case of parasite acquisition in which the exotic species becomes the preferred host compared to native ones. *E. infundibulifera* has been found in Europe (including the Iberian Peninsula), Asia and North America. Such cosmopolitan parasites are usually considered as acquired (Torchin et al. 2003; Prenter et al. 2004; Mastitsky et al. 2010), since it is much more likely that they have reencountered the parasites in the invaded area than that they were introduced with the alien host (Mastitsky et al. 2010). However, given the low prevalence of *E. infundibulifera* in native corixids, we cannot yet rule out the possibility that it has been introduced with *T. v. verticalis*. Studies of mite parasitism in corixid communities in parts of Iberia where *T. v. verticalis* has not yet arrived would shed light on this question. The means by which *T. v. verticalis* arrived on the peninsula are unknown, as is the date of arrival (Rodríguez-Pérez et al. 2009; Guareschi et al. 2013).

We are unaware of any other case in which an exotic insect in Europe has been shown to be more infected by parasites than native hosts. When an introduced species is a suitable host for a native parasite, this can seriously impact the exotic hosts, but can also amplify the infection ("spillback" from exotic to native species) with effects for native species at both the host individual and population level (Daszak et al. 2000; Tompkins and Poulin 2006). At the current stage of *T. v. verticalis* invasion our results provide no evidence of parasite spillback, but it remains a potential risk given the density and reproductive potential of the exotic host, high susceptibility for parasites and the high reproductive potential of parasites, all factors affecting the probability of spillback (Hershberger et al. 2010; Paterson et al. 2013). We can expect the opposite to the dilution effect hypothesis, which predicts that the introduction of a less competent host species may reduce infection prevalence in the native host (Telfer et al. 2005). Moreover, given the likely high dispersal abilities of *T. v. verticalis* (Guareschi et al. 2013), this species may enhance dispersal of mites and their introduction into new environments, as has been suggested for epibiotic mites infecting the invasive crab *Eriocheir sinensis* Milne-Edwards, 1853 (Normant et al. 2013).

Differences in parasite susceptibility observed in this study between native and alien corixids may be related to several factors. Firstly, hosts that rarely co-occur with mites in nature may be more susceptible to parasitism when spatial and temporal barriers are removed (Smith and McIver 1984a). This can apply to invasive species which represent new hosts for native parasitic fauna. Increased susceptibility of hosts to new parasites related to a lack of co-adaptation (“naïve host syndrome”, Mastitsky et al. 2010) has been reported for a wide range of parasites (Alderman et al. 1987; Burreson et al. 2000).

Alternatively, the increased susceptibility of *T. v. verticalis* to parasites may be caused by the differential level of sclerotization among hosts. Dark colour indicates a higher degree of sclerotization in water boatmen (Bennett 1993). The light aspect of *T. v. verticalis* compared with the darker *S. lateralis* and *S. scripta* suggests that the exotic corixid is less sclerotized, and that mites could perforate the integument of *T. v. verticalis* with less difficulty. The higher surface area susceptible to attachment (i.e., number of body regions in which mites were found) in *T. v. verticalis* compared to *S. lateralis* and *S. scripta* supports this hypothesis. Bennett (1993) showed that a smaller susceptible area for attachment in sclerotized *Cenocorixa bifida* (Hungerford, 1926) resulted in reduced overall susceptibility to *Eylais euryhalina* Smith, 1986 compared to the unsclerotized *C. expleta* (Uhler, 1895). In laboratory conditions, when equally exposed to water mites, 90 % of *C. expleta* and 25 % *C. bifida* were infected.

Another possibility is that biological and ecological factors affecting spatial distribution of the hosts would differentially expose them to water mite infection. Field observations (C. Coccia, personal observation) suggest that *T. v. verticalis* is more concentrated in the shallowest parts of ponds, where it may be more exposed to mites. Mite larvae are positively phototactic and swim to the water surface in search of hosts (Lanciani 1969), and it is also possible that *T. v. verticalis* coincides more often with the larvae within the water column. For example, *S. lateralis* feed more on benthic chironomid larvae (Tawfik et al. 1990) while *T. v. verticalis* may feed more on zooplankton in the water column (Wurtsbaugh 1992; Simonis 2013).

Behavioural factors may also play a role in our results. Some corixid species are able to limit infestations by eating larval mites (Lanciani 1985) or by defensive behaviours (Smith and McIver 1984b). Moreover, physiological aspects related with the ability of some species of corixids (*Sigara*) to impede engorgement of *Hydrachna* and *Eylais* species by reacting against the stilistoma of the mite (sometimes provoking the death of the parasite) (Davids 1973) may also partly explain our results. Experimental infection with equal exposure and behavioural tests would be necessary to discern between these hypotheses.

Effect of host sex, host size and attachment site

Like Smith (1977), we found no differences between sexes in parasite infection. Sexual preferences may be related with differences between sexes in size, time of emergence, differential exposure caused by different behaviors or different dispersal patterns. The low prevalence in *C. affinis* (by far the largest host species 7.2–10.5 mm Nieser et al. 1994) and high prevalence in *T. v. verticalis* (the smallest species in our study) suggests the mites show no preference for larger host species. Although host size has previously been shown to influence parasite growth for *Hydrachna* and *Eylais* species (Davids and Schoots 1975), we didn’t find differences in parasite size when infecting native and invasive species, suggesting that all hosts are equally suitable for engorgement. Although *T. v. verticalis* is significantly smaller that native species this difference is perhaps too small (<14 % difference in length) to have a noticeable effect on the mites. Bennett (1993) found fully engorged mites preferentially on lightly sclerotized corixids and rarely on highly sclerotized species, which suggests that parasite growth also depends on host sclerotization. Therefore, the low sclerotisation of *T. v. verticalis* may compensate for its smaller size. The size of the parasite relative to it host influences the degree of the damage it can induce (for example in fecundity, Davids and Schoots 1975). So for a given parasite size, we can expect more damage in a smaller host such as *T. v. verticalis*. However, laboratory growth experiments would be necessary to confirm that mite growth does not vary between host species.

The precise attachment site is relevant to the understanding of the effects of mites in their hosts, and to host-parasite coevolutionary interactions (Bennett and Scudder 1998). The attachment site for both mite species was highly species-specific and reflects different life histories. *Eylais* larvae are semi-aquatic requiring an air supply to survive, and are therefore restricted to areas such as under the wings, tergites, underside of the elytra and hemielytra (Lanciani 1969; Nielsen and Davids 1975; Davids et al. 1977). In our study they were invariably found attached to the abdominal tergites under the wings, which is likely to damage flight musculature (Smith 1988). In contrast, Hydrachnidae larvae are strictly aquatic and can use dissolved oxygen in the water. Therefore they can be found attached to all surfaces of the host (Harris and Harrison 1974), and in our study they were observed on the wings, head and legs. We did not find any preference between the right and left side of the host. In some species of *Sigara* the right hemelytron is more infected because it overlaps the left one (Davids 1973), although this is not a consistent result (Mitchell 1968).

Ecological impact of mite infection and consequences for *T. v. verticalis* invasion

Mites have the capacity to have a major influence on the extent of invasion by *T. v. verticalis*. Smith (1977) previously showed that the spatial distribution of two sympatric water boatmen was determined by the presence of water mites, which exclude one of them at lower salinity. In many host-parasite systems, values of prevalence exceeding 10 %, as in our study for *T. v. verticalis*, are enough to exert a negative influence on host density (Hall et al. 2011). Moreover, total prevalence and intensity of mites recorded in our study were probably underestimates. We often found brownish spots at the point of attachment of larval mites in all corixid species, indicating the previous presence of parasites (Fig. 5). In fact, in *Arrenurus* Dugès, 1833 species these marks have been used to accurately estimate the number of larvae that had been attached to the host (Lanciani 1979).

Mite-induced reduction in survival has been demonstrated for a variety of host-parasite associations (Lanciani 1982, 1986). Numerous studies have shown that parasitism by mites adversely affects insects (Smith 1988). Fernando and Galbraith (1970) reported disappearance of gerrid populations heavily infected by water mites. Hence mites have the potential to cause local extinctions of *T. v. verticalis*.

Specific information about the ecological impacts of *E. infundibulifera* and *H. skorikowi* larvae are lacking. However, the existing literature suggests that negative effects of infection can be expected at both the host individual and population levels. Both *Eylais* spp. and *Hydrachna* spp. experience a dramatic increase in size during the larval phase. The *Eylais* genus includes the largest species of all water mites (Lanciani 1971) and some species of *Hydrachna* can increase their volume by 600 times from birth (Davids 1973). Enlargement of the larvae is correlated with the time spent on the host, and in these genera the duration of the larval engorgement period can be very long (several months, Bennett 1993). Therefore, the time of the parasitic phase together with the size reached by the larvae in our study are both expected to negatively impact the hosts.

On the other hand, water mite larvae have been shown to destroy host tissue (Abro 1982) and adversely affect flight musculature (Smith 1988), consequently affecting the host's flight ability (Gillies and Wilkes 1972). The ability to fly and disperse is fundamental for the survival of aquatic insects living in temporary habitats, such as corixids (Savage 1989; Boda and Csabai 2009). Larval *Hydrachna* spp. and *Eylais* spp. infecting aquatic Hemiptera can also dramatically decrease fecundity by reducing egg production (Davids and Schoots 1975).

Other reproductive effects caused by mites in corixids include delayed maturation of the host (Lanciani 1975), reduction of nymphal growth (Lanciani and May 1982) that may affect competitiveness and survival (Martin 1975), and reduction of male mating success (Forbes 1991a, b; Forbes and Baker 1991). Deutonymphs and adults of *H. skorikowi* have also been shown to feed on eggs of water boatmen (Stevens and Greven 1999), as have other *Hydrachna* species (Davids 1979). High intensity of infection can induce mortality (Lanciani 1975), impacting at the population level. In this study, the values of infection intensity for *T. v. verticalis* (up to 7) are among the highest recorded for corixids. All these effects can potentially be stronger in the exotic species under the naïve host syndrome (Mastitsky et al. 2010).

Indirect effects can also be expected. *Eylais* and *Hydrachna* nymphs feed on Cladocera, where *T. v. verticalis* also occur and may compete for these prey (Simonis 2013). Since water mites can be very abundant (up to 13,000 eggs per female over a period of 12 months have been reported for *Eylais discreta*, Davids 1973), this may result in competition for food between mites and corixids. Further research should focus on the ecological impact of mites on the *T. v. verticalis* invasion and its interactions with native corixids, using naturally infected populations in combination with experimental laboratory infections.

Conclusion

T. v. verticalis showed consistently higher infection levels by water mite larvae compared with the native corixid hosts *S. lateralis* and *S. scripta*. We found evidence that the invasion success of *T. v. verticalis* in natural wetlands of low salinity has been limited owing to a higher susceptibility to parasites compared with native species. Since water mites strongly reduce reproductive success and increase mortality at high intensities, they are likely to play a key role in driving the outcome of ecological interactions between the invasive and the native species. This study suggests that mites may prevent *T. v. verticalis* from colonizing low salinity wetlands or outcompeting the native corixids there. As the invader spreads across Europe in future decades, the mites may play a vital role in conservation on native insect diversity.

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