Aquat Ecol (2010) 44:431–448
DOI 10.1007/s10452-009-9301-4

Larval parasitism of spring-dwelling alpine water mites (Hydrachnidia, Acari): a study with particular reference to chironomid hosts

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Received: 23 June 2009 / Accepted: 26 November 2009 / Published online: 12 December 2009

Abstract During faunistic investigations on spring habitats in the alpine National Park Berchtesgaden (Bavaria, Germany), water mites were found to be the group with the highest share of species strongly adapted to springs. At four sample sites at two spring complexes, insect emergence was screened for parasitism by larval water mites. A total of at least 36 host species were recorded as being parasitized by 19 water mite species. As in many other habitats, the most important host taxon was shown to be the nematoceran family Chironomidae, both in the number of species and individuals parasitized. Likewise, the number of water mite species attached to chironomids was high. Further host species were found among the Plecoptera, Trichoptera, Coleoptera, Limoniidae and Empididae (Diptera). These taxa were only parasitized by a single water mite species in each case. For 13 mite species, new hosts were recorded for the first time. For another six species, the known host spectrum could be confirmed and/or supplemented. The parasitological data presented (e.g., prevalences, selected attachment sites on the host, larval phenology, intensity of parasitism) provide, in most cases, basic information concerning previously unknown parasite–host associations. At this time, the reason for the strong crenobiosis in water mites cannot be explained by their parasitism.

Keywords Acari · Insects · Chironomids · Parasitology · Ectoparasites · Freshwater springs

Introduction

Springs are ecotone habitats with a diverse fauna composed of a large number of different groups of organisms. Both terrestrial and groundwater species coexist together with a wide range of limnic species which have different degrees of adaptations to this specific environment (Fischer et al. 1998). The spring-dwelling species can be separated into true crenobionts (preferring the eucrenal section within the spring habitat) and crenophiles, which were occasionally present in other habitats (lentobiontic, rhithrobiontic, stygobiontic and stygo-/hyporheobiontic crenophiles, see Gerecke et al. 1998). Springs are specific habitats that can be considered as “the

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ecologist's natural constant temperature laboratory", mainly on the basis of their constant water temperatures (Odum 1971). Because of the specific ecological adaptations of the animals and because springs may become subject to changes as a result of global warming (Williams and Williams 1998), spring fauna can be employed as a tool for the bio-monitoring of alpine springs. It is the focus of some current research (Cantonati et al. 2006; Gerecke and Franz 2006).

In many spring studies, water mites (Hydrachnidia, Acari) have been found to be the group with the highest share of crenobionts and crenophiles (e.g., Gerecke et al. 1998; Di Sabatino et al. 2003). By virtue of their consistently, high levels of diversity and abundance at all active instars in the life cycle (the predatory adult and nymph, the parasitic larva), water mites probably have a significant impact on the size and structure of insect populations in springs (Smith 1991). The species composition and the structure of water mite communities can be used both in monitoring and in assessing the biological impact of environmental changes on spring habitats and for characterizing various types of springs (Smith 1991). But life-cycle adaptations and especially larval parasitism (i.e., host use, prevalence, intensity, attachment sites etc.) have not been thoroughly investigated and understood.

Here, we study water mites in the springs in the German National Park of Berchtesgaden. Specifically we provide information on species composition, host range, attachment site, phenology, prevalence and intensity (sex differences) to understand better the basic mite biology and to provide first insight into the evolution of crenobiosis in water mites.

Materials and methods

The present research took place at Herrenroint and Schapbach, two long-term bio-monitoring sites in the National Park of Berchtesgaden (Germany, upper Bavaria; for a detailed description of the individual springs at these sites, see Gerecke et al. 2006). At these sites, adult insects with and without water mite parasites have been collected in emergence traps (I. Schrankel unpublished diploma thesis; methods partly published by Gerecke et al. 2006). In 1996, emergence traps were placed at Herrenroint on three individual sites (site numbers 308, 312, 318) and on one site at Schapbach (site number 360). Site 318 was at a spring brook located about 100 m downstream from the related springhead site 308. As it produced a diluted fauna of site 308, 318 should be considered a hypocrenal rather than a spring brook (as proposed by Gerecke et al. 2006).

Collections used in this study took place from May to October 1996, with the traps being emptied weekly. The insect fauna was identified by various specialists (see different chapters in Gerecke and Franz 2006). Insects parasitized by water mite larvae were selected and, after recording the attachment site, the mites were detached and fixed (for details of the methods see Gerecke and Martin 2006). An identification key for the local fauna based mainly on Martin (2003) was compiled by Gerecke and Martin (2006). At sites 308 and 360 all chironomid males and females were identified, at sites 312 and 318 only parasitized and not parasitized males. Most data deal with the material collected in 1996; additional data refer only to non-chironomid host taxa of *Feltria* spp., *Hydrovolzia placophora* and *Partnunia steinmanni*, which were collected at different dates in July 2000.

A statistical analysis (chi^2 tests) was performed only in taxa with more than 50 individuals for dorsal versus ventral and left versus right attachment. The significance between observed and expected values was calculated by 2 × 2 tables, using the software "PopTools" (Hood 2008).

The term "prevalence" is used here as the number of individuals of a host species infected with a particular parasite species divided by the number of hosts examined, the term "intensity" as number of individuals of a particular parasite species in each infected host in a sample (see e.g., Margolis et al. 1982; Bush et al. 1997). For the advanced statistical analyses of parasitism parameters of the mite–chironomid associations from sites 308 and 360, the free software "Quantitative Parasitology" was applied (Rózsa et al. 2000; Reiczigel and Rózsa 2005). Data presentation is performed according to the recommendation of Rózsa et al. (2000) and was computed on pooled water mites and chironomids of sites 308 and 360, separately for each of the sites and, on species level, for *Hygrobates norvegicus*, the most abundant species of the study. Data were given for host sample size (n), prevalence and 95% confidence interval (CI) for the prevalence based on the binomial distribution, median intensity, mean intensity and

95% bootstrap confidence interval (BCA), variance to mean ratio (including uninfected hosts in the calculations), discrepancy index (*D*), which describes the disparity between observed and uniform distributions, as defined by Poulin (1993) and the result of the test for negative binominal distribution (level of significance $P = 0.05$; Bliss and Fisher 1953). Comparisons between prevalences were calculated by chi^2 tests and those of mean intensities by Bootstrap 2-sample *t*-tests also using Quantitative Parasitology.

Results

Hosts, site-specific distribution and host specificity

Larvae of at least 20 water mite taxa were found as ectoparasites (Table 1), 19 of them determined to species level, plus at least one species of *Feltria* (identified to genus level only).

At least 36 species were detected as hosts (Table 1); 26 of them belonged to the non-biting midges (Diptera, Chironomidae). Additional host taxa were Limoniidae and the Empididae (Diptera), Nemouridae and Leuctridae (Plecoptera), Brachycentridae and Limnephilidae (Trichoptera) and Scirtidae (Coleoptera). *Hydrovolzia placophora* was the only species whose larvae were never found attached to chironomids but to coleopterans and empidids. Two mite taxa were parasitic not only on chironomids, but also on other hosts: *Feltria* on a trichopteran larva, *Partnunia steinmanni* on Plecoptera, Trichoptera, Limoniidae and Empididae.

Host species were parasitized by between one and nine water mite species. For most water mite species only one (19, i.e., 53% of all host species) or a few host species were recorded, but for single species up to 14 host species were found (Table 1). Of the 816 water mite larvae were present in the emergence traps for the year 1996, 780 attached to chironomids and 36 attached to Trichoptera (see Table 2 for details). *Bandakia concreta* and *Sperchon resupinus* were found detached but in vials together with chironomids and thus members of this family acted as hosts.

For *Hygrobates norvegicus*, the most abundant water mite species in the study, at least 14 chironomid species were found as hosts (Table 1), with 5–7 host species for each collection site. More than 50% of the host individuals belonged to *Rheocricotopus effusus*, *Parametriocnemus stylatus* and *Micropsectra* spp. and nearly 60% of *H. norvegicus* larvae were attached to these. *Rheocricotopus effusus* was most frequently parasitized at sites 308 and 360, *Micropsectra* species at site 312, *Cricotopus* cf. *curtus* and *Stempellinella flavidula* at site 318.

In the majority of cases (388 chironomid specimens), only one water mite species was attached to one host individual. Only 32 midges were parasitized by two and two chironomids by three water mite species. The mite species most frequently found together on one host specimen were *Hygrobates norvegicus* with *Atractides panniculatus* (11 cases), *Feltria* spp. with *L. maculosa* (7 cases) and *Feltria* spp. with *H. norvegicus* (4 cases).

Attachment sites

For the 664 mite larvae parasitizing chironomids, two groups of parasites within the most abundant taxa were observed: larvae of *Feltria* spp., *Hygrobates norvegicus* and *Atractides* spp. preferring attachment to the abdomen, whereas *Sperchon mutilus* and *Lebertia* spp. larvae choosing the thorax, mostly the base of the front legs (Table 3). Most of the abdominal parasites were attached to the intersegmental areas. The only exception was *Atractides adnatus* whose larvae were often attached to the first abdominal segment, in most cases at the anterior end. While larvae of *A. panniculatus* were attached more or less equally to all possible sites, larvae of *Feltria* spp. had an obvious preference for the abdominal intersegmental area 5/6, those of *A. walteri* for the intersegmental area 1/2, *A. adnatus* for the two anterior segments and of *H. norvegicus* for the proximal abdominal segments. Leg 2 was never parasitized whereas thoracic parasites were regularly present on leg 1 and abdominal parasites were occasionally attached to leg 3.

The dorsal side of the abdomen was more frequently parasitized than the ventral side by *Feltria* spp. (chi$^2 = 11.96$, $P < 0.05$), *Hygrobates norvegicus* (chi$^2 = 23.56$, $P < 0.05$) and *Atractides walteri* (chi$^2 = 21.9$, $P < 0.05$), while *A. panniculatus* and *A. adnatus* preferred ventral attachment, but without statistical significance (chi$^2 = 3.10$, $P = 0.078$; chi$^2 = 1.86$, $P = 0.172$). The equal left–right distribution seemed to be present, as expected (no significance of chi^2-tests for *Feltria* spp., *Hygrobates*

Table 1 Combined parasite–host associations of the water mites and their hosts at the two spring sites Herrenroint and Schapbach

	Atractides adnatus Lundblad, 1956	*Atractides macrolaminatus* Láska, 1956	*Atractides panniculatus* (K. Viets, 1925)	*Atractides walteri* (K. Viets, 1925)	*Bandakia concreta* Thor, 1913	*Feltria* spp.	*Hydrovolzia placophora* (Monti, 1905)	*Hygrobates norvegicus* (Thor, 1897)	*Lebertia cuneifera* Walter, 1922	*Lebertia lativentris* K. Viets, 1922
PLECOPTERA										
Nemouridae										
Nemoura marginata Pictet, 1836										
Nemoura sinuata Ris, 1902										
Nemurella pictetii Klapálek, 1900										
Leuctridae										
Leuctra armata Kempny, 1899										
TRICHOPTERA										
Brachycentridae										
Micrasema morosum (McLachlan, 1868)										
Limnephilidae										
Parachiona picicornis (Pictet, 1834)										
Limnephilidae indet. (larva)						x				
COLEOPTERA										
Scirtidae										
Scirtidae indet.							x			
DIPTERA										
Brachycera										
Empididae										
Rhamphomyia flaviventris Macquart, 1827										
Empididae indet.							x			
Nematocera										
Limoniidae										
Pedicia straminea (Meigen, 1838)										
Chironomidae										
Podonominae										
Parochlus kiefferi (Garret, 1925)										
Orthocladiinae										
Brillia bifida (Kieffer, 1909)			x					x		
Corynoneura lobata Edwards, 1924	x			x						

Table 1 continued

	Atractides adnatus Lundblad, 1956	*Atractides macrolaminatus* Láska, 1956	*Atractides panniculatus* (K. Viets, 1925)	*Atractides walteri* (K. Viets, 1925)	*Bandakia concreta* Thor, 1913	*Feltria* spp.	*Hydrovolzia placophora* (Monti, 1905)	*Hygrobates norvegicus* (Thor, 1897)	*Lebertia cuneifera* Walter, 1922	*Lebertia lativentris* K. Viets, 1922
Corynoneura sp. 1				x						
Cricotopus cf. *curtus* Hirvenoja, 1973			x			x		x		
Cricotopus sp.			x					x		
Eukiefferiella tirolensis Goetghebuer, 1938	x					x				
Eukiefferiella sp. (♀♀)						x				
Heleniella spp.			x	x				x	x	
Krenosmittia boreoalpina (Goetghebuer, 1944)						x				
Metriocnemus sp. (♀♀)										
Orthocladius sp. (♀♀)			x							
Parametriocnemus stylatus (Spärck, 1923)	x	x	x	x		x		x		
Paratrichocladius skirwithensis (Edwards, 1929)								x	x	
Rheocricotopus effusus (Walker, 1856)			x			x		x	x	x
Rheocricotopus sp. (♀♀)								x		
Thienemannia libanica Laville and Moubayed, 1985						x				
Thienemanniella spp.	x	x	x	x				x		
Tvetenia bavarica (Goetghebuer, 1934)	x									
Tvetenia calvescens (Edwards, 1929)	x			x		x				
Orthocladiinae indet.	x		x			x		x		
Chironominae-Tanytarsini										
Micropsectra attenuata Reiss, 1969			x					x		
Micropsectra pharetrophora Fittkau and Reiss, 1999			x					x		
Micropsectra seguyi Casas and Laville, 1990	x		x							
Micropsectra sofiae Stur and Ekrem, 2006	x									
Micropsectra sp. (♀♀)	x		x			x		x		
Neozavrelia nr. *improvisa*								x		
Parapsectra mendli Reiss, 1983								x		
Stempellinella ciliaris (Goetghebuer, 1944)			x					x		
Stempellinella flavidula (Edwards, 1929)			x					x		
Tanytarsus heusdensis Goetghebuer, 1923								x		

Table 1 continued

	Atractides adnatus Lundblad, 1956	*Atractides macrolaminatus* Láska, 1956	*Atractides panniculatus* (K. Viets, 1925)	*Atractides walteri* (K. Viets, 1925)	*Bandakia concreta* Thor, 1913	*Feltria* spp.	*Hydrovolzia placophora* (Monti, 1905)	*Hygrobates norvegicus* (Thor, 1897)	*Lebertia cuneifera* Walter, 1922	*Lebertia lativentris* K. Viets, 1922
Tanytarsini indet.			x							
Chironomidae indet.	x	x	x	x	x	x		x	x	x
Host taxa (minimum number of host species)	8	2	12	6	1	9	2	14	3	1

	Lebertia maculosa Koenike, 1908	*Lebertia sefvei* Walter, 1911	*Lebertia* cf. *schechteli* Thor, 1913	*Panisopsis curvifrons* (Walter, 1907)	*Partnunia steinmanni* Walter, 1906	*Protzia distincta* Walter, 1922	*Sperchon mutilus* Koenike, 1895	*Sperchon resupinus* K. Viets, 1922	*Tartarothyas romanica* Husiatinschi, 1937	*Todothyas palustris* (Koenike, 1912)	Number of parasitizing mite species
PLECOPTERA											
Nemouridae											
Nemoura marginata Pictet, 1836					x						1
Nemoura sinuata Ris, 1902					x						1
Nemurella pictetii Klapálek, 1900					x						1
Leuctridae											
Leuctra armata Kempny, 1899					x						1
TRICHOPTERA											
Brachycentridae											
Micrasema morosum (McLachlan, 1868)					x						1
Limnephilidae											
Parachiona picicornis (Pictet, 1834)					x						1
Limnephilidae indet. (larva)											1
COLEOPTERA											
Scirtidae											
Scirtidae indet.											1
DIPTERA											
Brachycera											

Table 1 cotinued

	Lebertia maculosa Koenike, 1908	*Lebertia sefvei* Walter, 1911	*Lebertia* cf. *schechteli* Thor, 1913	*Panisopsis curvifrons* (Walter, 1907)	*Partnunia steinmanni* Walter, 1906	*Protzia distincta* Walter, 1922	*Sperchon mutilus* Koenike, 1895	*Sperchon resupinus* K. Viets, 1922	*Tartarothyas romanica* Husiatinschi, 1937	*Todothyas palustris* (Koenike, 1912)	Number of parasitizing mite species
Empididae											
Rhamphomyia flaviventris Macquart, 1827					x						1
Empididae indet.											1
Nematocera											
Limoniidae											
Pedicia straminea (Meigen, 1838)					x						1
Chironomidae											
Podonominae											
Parochlus kiefferi (Garret, 1925)										x	1
Orthocladiinae											
Brillia bifida (Kieffer, 1909)											2
Corynoneura lobata Edwards, 1924						x					3
Corynoneura sp. 1						x					2
Cricotopus cf. *curtus* Hirvenoja, 1973											3
Cricotopus sp.											2
Eukiefferiella tirolensis Goetghebuer, 1938											2
Eukiefferiella sp. (♀♀)											1
Heleniella spp.		x				x					6
Krenosmittia boreoalpina (Goetghebuer, 1944)											1
Metriocnemus sp. (♀♀)					x						1
Orthocladius sp. (♀♀)											1

Table 1 cotinued

	Lebertia maculosa Koenike, 1908	*Lebertia sefvei* Walter, 1911	*Lebertia* cf. *schechteli* Thor, 1913	*Panisopsis curvifrons* (Walter, 1907)	*Partnunia steinmanni* Walter, 1906	*Protzia distincta* Walter, 1922	*Sperchon mutilus* Koenike, 1895	*Sperchon resupinus* K. Viets, 1922	*Tartarothyas romanica* Husiatinschi, 1937	*Todothyas palustris* (Koenike, 1912)	Number of parasitizing mite species
Parametriocnemus stylatus (Spärck, 1923)	x	x			x						9
Paratrichocladius skirwithensis (Edwards, 1929)											2
Rheocricotopus effusus (Walker, 1856)	x	x									7
Rheocricotopus sp. (♀♀)											1
Thienemannia libanica Laville and Moubayed, 1985											1
Thienemanniella spp.						x					5
Tvetenia bavarica (Goetghebuer, 1934)											2
Tvetenia calvescens (Edwards, 1929)											3
Orthocladiinae indet.	x					x					6
Chironominae-Tanytarsini											
Micropsectra attenuata Reiss, 1969											2
Micropsectra pharetrophora Fittkau and Reiss, 1999							x		x		4
Micropsectra seguyi Casas and Laville, 1990											2
Micropsectra sofiae Stur and Ekrem, 2006							x				2
Micropsectra sp. (♀♀)		x	x				x		x		8
Neozavrelia nr. *improvisa*											1
Parapsectra mendli Reiss, 1983											1

Table 1 cotinued

	Lebertia maculosa Koenike, 1908	*Lebertia sefvei* Walter, 1911	*Lebertia* cf. *schechteli* Thor, 1913	*Panisopsis curvifrons* (Walter, 1907)	*Partnunia steinmanni* Walter, 1906	*Protzia distincta* Walter, 1922	*Sperchon mutilus* Koenike, 1895	*Sperchon resupinus* K. Viets, 1922	*Tartarothyas romanica* Husiatinschi, 1937	*Todothyas palustris* (Koenike, 1912)	Number of parasitizing mite species
Stempellinella ciliaris (Goetghebuer, 1944)											2
Stempellinella flavidula (Edwards, 1929)											2
Tanytarsus heusdensis Goetghebuer, 1923											1
Tanytarsini indet.							x				2
Chironomidae indet.	x	x		x	x	x	x	x	x	x	
Host taxa (minimum number of host species)	2	4	1	1	10	4	2	1	1	1	

Atractides adnatus: also some associations with atypical specimens especially from site 360 were included here; possibly the unknown larva of the closely related but not yet described larva of *Atractides vaginalis* (Koenike, 1905) is present in these associations. For the species of *Feltria* spp. see text

Table 2 Distribution of the mites to the different collecting sites

	Herrenroint			Schapbach	Detached	Total
	Site 308	Site 312	Site 318	Site 360		
Atractides sp.	6			1	1	8
A. adnatus		1		70	1	72
A. macrolaminatus			2	3		5
A. panniculatus	15		30	28	2	75
A. walteri	6		5	43	3	57
Bandakia concreta					2	2
Feltria spp.	141	8	49	33	3	234
Hygrobates norvegicus	48	32	26	60	4	170
Lebertia sp.					1	1
L. cuneifera		10			1	11
L. lativentris		2			1	3
L. maculosa	13		1		2	16
L. sefvei		4	1		3	8
L. cf. *schechteli*			6			6
Panisopsis curvifrons					1	1
Partnunia steinmanni	2				3	41
P. steinmanni (Trich.)	35				1	
Protzia distincta				7	4	11
Sperchon mutilus	10			5	35	50
S. resupinus					1	1
Tartarothyas romanica	2				4	6
Todothyas palustris		1			1	2
Total	302	71	127	280	74	780

Sites 308, 312 and 318 are part of the Herrenroint spring complex, site 360 belongs to Schapbach spring complex. The numbers of mites are separated into attached and detached larvae (all from chironomid hosts except for some *P. steinmanni* larvae attached to Trichoptera)

norvegicus, *Atractides panniculatus*, *A. adnatus* and *A. walteri*).

Phenology, prevalence and intensity

Seasonal fluctuations in phenology of all larval water mites were similar at all collection sites, with 3–4 peaks (Fig. 1a). The parasitization of chironomids extended from the beginning of the emergence, at the end of May, until the end of October. Species phenology revealed differences from site to site: For example, *Feltria* spp. larvae appeared almost exclusively in spring at site 308, but in late summer at site 360. This difference could well be explained by the presence of different *Feltria* species at the two sites, but similar discrepancies were found in well-defined species such as *Atractides panniculatus*. Some species were present only for a short time (e.g., *Sperchon mutilus* at site 308: end of August–September), others showed two periods of occurrence (e.g., *Lebertia maculosa* at site 308: June and end of August/beginning of September). *Hygrobates norvegicus* and *Atractides walteri* were present during the whole period but with different peaks at different sites. At site 360, for example, they produced two peaks, one in early summer and one in August/September.

The distribution of water mites on the hosts fits the negative binominal distribution at sites 308 and 360 in some cases (Table 4). For example, for the females of sites 308 + 360 chi^2 = 12.3286, $df = 6$, $k = 0.030$ or for the males of site 308 chi$^2 = 5.2507$, $df = 4$, $k = 0.052$. The overall prevalence was low at both sites (site 308: 3.8%, 113 of 3011 chironomids infected by 245 mites; site 360: 3.9%, 180 of 4562

Table 3 Attachment sites for the chironomid parasites

	n	Caput/Thorax		Thorax		Abdomen intersegments								Abdomen segments				Dorsal	Ventral	Left	Right	Centred
		Dorsal	Ventral	Frontleg	3rd leg	0/1	1/2	2/3	3/4	4/5	5/6	6/7	7/8	1	2	3	4					
Feltria spp.	229					1	27	29	34	47	88	3						152	77	86	121	22
H. norvegicus	166						55	42	51	7	4	2		4	1			123	43	70	80	16
A. panniculatus	73				1		12	9	16	8	12	8	3	1	1	1	1	48	25	36	34	3
A. adnatus	70				1	3	24	11	4		6	1		20				26	44	19	32	19
A. walteri	54						34	11	6	3								50	4	28	26	
S. mutilus	14	3		11														5	9	6	5	3
L. maculosa	13			13														1	12	7	6	
L. cuneifera	10			10														3	7	2	8	
Atractides sp.	7							3	2	1	1							5	2	6	1	
L. cf. *schechteli*	6	2	1	3														2	4	0	6	
P. distincta	6			2					3	1								3	3	2	4	
L. sefvei	5			5														4	1	5	0	
A. macrolaminatus	4						3			1								4		2	2	
L. lativentris	2			2														1	1	1	1	
P. steinmanni	2		2															0	2	0	0	2
T. romanica	2						1							1				0	2	1	0	1
Todothyas palustris	1			1														1	0	1	0	
Number of individuals	664	5	3	47	2	4	156	105	116	68	111	14	3	26	2	1	1	428	236	272	326	66

Aside of the attachment sites, also attachment to dorsal versus ventral sites and attachment to left/right and centred attachment sites was given. Intersegment 0/1 means the area between metathorax and first abdominal segment

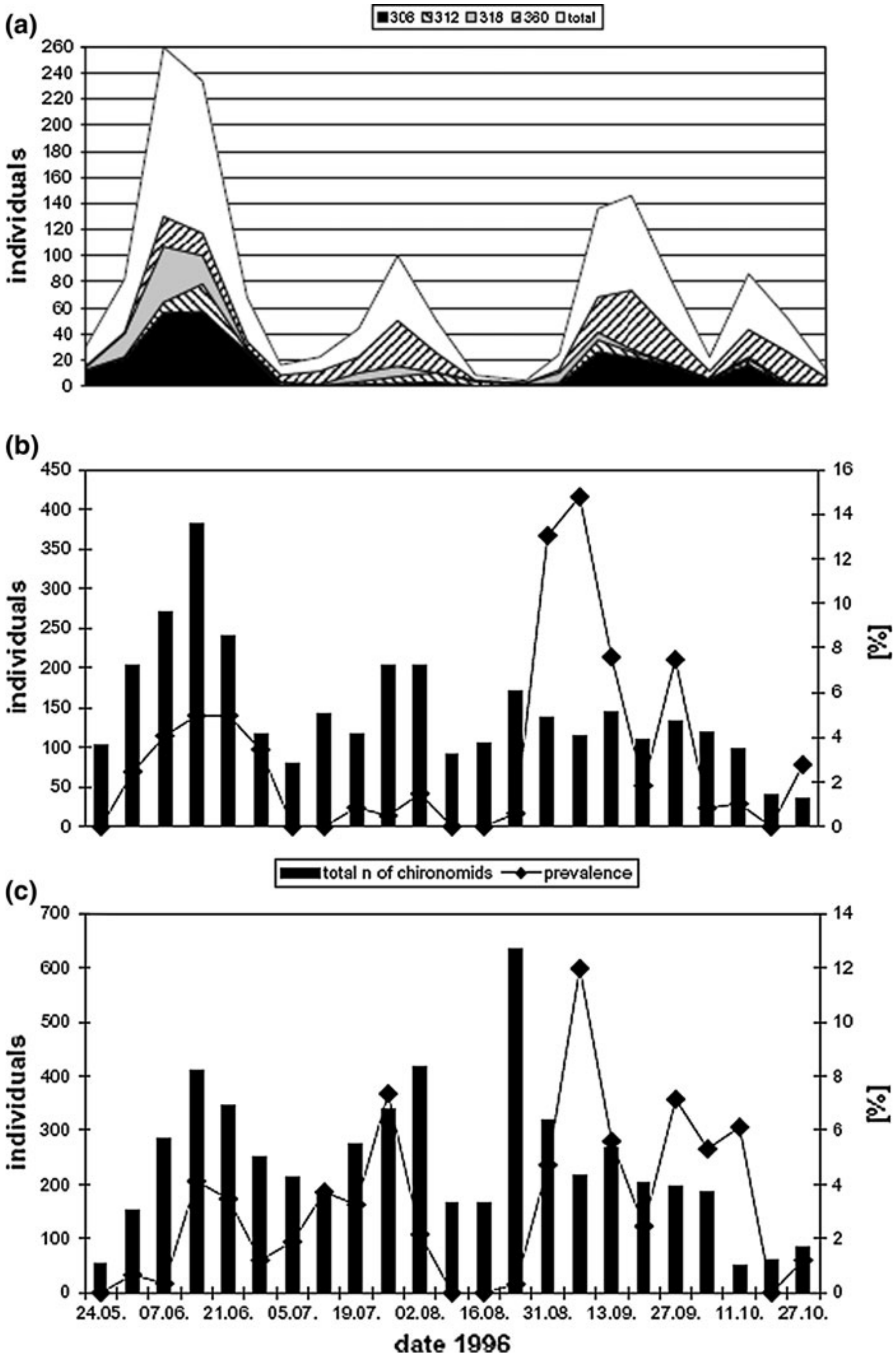

Fig. 1 Combined seasonal data of the present study: **a** Phenology of all water mite larvae attached to chironomid hosts at the four sites. **b** Phenology of all chironomids (parasitized and not parasitized) and the prevalence (%) of parasitism at site 308. **c** Phenology of all chironomids (parasitized and not parasitized) and the prevalence (%) of parasitism at site 360

chironomids infected by 252 mites). However, at the species level, prevalence in some species reached levels of nearly a third of a population (Table 5). Some of the more abundant species were heavily parasitized (e.g., *Parametrionemus stylatus*, 21%). During the year, the prevalence fluctuated with no parasitized chironomids observed in some weeks, whereas in other periods, prevalence reached more than 14% (Fig. 1b, site 308) or more than 12% (Fig. 1c, site 360). Comparing the whole chironomid community at the two sites, the prevalence variation is mostly similar over the seasons, but with a peak

Table 4 Quantitative data for water mites and their chironomid hosts

	No. of hosts (*n*)		Prevalence		Intensity			Var/mean ratio	*D*	Negative binominal distribution
	Total	Infected		95% CI	Median	Mean	BCA 95CI			
308 + 360 total	7573	293	0.039	0.0346–0.0433	1.0	1.70	1.54–1.89	2.95	0.974	–
308 + 360 ♂♂	3004	142	0.047	0.0402–0.0555	1.0	1.52	1.35–1.76	2.44	0.966	–
308 + 360 ♀♀	4569	151	0.033	0.0282–0.0387	1.0	1.86	1.61–2.16	3.34	0.979	+
308 total	3011	113	0.038	0.0313–0.0450	1.0	2.17	1.81–2.60	4.14	0.978	–
308 ♂♂	1141	61	0.053	0.0418–0.0682	1.0	1.82	1.48–2.34	3.23	0.965	+
308 ♀♀	1870	52	0.028	0.0212–0.0364	1.0	2.58	2.02–3.40	4.89	0.984	–
360 total	4562	180	0.039	0.0342–0.0455	1.0	1.40	1.29–1.52	1.79	0.969	+
360 ♂♂	1863	81	0.043	0.0351–0.0538	1.0	1.30	1.16–1.53	1.59	0.964	–
360 ♀♀	2699	99	0.037	0.0302–0.0445	1.0	1.93	1.33–1.67	1.93	0.972	+
H. norvegicus total	7573	81	0.011	0.0086–0.0133	1.0	1.33	1.19–1.56	1.84	0.991	+
H. norvegicus ♂♂	3004	43	0.014	0.0106–0.0193	1.0	1.28	1.09–1.77	2.00	0.988	+
H. norvegicus ♀♀	4569	38	0.008	0.0060–0.0114	1.0	1.39	1.18–1.58	1.67	0.993	Not tested

Data were given for the sites 308, 360, 308 + 360 and *Hygrobates norvegicus* of both sites, each additionally separated for host sexes. Data were given for host sample size (total and infested), prevalence and 95% confidence interval (CI), median intensity, mean intensity and 95% bootstrap confidence interval (BCA 95 CI), variance to mean ratio (Var/mean ratio), discrepancy index (*D*) and the result of the test for negative binominal distribution (could not be tested for females of *H. norvegicus* due to not enough categories). For details see text

Table 5 Prevalence of chironomid host species and their water mite parasites

Chironomid host species	Total	Parasitized	Prevalence (%)
Parochlus kiefferi	3	1	33
Cricotopus cf. *curtus*	16	5	31
Micropsectra sofiae	34	10	29
Micropsectra attenuata	22	5	23
Rheocricotopus effusus	133	30	23
Parametriocnemus stylatus	259	54	21
Stempellinella cililaris	41	6	15
Paratrichocladius skirwithensis	23	2	9
Eukiefferiella tirolensis	30	2	7
Tvetenia calvescens	33	2	6
Thienemanniella spp.	288	16	6
Tvetenia sp.	19	1	5
Micropsectra pharetrophora	165	8	5
Corynoneura lobata	243	7	3
Tvetenia bavarica	97	2	2
Micropsectra seguyi	274	5	2
Parapsectra mendli	82	1	1
Heleniella spp.	261	2	1
Thienemannia libanica	702	1	<1

Data were pooled for males of the sites 308, 312 and 360

prevalence in July (>6%) at site 360, whereas prevalence did not reach 2% in the same month at site 308. Such seasonal variations are presumably also valid at species level, but our dataset does not allow for statistical considerations in this sense. At sites 308 and 360 the overall prevalence is higher in males than in females, but only significant for site 308 (Table 4; 308: ♂♂ 5.3%, ♀♀ 4.3%, $\text{chi}^2 = 12.912$, $P < 0.05$; 360: ♂♂ 4.3%, ♀♀ 3.7%, $\text{chi}^2 = 1.344$, $P = 0.246$). Pooling both sites, the higher prevalence in males is also significant ($\text{chi}^2 = 9.856$, $P < 0.05$). At the species level, *Hygrobates norvegicus* (only this species was regarded) showed a higher prevalence in males than in females ($\text{chi}^2 = 6.161$, $P = 0.013$) and reached a prevalence of 1.1%.

No correlation could be observed between the abundance of emerged chironomid species and the numbers of parasitized individuals (data for males only): For example, no individual of the most abundant species at site 308 (*Thienemannia libanica*) was parasitized. At site 360, of the five most abundant taxa (*T. libanica*, *Micropsectra seguyi*, *Corynoneura lobata*, *Heleniella* spp., *Krenosmittia boreoalpina*), only 1% of the 1118 individuals was parasitized and *Heleniella* spp. and *K. boreoalpina* remained completely uninfected.

In total, 422 chironomid hosts were parasitized by 671 larval water mites, i.e., a mean intensity of 1.6 larvae per host. Some 303 chironomids were parasitized by one water mite larva, 56 by two, 40 by three and 23 by four or more mites. Regarding the two sites 308 and 360, the maximum number of mite larvae on a single host (13) was found on a female *Parametriocnemus stylatus*. The mean intensity for *Feltria* spp. was 2.2 mites per host at site 308, but only 1.4 mites per host at site 360, a difference probably caused by the smaller share of *Feltria* larvae at site 360. Comparing other mite species with regard to intensity of parasitism, differences between the two sites also reflect the relative abundance of the species *Atractides panniculatus* had a higher mean intensity at site 360 (1.3, 1.0 at site 308).

At both sites, chironomid females were parasitized with a slightly higher mean intensity than males (Table 4; 2.58 vs. 1.82 and 1.93 vs. 1.30, respectively), but this was not significant for either of the sites 308 and 360 separately ($t = 1.860$, $P = 0.069$; $t = 1.642$, $P = 0.175$) nor for both sites regarded together ($t = 1.971$, $P = 0.051$). At the species level, the differences in mean intensities for *Hygrobates norvegicus* were not different comparing both sites ($t = 0646$, $P = 0.543$). The mean intensity of parasitism was slightly biased towards females (1.39 vs. 1.28) but there was no statistical significance ($t = 0.634$, $P = 0.054$).

Discussion

Host spectra and host specificity

In the past, parasitism was doubted for spring-living water mites (e.g. Schwoerbel 1959; Besch 1969). The present results support the recent views of, for example, Smith (1991, 1998) and Martin and Stur (2006) that parasitism is also the rule for spring-living species. Loss of larval parasitism has not been observed in the present study but is assumed for one species abundant at site 360, viz. *Sperchon violaceus* Walter, 1944, because of the morphology of the reared larvae (Martin 2003; Gerecke and Martin 2006). From one clutch of *Atractides walteri* reared in the laboratory, no larvae hatched, but deutonymphs (P. Martin, unpublished observation); thus, at least for this species, a facultative loss of parasitism can be supposed. Further investigations on spring-dwelling water mites are necessary before firm conclusions can be drawn.

The present study provides the first data concerning the water mite-host spectra from spring sites in the Alps. A similar dataset has been presented only once before, from an investigation on spring habitats in Luxembourg (Martin and Stur 2006). As in the results from studies dealing with other habitat types (e.g., Ullrich 1978; Martin 2000 for streams, or Smukalla and Meyer 1988 for lakes), chironomids have been shown to be the most important host taxon. No members of the subfamilies Tanypodinae and Diamesinae were found to be parasitized, although they are present in the spring complexes (Stur and Wiedenbrug 2006).

For 13 species (*Atractides adnatus*, *A. macrolaminatus*, *A. panniculatus*, *A. walteri*, *Lebertia cuneifera*, *L. lativentris*, *L. maculosa*, *L.* cf. *schechteli*, *Panisopsis curvifrons*, *Protzia distincta*, *Sperchon mutilus*, *S. resupinus* and *Tartarothyas romanica*), hosts are recorded for the first time. For five other species, known host spectra are confirmed and/or supplemented: *Bandakia concreta*, *Hydrovolzia placophora*, *Hygrobates norvegicus*, *Lebertia sefvei*, *Partnunia steinmanni* and *Todothyas palustris*.

In the present study, *Bandakia concreta* has only been detected as a parasite of an unidentified chironomid; two species of the subfamily Tanypodinae are previously known hosts (Martin and Stur 2006) and also other *Bandakia* species have been found to be parasites of the Tanypodinae (Smith 1982).

Hygrobates norvegicus is the only species for which data are sufficiently complete to allow a comparison with a similar study from Luxemburg (Martin and Stur 2006). Interestingly, in this species, which generally seemed to be a host generalist rather than a specialist (see Martin and Stur 2006), a kind of host specificity can be shown: the host species most intensely parasitized (>50% of the attached larvae) was *Rheocricotopus effusus* and also other less frequent host species were the same in both studies.

The finding of a trichopteran larva parasitized by larval *Feltria* is interesting because parasitism on larval Trichoptera and Plecoptera by *Feltria* was also noted by Efford (1963, 1966), but rejected by Smith and Oliver (1986) as probably an accidental association. The possible parasitism of larval insects by *Feltria* (but perhaps also by larvae of other water mite genera) is obviously more common than expected and should be taken into consideration and given more attention in future investigations.

For most water mites, the known host spectrum at species level is directly reflected by the (mostly rare) number of investigations (see also Böttger and Martin 2003). Mites can be specialists with a single host species per site as shown by the example of *Feltria rouxi* in a British stream (Efford 1963). However, at other sites, the same mite species can have a broader host spectrum. Because of our sparse knowledge and the difficulties of laboratory investigations in most of the chironomid species, a detailed discussion of these questions cannot take place at the present time (see Martin and Stur 2006).

Possible preference for spring-adapted hosts

Gerecke and Di Sabatino (1996a) hypothesized that most crenobiontic water mites are associated with spring-preferring hosts, since only these enable a post-parasitic return to a well-suited habitat. However, while most water mite species in the present study are crenobionts or crenophiles (Gerecke and Martin 2006), the degree of spring-preference of their chironomid hosts is mostly uncertain (Lindegaard 1995; Stur et al. 2005; Stur and Wiedenbrug 2006). Some of the abundant hosts are crenophiles to crenobionts (e.g., most *Micropsectra* species), others are more euryoecious (e.g., *Parametriocnemus stylatus*; see Stur and Wiedenbrug 2006). The regional crenobiosis is also unknown for non-chironomid hosts to a large extent. Although at least some of them could be estimated as crenobionts and/or crenophiles (e.g., *Nemoura marginata*, *N. sinuata*, *Leuctra armata*; Weinzierl and Graf 2006, *Micrasema morosum*, *Parachiona picicornis*; Graf et al. 2006) the low number of parasitic associations with these hosts does not enable an interpretation. Summarizing, water mite-host relationships are difficult to assess with regard to their spring-preference. As in water mites from the Luxembourg springs, where larvae of only a few water mite species were found to attach exclusively to hosts considered as crenobionts or crenophiles (Martin and Stur 2006), in the present study also, no general preference for strictly spring-preferring hosts could be shown. As in the study area, springs and small streams are present almost exclusively (perhaps with a similar thermal regime), also non–spring-preferring host imagos will preferably stay in areas suited for spring-preferring mite parasites. A manipulation of the hosts by the parasitic mite larvae has also been seen as a possible strategy for water mite larvae by Gerecke and Di Sabatino (1996a). Manipulative parasites can have an important and interesting significance for the whole ecology of their habitats (Lefèvre et al. 2008), but no indications have been noted so far suggesting such kind of effects in water mites, and a study directed to answering these questions would need an ambitious study design.

Attachment sites, phenology and prevalence

The present results concerning attachment sites of water mite larvae on their host's body in general accord with data reported elsewhere, for example, by Smith and Oliver (1986) and Smith et al. (2001) at genus level. Also in the Luxembourg springs (Martin and Stur 2005), most *Hygrobates norvegicus* larvae had a clear preference for the dorsal area anterior to abdominal intersegment 3/4. This stability of attachment patterns, within geographically distant populations of a water mite species, is shown by some of its common host species in both studies.

As suggested by Martin (2004) and Martin and Stur (2005), attachment site preference is a prerequisite for host partitioning, allowing for more than one species to attach to the same host individual. Such multiple parasitized chironomids exhibit possible co-occurrence: *Lebertia* spp. larvae as thorax parasites were found together with several species of abdominal parasites; *Feltria* spp. larvae attached more distally than co-occurring *Hygrobates norvegicus* larvae. *Atractides panniculatus* and *H. norvegicus* larvae do not show distinct differences in their preferred attachment sites along the host's longitudinal axis but avoid competition by alternating dorsal/ventral attachment. In the present study, only 8.8% of the parasitized chironomids were found as hosts for more than one species. Similar values were found during a study in the Luxembourg springs (11.5%; Martin and Stur 2005) and in a small north German stream (6.4%; Martin 2004), and we conclude that the extent of host partitioning by using different attachment sites is not high in the populations studied. Such host partitioning by attachment site differentiation has been shown for other water mite-host relationships (e.g., Lanciani 1970). Perhaps, the potential of host partitioning by selective attachment site, as found here, can be seen as the possible avoidance of competition, e.g., in years with a poor supply of hosts or at other sites with higher interspecific competition.

Most mite species obviously emerge throughout the sampling period, but various species showed restricted seasonal emergence patterns, but results have to be interpreted cautiously due to generally low individual numbers in most species. The only possible comparison at species level concerns *Hygrobates norvegicus*, a species that shows (summarizing all data), a two-peaked occurrence. Instead, in Luxembourg (Martin and Stur 2005), *H. norvegicus* was present almost exclusively in springtime and consequently might display another type of life-cycle strategy. The phenology observed in Berchtesgaden, together with the data from Luxembourg, also indicate that spring-dwelling mites show geographical and ecological variability in their life-cycle strategies, e.g., by different modes of hibernation or different periods of oviposition. Such differences in life cycles were also found concerning stream-living water mites, e.g., by Ullrich (1978) and Martin (1998, in press).

The present data show a relatively low total prevalence for parasitized chironomid hosts (about 3–3.5%) and fall below the values from the Luxembourg springs (7.8% of parasitized male hosts, Stur et al. 2005). Other habitats also exhibit a higher overall prevalence of parasitized chironomids than in the present study (e.g., stream: 16.9%, P. Martin, unpublished data, lake littoral: 14–23%, Smukalla and Meyer 1988). However, as in the other studies referred to, also in Berchtesgaden, at least during some seasons, almost the complete population of some species could be found parasitized by mites. In the study by Stur et al. (2005) for example, the chironomid species *Parametriocnemus stylatus* shows a similar overall prevalence as in the present study (>20%).

Intensity of parasitism and possible preferences for host sex

The total mean intensity of water mite parasitism is lower than that in a study of parasitized chironomids from a lake (males: 2.35 larvae/host, females: 2.92 larvae/host; Kouwets and Davids 1984), but many chironomid parasites show a high maximum intensity, both in springs (the present study; e.g., *Ljania bipapillata* Thor, 1898: 21 larvae/host; Martin and Stur 2006), streams (e.g., *Feltria rouxi* Walter, 1907: 19 larvae/host; Martin 1998; Martin in prep.) and in lakes (species not reported: 42 larvae/host; Kouwets and Davids 1984). Differences in specific intensities of parasitism between different spring sites have also been reported in Martin and Stur (2006). Their statistical analysis shows no sex-biased differences in the distribution and intensities of the parasitic mites. Due to the low number of specimens, our data does not allow a thorough statistical analysis of this phenomenon.

Conclusions and perspectives

The results of the present investigation and data from other studies (Martin and Stur 2005, 2006; Stur et al. 2005) allow us to conclude that, in general, water mite parasitism in spring habitats does not differ from that in other freshwater habitats. To date, no clear explanation has been proposed for crenobiosis of spring-dwelling water mites. Since crenobiosis is a phenomenon that has evolved over large-scale climatic periods of time and has to be regarded on a regional or local scale (Gerecke and Di Sabatino 1996b), habitat preference of many of the host species should probably be re-defined for the alpine region and little data from springs exist (Cantonati et al. 2006). Potentially, the numbers of chironomid host species that have to be classified as local crenobionts may be higher than believed so far.

Nevertheless, the alternative assumption of Gerecke and Di Sabatino (1996a) is still valid: more euryoecious hosts might show a behavioural pattern, possibly induced by the parasites, that allows the parasites to return to their preferred spring habitat. This is especially possible in the area in which the present investigation has been undertaken. Here, except for springs, only small streams are present in the surroundings of large spring complexes in which mostly a diluted spring fauna is found (Franz et al. 2006) and which obviously offer suitable conditions for the spring-preferring mites.

Smith (1991) suggested that the evolution of water mites has led to at least 30 independent invasions of spring habitats. Thus, the enormous diversity of stenotopic water mites in springs might be based on the fact that springs, as ecotone habitats between aquatic and terrestrial life, are a key habitat in which the evolution of water mites originated from terrestrial ancestors. This could be reflected by high numbers of early derivative taxa of mites bound to springs (Smith 1991). Additionally, because of the high abundance of chironomids, spring habitats are obviously favourable habitats not only for the larval parasites, for the predatory nymphs and for the adults, but probably also for the quiescent inactive stages in the life cycle of water mites.

The investigation of water mite parasitism in springs requires data from other geographical areas (e.g., from northern or southern Europe). Indeed, further research in the National Park of Berchtesgaden offers challenging perspectives including the analysis of water mite parasitism by long-term monitoring of the insect fauna using emergence traps (see Gerecke et al. 2006). Such an analysis would reveal the stability or variability of parasite–host associations and also possible climatic changes which could have a strong impact on the spring communities as a whole.

Acknowledgments This study was financially supported by a postdoc-grant of the foundation “Pro Acarologia Basiliensis” (PAB), Basel, Switzerland to the first author. The second and third authors received funding from the National Park of Berchtesgaden. Helmut Franz from the National Park kindly supported the field stays of all authors. Special thanks are extended to H. Reusch (Suhlendorf, Germany) and H. Meyer (Ecology Centre of Kiel University) for identifying limoniid and empidid hosts as well as to R. Gerecke (Tübingen, Germany) for support in an earlier version of this paper. Four anonymous, constructive reviewers helped to improve the manuscript. Sincere thanks also to Dr. R. A. Baker (University of Leeds) for correcting the English.

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