Primary Research Paper

Parasite-host associations and life cycles of spring-living water mites (Hydrachnidia, Acari) from Luxembourg

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Abstract

Larval water mites are parasites of various insect species. The main aim of the present study was to analyse the host range of spring dwelling water mites. The investigation focuses on seven spring sites in Luxembourg. Some 24 water mite species were recorded either from the benthos or as parasites attached to flying insects captured in emergence traps. For 20 mite species 35 host species from four Nematocera (Diptera) families were recorded. About 80% of the host species and over 90% of the host individuals were Chironomidae, the others were Limoniidae, Dixidae and Simuliidae. For all water mite species recorded we present the observed host spectrum and/or potential hosts as well as the intensity of parasitism and the phenology of the mites. For 10 mite species the hosts were previously unknown. For another ten species the known host spectrum can be confirmed and extended. The host spectrum ranged from one host species (e.g. for *Sperchon insignis*) to at least 10 host species (for *Sperchon thienemanni*, *Ljania bipapillata*), but the effective host range could not be definitively estimated due to the lack of corresponding data. The hypothesised host preference of the water mites, of which most are strictly confined to spring habitats, for similarly spring-preferring hosts could not be proven. The mean intensity of parasitism was highest for *Thyas palustris* (10.8 larvae/host) and lowest for *Sperchon insignis* and *Hygrobates norvegicus* (1.2 larvae per host for each). The hydryphantid mite *Thyas palustris* occurred at maximal intensity (41 larvae per host) and the two abdominal parasites *Ljania bipapillata* and *Arrenurus fontinalis* showed higher mean intensities than the thoracic parasites did. Larval water mites parasitising chironomids did not exhibit a preference for host sex. The phenology of the larval mite species was varied, some species were only present in samples early in the year and others exclusively in the summer. Another species showed two peaks of occurrence, springtime/early summer and late summer/autumn. In conclusion, the water mite larvae in the studied springs showed differences in host spectra and phenology but there are no clear evidences in both for host partitioning. Maybe, the relative low species diversity of water mites in individual springs and the low inter-specific competition for suitable hosts in combination with the high host abundances and species richness makes springs such favourable habitats for the mites.

Introduction

In general, the species-rich water mites or Hydrachnidia which have invaded nearly all kinds of aquatic habitats, have a parasitic larva associated to various host taxa (Smith & Oliver, 1986; Smith et al., 2001). In spring habitats, many mite species are known to be more or less strictly restricted to

these habitats and are called crenobiont and/or crenophilous (see e.g. Gerecke et al., 1998; Di Sabatino et al., 2003). On the other hand, our knowledge of the host species of water mites from spring habitats is very poor. It has been suggested, because of the difficulties in synchronising the life cycles between parasitic mites and their hosts in the stenothermous springs, that water mites from spring habitats had lost their parasitic larval stage (Walter, 1917; Viets, 1940; Mitchell, 1957; Schwoerbel, 1959; 1961; 1967; Besch, 1969). Following first findings from North America (compiled in Smith, 1991 and various later publications of I.M. Smith concerning that subject for different genera and species) larval descriptions of spring-inhabiting species and their hosts were also published from European springs (Cicolani et al., 2001; Martin, 2000; 2003; 2006; Martin et al., 2002; Gerecke & Martin, 2006).

Nevertheless, there are not many studies concerning parasite-host associations at species level because of various problems. For most water mite species no larval taxonomic description exists and thus there is no way to establish associations with host species. Moreover, mite diversity in many habitats is high and the separation of mites at species level is difficult. At the host level, diversity is also high since most water mites have more than one single host species and the most important hosts belong to the species-rich dipteran family Chironomidae (Smith & Oliver, 1986).

Because of these taxonomic and practical difficulties springs seem to be suitable habitats to investigate larval morphology and parasitism since most are small habitats with relatively small numbers both of mite and host species in any one individual spring site.

Aside a similar study from the Alps (see Martin, 2003; Gerecke & Martin, 2006) the present study is the only one that covers all mite species from particular spring habitats. Here, we investigated the hypothesis that water mite parasitism is the rule in this specific habitat. In the present study results from seven Luxembourg springs are presented, where mite diversity is largely known from benthic samples (Gerecke et al., 2005). Based on determinations of mites (see Martin, 2006) and hosts at species level, host spectra and larval phenology of all mite species collected was investigated. Moreover, we asked some more general questions which were partly contradictorily treated in the literature: Is there evidence for host preference? Do the water mites prefer female hosts? Are there differences in seasonality of parasitism in spring living water mites?

Material and methods

This study deals with the parasitism of water mites in seven Luxembourg springs. The sample sites were described in detail by Gerecke et al. (2005) and were named there as qu11, qu19, qu20, qu21, qu23, qu24 and qu25. At these sites emergence traps (base 0.8×0.8 m, for details see Stur et al., 2005) were positioned and emptied at intervals of 2 weeks from May 26th to November, 3rd 1999. In the present study the sites were simplifying named according to the numbers of the emergence traps located at the respective sites, i.e. as E1 (= qu19), E2 (= qu20), E3 (= qu23), E4 (= qu11), E5 (= qu21), E6 (= qu24) and E7 (= qu25). The springs belongs to different types, sites E1, E7 were classified as rheocrenes, site E2 as a helocrene and sites of E3, E4, E5 and E6 as rheohelocrenes (see Gerecke et al., 2005). The E1 sample for the period June 29th to July 13th was lost and thus could not be analysed.

The insects collected from the traps were checked for parasitic larval water mites. The mite larvae were removed from their hosts, attachment sites were noted and the mites could be identified according to Martin (2006). All hosts except the chironomids were identified by different specialists (see Acknowledgements).

The species inventory of water mites from the seven sites was compiled from the samplings of Gerecke et al. (2005), benthic samples of the first author and the results of Martin (2006).

For all statistical analyses, χ^2-tests of uniform distribution were applied by using STATISTICA 6.0, StatSoft Inc. The significance between observed and expected values was calculated by the use of 2×2 tables and the χ^2-test with contingency tables. The applied limits of the significance levels were: * = $0.01 < p < 0.05$, ** = $0.001 < p < 0.01$, *** = $p < 0.001$.

Concerning statistical analyses of host preference, intensities of parasitism and preferences of

hosts' sexes the following assumptions were made and procedures were conducted:

For answering the question of evidence for host preferences the distribution of larvae of a water mite species was checked for different chironomid host species from one or different sample sites. As a first approximation, a higher intensity was considered as a measurement for a higher preference for a host. A χ^2-test was applied to the intensity of parasitism for larvae of a mite species between two host species. The following associations were statistically analysed: *Sperchon thienemanni* attached to *Tvetenia calvescens* (E1) and *Micropsectra* spp. (E1), *S. thienemanni* attached to *T. calvescens* (E1) and *Stempellinella flavidula* (E5), *S. thienemanni* attached to *Micropsectra* spp. (E1) and *St. flavidula* (E5), *Atractides fonticolus* attached to *Brillia bifida* (E1) and *Micropsectra* spp. (E1), *A. fonticolus* attached to *B. bifida* (E1) and *Corynoneura lobata* (E7), *A. fonticolus* attached to *Micropsectra* spp. (E1) and *C. lobata* (E7), *Ljania bipapillata* attached to *B. bifida* (E1) and *Parametriocnemus stylatus* (E1), *L. bipapillata* attached to *B. bifida* (E5) and *St. flavidula* (E5), *L. bipapillata* attached to *B. bifida* (E5) and *P. stylatus* (E5). *L. bipapillata* attached to *St. flavidula* (E5) and *P. stylatus* (E5).

On the other hand, the intensity of parasitism can be compared if a host species is parasitised by different parasitic mites. For that reason the following chironomid taxa host-parasite associations were checked for differences in intensities by applying a χ^2-test: *Micropsectra* species as host for *Sperchon thienemanni* (E1) and *Atractides fonticolus* (E1), *Stempellinella* species as host for *S. thienemanni* (E5) and *Ljania bipapillata* (E5), *Brillia bifida* as host for *A. fonticolus* (E1) and *L. bipapillata* (E1), *B. bifida* as host for *A. fonticolus* (E1) and *L. bipapillata* (E5), *B. bifida* as host for *L. bipapillata* (E1) and *L. bipapillata* (E5), *Parametriocnemus stylatus* as host for *L. bipapillata* (E1) and *L. bipapillata* (E5).

The distribution of mites relating to the host sex was statistically tested for the most numerous parasite-host associations in chironomid hosts: *Sperchon longissimus* vs. *Micropsectra* spp. (E1), *S. squamosus* vs. *Micropsectra* spp. (E3), *S. thienemanni* vs. *Tvetenia calvescens* (E1), *S. thienemanni* vs. *Stempellinella flavidula* (E5), *Lebertia glabra* vs. *Micropsectra* spp. (E7), *L. sefvei* vs. *Micropsectra* spp. (E7), *Hygrobates norvegicus* vs. *Rheocricotopus*

effusus (E3), *Atractides fonticolus* vs. *Brillia bifida* (E1), *A. fonticolus* vs. *Micropsectra* spp. (E1), *A. fonticolus* vs. *Corynoneura lobata* (E7), *L. bipapillata* vs. *B. bifida* (E1), *Ljania bipapillata* vs. *Parametriocnemus stylatus* (E1), *L. bipapillata* vs. *B. bifida* (E5), *L. bipapillata* vs. *Stempellinella flavidula* (E5). For answering the question whether or not the intensity of parasitism is higher in host females than in males or vice versa, parasite-host associations were tested for pairs with more than 50 specimens of one mite species for one host species (range of host individuals 23–185): *Sperchon longissimus* vs. *Micropsectra* spp. (E1), *S. squamosus* vs. *Micropsectra* spp. (E3), *S. thienemanni* vs. *Tvetenia calvescens* (E1), *S. thienemanni* vs. *Stempellinella flavidula* (E1), *Lebertia sefvei* vs. *Micropsectra* spp. (E7), *Ljania bipapillata* vs. *Brillia bifida* (E1), *L. bipapillata* vs. *B. bifida* (E5), *L. bipapillata* vs. *St. flavidula* (E5).

The data for the species in the results were given as follows: For all sites with 20 or more mites of the respective species: site no 1: total hosts/total attached mites (additionally detached mites), total mean intensity, host 1 parasitised individuals (percentage)/attached mites (percentage), mean intensity (range; if present), host 2 etc., site no. 2: etc. For sites with < 20 mites: host 1 parasitised individuals/ attached mites (additionally detached mites), host 2 etc., site no. 2: etc.

Results and former findings for the parasitism of the mites

Twenty taxa of 24 water mite species, known from the seven investigated spring sites, were found as parasites of at least 35 host species (Table 1). Host taxa were exclusively Diptera-Nematocera: Limoniidae (five taxa), Simuliidae (one species), Dixidae (two species) and Chironomidae (26 species and one genus). The limoniids were hosts to two mite species, the simuliids and dixids to one species each and the chironomids for 16 taxa.

Among the total individuals of chironomids for all seven sites, *Stempellinella flavidula* was most frequently found with attached water mites (81 individuals, see Table 1). At most five different water mites species were found parasitising the same host species (*Parametriocnemus stylatus*,

Table 1. A survey on the host taxa and their parasitic water mites of seven spring sites in Luxembourg (E1–E7)

Host taxon	Arrenurus fontinalis*	Atractides fonticolus*	Atractides pennatus*	Bandakia concreta*	Feltria rouxi	Hygrobates norvegicus*	Lebertia glabra*	Lebertia holsatica*	Lebertia sefvei*	Ljania bipapillata*	Mideopsis willmanni*	Pionidae indet.	Pseudofeltria scourfieldi*	Sperchon insignis*	Sperchon longissimus*	Sperchon squamosus*	Sperchon thienemanni*	Sperchonopsis verrucosa	Thyas palustris*	Thyopsis cancellata	# parasitised hosts	# mite species/host taxon
Limoniidae																						
Molophilus sp.																			284	1	26	2
Paradelphomyia sp.																			9		2	1
Pilaria fuscipennis (Meigen, 1818)																			9		1	1
Erioptera flavata (Westhoff, 1882)																				1	1	1
Helius longirostris (Meigen, 1818)																				2	1	1
Simuliidae																						
Simulium crenobium (Knoz, 1961)*														21							19	1
Dixidae																						
Dixa dilatata Strobl, 1900*	22																				7	1
Dixa submaculata Meigen, 1818*	42																				10	1
Chironomidae																						
Tanypodinae																						
Krenopelopia sp.*				9																	7	1
Trissopelopia longimana (Staeger, 1839)				1																	1	1
Orthocladiinae																						
Brillia bifida (Kieffer, 1909)		36				7				261							1				34	4
Corynoneura lobata Edwards, 1924		47								1							8	13			37	4
Heleniella ornaticollis (Edwards, 1929)		1																			1	1
Heterotanytarsus apicalis (Kieffer, 1921)								1													1	1
Orthocladius oblidens (Walker, 1856)		3								27							1				15	3
Orthocladius rubicundus (Meigen, 1818)						1															1	1

Taxon																					
Parametriocnemus stylatus (Kieffer, 1924)	18					1	1		88					18				30		41	5
Rheocricotopus atripes (Kieffer, 1913)		1							8											2	2
Rheocricotopus effusus (Walker, 1856)		45							9											20	2
Rheocricotopus fuscipes (Kieffer 1909)									20											11	1
Tvetenia bavarica (Goetghebuer, 1934)																		3		1	1
Tvetenia calvescens (Edwards, 1929)	6												2					77		24	3
Orthocladiinae indet. (♀)										1										1	1
Chironominae																					
Micropsectra attenuata Reiss, 1969*	3								1			1						9		7	4
Micropsectra calcifontis Stur & Ekrem, 2006*	1																			1	1
Micropsectra junci (Meigen, 1818)*		5			23		2		2				29					11		27	5
Micropsectra longicrista Stur & Ekrem, 2006*					3				2									4		3	3
Micropsectra notescens (Walker, 1856)*						1														1	1
Micropsectra pallidula (Meigen, 1830)		15			36								37							9	3
Micropsectra schrankelae Stur & Ekrem, 2006*	11	22			1						25		23						48	5	
Micropsectra spp. ♀♀							1												1		
Microtendipes tarsalis (Walker, 1856)									3									2		4	2
Polypedilum albiorne (Meigen, 1838) ♀♀																		2		2	1
Polypedilum convictum (Walker, 1856) ♀♀	13																	1		1	2
Stempellinella flavidula (Edwards, 1929)	7								96				64					64		81	3
Stempellinella sp. 1 *	9																			9	1
Tanytarsus heusdensis Goetghebuer, 1923*		10			2											3		3		6	4
number of host taxa	2	11	1	2	1	6	2	1	13	1	1	3	3	3	3	14	1	3	3		
total mite individuals	73	203	6	22	1	89	2	1	526	1	22	122	152	387	464	4	50	101			
total mite individuals detached	9	24	0	11	0	5	1	12	3	0	0	37	37	93	162	0	26				
E1 total	1	129							151		112		261								
E1 detached		15									34		73								
E2 total																		58			
E2 detached																		36			

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Table 1. (Continued)

	Arrenurus fontinalis*	Atractides fonticolus*	Atractides pennatus*	Bandakia concreta*	Feltria rouxi	Hygrobates norvegicus*	Lebertia glabra*	Lebertia holsatica*	Lebertia sefvei*	Ljania bipapillata*	Mideopsis willmanni*	Pionidae indet.	Pseudofeltria scourfieldi*	Sperchon insignis*	Sperchon longissimus*	Sperchon squamosus*	Sperchon thienemanni*	Sperchonopsis verrucosa	Thyas palustris*	Thyopsis cancellata	# parasitised hosts	# mite species/host taxon
E3 total	64			21		88			73	8						93	3		461			
E3 detached	9			11		5			21										159			
E4 total	8										1		1		9		1			4		
E4 detached													1		3							
E5 total									28	353						1	121	2				
E5 detached									5	2						1	20	2				
E6 total				1									4									
E6 detached				1																		
E7 total	9		74					50		14		1		22			1	22				
E7 detached			6					12		1				1				9				

As a rule, higher taxa of hosts (genera or others) were omitted if hosts at species level were known. In addition to the total number of collected mites, detached larvae are reported. No. of parasitised chironomids: if not otherwise indicated, only parasitised ♂♂ were given. Marked by "*": taxa which were considered as crenobionts and crenophiles.

Micropsectra junci, *M. pallidula* and *M. schrankelae*).

In Table 1 also the numbers of larval water mites are presented for all seven sample sites. Larvae were either attached to their hosts (1823 individuals) or found detached in the samples (430 larvae). Most water mite larvae were found at site E3 (811 larvae), the fewest at site E6 (seven larvae). A total of 2253 larvae were collected, the most numerous being *Ljania bipapillata* (526 ind.), *Thyas palustris* (464 ind.) and *Sperchon thienemanni* (387 ind.).

In the following, for all 24 water mite species of the spring sites, results on parasite-host associations are given and discussed for each species separately (for the host systematics see Table 1). These data are followed by investigation into questions concerning host preferences, the intensity of parasitism and possible preferences of the mites for host sexes.

Hydryphantidae Piersig, 1896
Thyadinae K.Viets, 1926
Panisellus thienemanni (K.Viets, 1920)

No host species were found in this investigation.

Remarks: In the present study adults of *Panisellus thienemanni* were only found in the benthos at site E5. This species is known as a parasite of collembolans (Boehle, 1996). Since in this investigation mainly merolimnic insects were caught in the traps, collembolans were only accidentally present. Parasitism occurs in the early spring, from the beginning of April to middle of June (Boehle, 1996; A. Wohltmann, Bremen, pers. comm.).

Thyas palustris Koenike, 1912

E3: 28/302 (159), 10.8, *Molophilus* sp. 25 (89.3%)/284 (94.0%), 11.4 (1–41), *Paradelphomyia* sp. 2 (7.1%)/9 (3.0%), 4.5 (3–6), *Pilaria fuscipennis* 1 (3.6%)/9 (3.0%), 9.0, E5: 2 detached mites, E7: 1 detached mite.
Thyas palustris larvae were collected from July to the beginning of September, but were most numerous in early August (Fig. 1).

Remarks: For alpine springs, Limoniidae were already reported as hosts for *Thyas palustris*

(Gerecke & Martin, 2006). Also, Rack (1977) found different limoniids as hosts for *T. palustris*.

Thyopsis cancellata (Protz, 1896)

E4: *Molophilus* sp. (1/1), *Erioptera flavata* (1/1), *Helius longirostris* (1/2).
The four individuals occurred on July 13th 1999.
Remarks: Helius longirostris has been reported as host for *Thyopsis cancellata* by Martin (2000). Münchberg (1936; 1956) also reported some limoniid and tipulid species as hosts but some of his data are considered to be ambiguous (Smith & Oliver, 1986).

Tartarothyadinae K.Viets, 1934
Tartarothyas romanica Husiatinschi, 1937

No larva of *Tartarothyas romanica* was found in samples during the present study.

Remarks: Adult *Tartarothyas romanica* specimens were only collected in benthic samples at sites E4 and E6 (Martin, 2006). In another investigation Chironomidae are reported hosts for *T. romanica* (Gerecke & Martin, 2006).

Sperchontidae Thor, 1900
Sperchonopsis verrucosa (Protz, 1896)

E7: 12/13 (9), 1.1, *Corynoneura lobata* 12 (100.0%)/13 (100.0%), 1.1 (1–2).

The 22 individuals of *Sperchonopsis verrucosa* occurred in the emergence traps from May 4th to June 29th 1999, with a maximum on June 15th (Fig. 1).

Remarks: Corynoneura lobata was reported as the most important host species for *Sperchonopsis verrucosa* in a small stream in Northern Germany (Martin, 1998; 2000). Other hosts found in that study were *Micropsectra* sp. and *Thienemanniella* sp. For further known hosts of the genus *Sperchonopsis* see Smith & Oliver (1986) and Martin (2000).

Sperchon clupeifer Piersig, 1896

No larva of *Sperchon clupeifer* was detected in the emergence traps.

Remarks: Sperchon clupeifer was only found as a single adult specimen in a benthic sample at site E1 (see Gerecke et al., 2005). Martin (2000) reported

different chironomid species from the subfamilies Chironominae and Orthocladiinae as hosts for *S. clupeifer*.

Sperchon insignis (Walter, 1906)

E7: 9/20 (0), 1.16, *Simulium crenobium* 9 (100.0%)/20 (100.0%), 1.16 (1–2).

The first larvae of *S. insignis* appeared on April 20th, the last on July 27th 1999. Possibly, there are two peaks of occurrence, at the beginning of May and at the end of July.

Remarks: The host of *S. insignis* was previously unknown. Since only one simuliid species was found as host, *S. insignis* may preliminary be considered as host-specific. This is supported by knowing that in emergence trap E7 another simuliid species was collected (M. Car, Brunn a. Gebirge, pers. comm.). *Sperchon insignis* was considered as a subspecies of *S. setiger* Thor, 1898 for a long time. *Sperchon setiger* obviously prefers different species of Simuliidae as hosts (Ullrich, 1978; Semushin, 1981; Gledhill et al., 1982) although Martin (2000) found besides simuliids also occasionally chironomids as hosts.

Sperchon longissimus K.Viets, 1920

E1: 47/78 (34), 1.7, *Micropsectra* sp. ♀♀ 32 (68.1%)/51 (65.4%), 1.6 (1–6), *M. schrankelae* 13 (27.7%)/24 (30.8%), 1.8 (1–5), *Tvetenia calvescens* 1 (2.1%)/2 (2.6%), 2.0, *M. attenuata* 1 (2.1%)/1 (1.3%), 1.0, E4: *Micropsectra* sp. ♀♀ 6/6 (3), E7: *M. schrankelae* 1/1.

The larvae of *S. longissimus* were recorded at site E1 from May 18th to July 27th 1999 with the maximum on June 27th (Fig. 1). At E4, all larvae were found in October 1999. The only larva at site E7 was collected in June 15th 1999.

Remarks: In this study, the first records of the host spectrum of *S. longissimus* are presented. Until now, the mite species appeared to be host-specific to the genus *Micropsectra*. The appearance of the larvae in a relative narrow time frame is remarkable and may be based on a stringently synchronised ovipositing by the mite females.

Sperchon squamosus Kramer, 1879

E2: 19/22 (36), 1.2, *Micropsectra pallidula* (♂♂ + ♀♀) 14 (73.7%)/16 (72.7%), 1.1 (1–2), *M. junci* (♂♂ + ♀♀) 5 (26.3%)/6 (27.3%), 1.2 (1–2), E3: 35/55 (38), 1.6, *M. pallidula* (♂♂ + ♀♀) 19 (54.3%)/21 (52.7%),

M. junci (♂♂ + ♀♀) 13 (37.1%)/23 (41.8%), 1.8 (1–5), *Tanytarsus heusdensis* 3 (8.6%)/3 (5.5%), 1.0, E5: 1 detached larva.

With the exception of *Tanytarsus heusdensis*, only *Micropsectra* species were found as hosts (*M. pallidula* and *M. junci*). At sites E2 and E3, parasitic larvae occurred early in the year (Fig. 1), from April until July with a maximum on May 5th. At E3 a few additional individuals were found at the beginning of November.

Remarks: Ullrich (1978) found larvae of *Sperchon squamosus* exclusively attached to *Micropsectra* hosts, indicating a preference for that host genus which is reflected by our new data.

Sperchon thienemanni Koenike, 1907

E1: 114/188 (73), 1.6, *Tvetenia calvescens* 48 (42.1%)/76 (40.4%), 1.6 (1–4), *Micropsectra* spp. ♀♀ 25 (21.9%)/40 (21.3%), 1.6 (1–4), *Parametriocnemus stylatus* 13 (11.4%)/28 (14.9%), 2.2 (1–4), *M. schrankelae* 15 (13.2%)/23 (12.2%), 1.5 (1–3), *M. attenuata* ♂♂ 5 (4.4%)/ 9 (4.8%), 1.8 (1–4), *T. calvescens/bavarica* ♀♀ 4 (3.5%)/6 (3.2%), 1.5 (1–2), *T. bavarica* ♂♂ 1 (0.9%)/3 (1.6%), 3.0, *Brillia bifida* 1 (0.9%)/1 (0.5%), 1.0, *Corynoneura lobata* 1 (0.9%)/1 (0.5%), 1.0, *Orthocladius oblidens* 1 (0.9%)/1 (0.5%), 1.0, E3: *M. junci* 1/1, *Micropsectra* spp. ♀♀ 2/2, E4: *C. lobata* 1/1, E5: 83/101 (20), 1.2, *Stempellinella flavidula* 59 (71.1%)/64 (63.4%), 1.1 (1–3), *M. junci* ♂♂ 5 (6.0%)/10 (9.9%), 2.0 (1–4), *Micropsectra* spp. ♀♀ 4 (4.8%)/9 (8.9%), 2.3 (1–3), *C. lobata* 5 (6.0%)/6 (5.9%), 1.2 (1–2), *M. longicrista* ♂♂ 2 (2.4%)/4 (4.0%), 2.0 (1–3), *Tanytarsus heusdensis* 3 (3.6%)/3 (3.0%), 1.0, *Microtendipes tarsalis* 2 (2.4%)/2 (2.0%), 1.0, *P. stylatus* 2 (2.4%)/2 (2.0%), 1.0, *Polypedilum albicorne* 1 (1.2%)/1 (1.0%), 1.0, e7 *T. calvescens* 1/1.

The host spectrum is broad and contains more than 10 species of chironomids from the subfamilies Orthocladiinae and Chironominae (Table 1). *Sperchon thienemanni* larvae were found in the emergence traps E1 and E5 from April to October 1999 (Fig. 1). The maximum abundance was in July, but the lack of data from trap E1 (July 13th) does not allow a clear interpretation. There were no remarkable differences between the results from the two sample sites. Parasitism by larvae of *S. thienemanni* was different at E1 and E5, where the species was abundant. More than half the mite larvae were attached to specimens of the orthocladiid species *Tvetenia calvescens* and *Parametriocnemus stylatus* in E1 whereas in E5 more than 60% of larvae were attached to *Stempellinella flavidula* (Chironominae,

Tanytarsini). *Micropsectra* spp. imagos were used as hosts at both sites but species which were seldom parasitised were other taxa.

Remarks: Ullrich (1978) and Martin (1998; 2000) found a broad range of chironomid host species for *S. thienemanni*. The most important host genus in both studies was *Micropsectra*.

<div align="center">

Anisitsiellidae Koenike, 1910
Bandakia concreta Thor, 1913

</div>

E3: 10/10 (11), 1.0, *Krenopelopia* sp. 9 (90.0%)/9 (90.0%) 1.0, *Trissopelopia longimana* 1 (10.0%)/1 (10.0%), 1.0, E6: *Krenopelopia* sp. 1/1.

Larvae of *B. concreta* were found from May 18th to July 13th with a maximum abundance in June.

Remarks: Chironomids as hosts at family level are reported for *Bandakia concreta* by Gerecke & Martin (2006) and generally for the genus *Bandakia* by Smith (1982). The observed parasitism of species of the subfamily Tanypodinae in this study
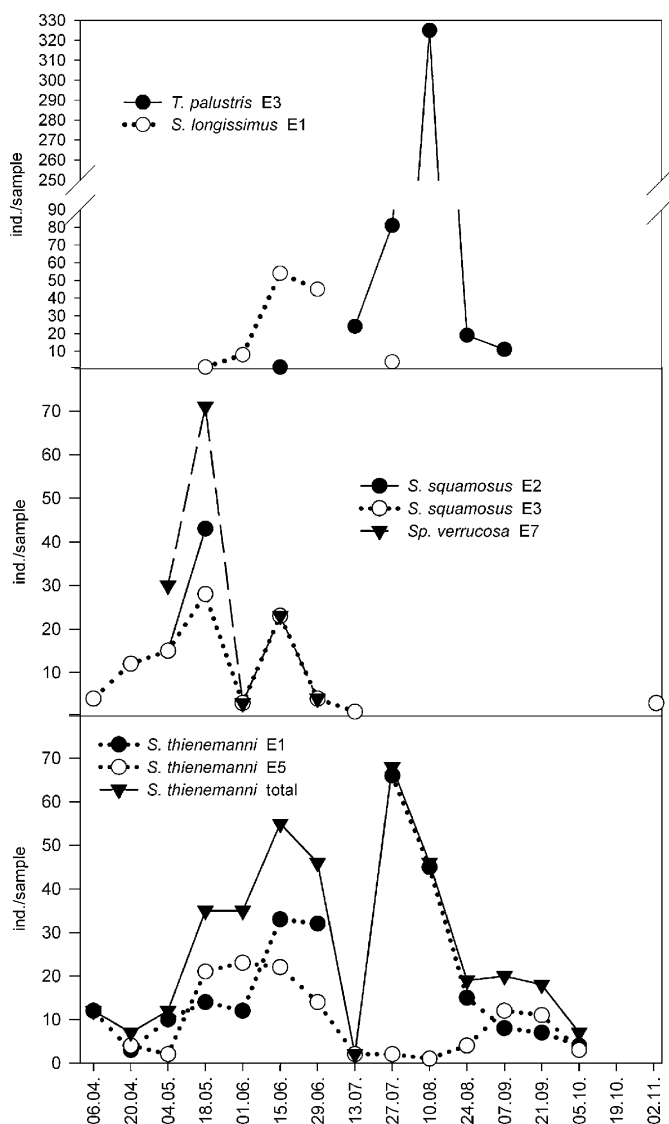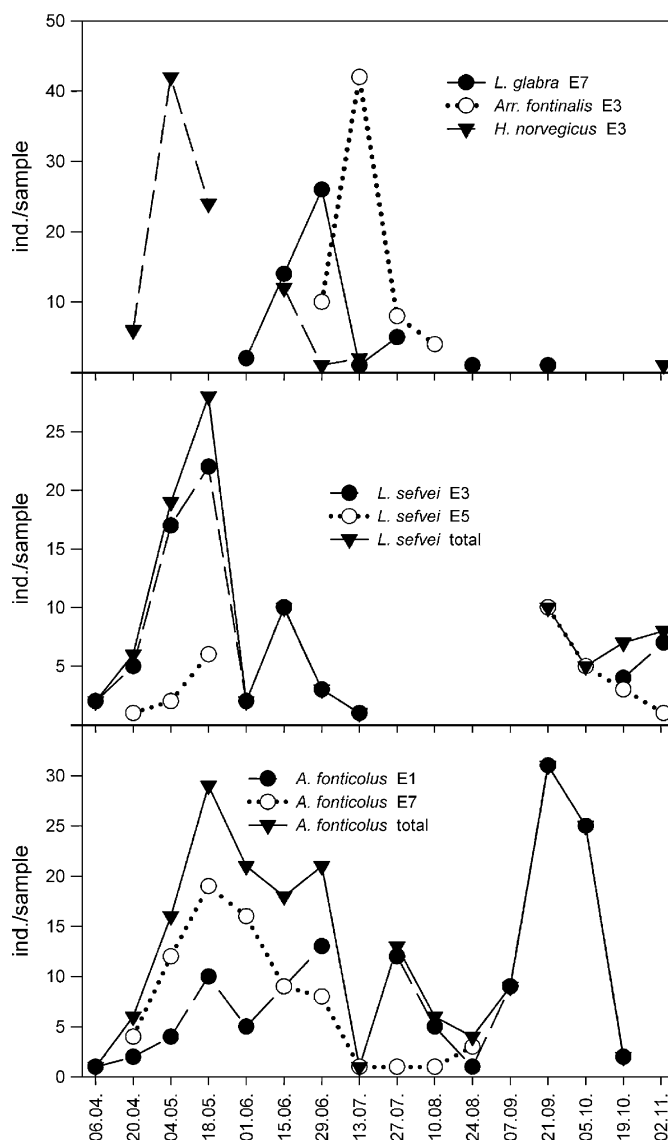

Figure 1. Phenology of attached and detached larvae of water mites from different springs in Luxembourg: top: *Thyas palustris* (E3) and *Sperchon longissimus* (E1), center: *Sperchon squamosus* (E2, E3) and *Sperchonopsis verrucosa* (E7), bottom: *Sperchon thienemanni* (E1, E5, totally).

fits the observations of Smith (1982). In the springs of Luxembourg, *B. concreta* was the only species parasitising Tanypodinae, but Tanypodinae are also known hosts for other mite species (Smith & Oliver, 1986).

Lebertiidae Thor, 1900
Lebertia holsatica K.Viets, 1920

E1: *Parametriocnemus stylatus* 1/1 (1).

One attached larva was found on August 10th and a detached one on July 27th 1999.

Remarks: No other data on the parasitology of *Lebertia holsatica* has been reported.

Lebertia glabra Thor, 1897

E7: 27/38 (12), 1.4, *Micropsectra schrankelae* 15 (55.6%)/22 (57.9%), 1.5 (1–2), *Micropsectra* spp. ♀♀ 11 (40.7%)/15 (39.5%), 1.4 (1–3), *Parametriocnemus stylatus* 1 (3.7%)/1 (2.6%), 1.0.

Larvae of *L. glabra* were found from June 1st to September 15th (Fig. 2). The maximum of abundance was the end of June. In August and September only single individuals were found.

Remarks: Host species of *Lebertia glabra* were reported by Efford (1963) and Martin (1998; 2000), the most important hosts were *Micropsectra junci* and *Micropsectra notescens*, respectively. *Lebertia glabra* appears to be host-specific to the genus *Micropsectra*.

Lebertia sefvei Walter, 1911

E3: 41/52 (21), 1.3, *Micropsectra pallidula* (♂♂ + ♀♀) 29 (70.7%)/36 (69.3%), 1.2 (1–3), *M. junci* (♂♂ + ♀♀) 12 (29.3%)/16 (30.8%), 1.3 (1–2), E5: 16/23 (1), 1.4, *Micropsectra* spp. ♀♀ 7 (43.8%)/11 (47.8%), 1.6 (1–3), *M. junci* ♂♂ 6 (37.5%)/7 (30.4%), 1.2 (1–2), *M. longicrista* 1 (6.3%)/3 (13.0%), 3.0, *Tanytarsus heusdensis* 2 (12.5%)/2 (8.7%), 1.0.

In both emergences, larvae were present from April to November (Fig. 2) and absent from the end of July to October. Most larvae in the first period were found at both sites in May. In autumn they were found earlier at E5 (end of September) than in the emergence at E3. At both sites *Micropsectra* spp. is the most important host.

Remarks: Since Gerecke & Martin (2006) only reported the family Chironomidae as hosts of *Lebertia sefvei* from alpine springs, this study presents the first records of host species and/or

genera. Obviously, a preference for *Micropsectra* hosts is developed, similar as in *L. glabra*.

Lebertia stigmatifera Thor, 1900

No larva of *L. stigmatifera* was present in the emergence traps.

Remarks: Lebertia stigmatifera was only recorded as an adult individual in benthic samples at E4 (see Gerecke et al., 2005; Martin, 2006). Lundblad (1924) observed non-parasitic larvae in the development of *L. stigmatifera* but Martin (2000) reported larvae of that species as parasites of the chironomid species *Micropsectra notescens*.

Hygrobatidae Koch, 1842
Hygrobates norvegicus (Thor, 1897)

E3: 68/83 (5), 1.2, *Rheocricotopus effusus* 35 (51.5%)/45 (54.2%) 1.3 (1–3), *Micropsectra pallidula* ♀♀ 11 (16.2%)/15 (18.1%), 1.4 (1–3), *Tanytarsus heusdensis* 10 (14.7%)/10 (12.0%), 1.0, *Brillia bifida* 6 (8.8%)/7 (8.4%), 1.2 (1–2), *M. junci* (♂♂ + ♀♀) 4 (5.9%)/4 (4.8%), 1.0, *Heterotanytarsus apicalis* 1 (1.5%)/1 (1.2%), 1.0, *Rheocricotopus atripes* 1 (1.5%)/1 (1.2%), 1.0, E6: *M. junci* 1/1.

The larva from E1 was found on July 29th. The larvae from E3 were found from the end of April to mid July (Fig. 2). There was a distinct maximum in early May and additionally a single *Hygrobates* larva was found at the beginning of November.

Remarks: Chironomids at family level are already reported as hosts for *Hygrobates norvegicus* by Gerecke & Martin (2006) and some host species of that study were already named by Martin et al. (2002). Some host species were identical in the latter and the present study (e.g. *Rheocricotopus effusus*).

Atractides fonticolus (K.Viets, 1920)

E1: 68/114 (15), 1.7, *Brillia bifida* 17 (25.0%)/36 (31.6%), 2.1 (1–4), *Micropsectra* spp. ♀♀ 13 (19.1%)/19 (16.7%), 1.5 (1–3), *Parametriocnemus stylatus* 15 (22.1%)/17 (14.9%), 1.1 (1–2), *Polypedilum convictum* 1 (1.5%)/13 (11.4%), 13.0, *Corynoneura lobata* 9 (13.2%)/12 (10.5%), 1.3 (1–2), *Micropsectra schrankelae* 8 (11.8%)/11 (9.6%), 1.4 (1–2), *M. attenuata* 3 (4.4%)/3 (2.6%), 1.0, *Orthocladius oblidens* 2 (2.9%)/3 (2.6%), 1.5 (1–2), E7: 58/65 (9), 1.1, *C. lobata* 30 (51.7%)/35 (53.8%), 1.2 (1–2), *Stempellinella* sp.1 9 (15.5%)/9 (13.8%), 1.0, *St. flavidula* 6 (10.3%)/7 (10.8%), 1.2 (1–2), *Stempellinella* spp. ♀♀ 5 (8.6%)/6 (9.2%), 1.2 (1–2),

Heleniella spp. ♀♀ 3 (5.2%)/3 (4.6%), 1.0, *H. ornaticollis* 1 (1.7%)/1 (1.5%), 1.0, *P. stylatus* 1 (1.7%)/1 (1.5%), 1.0, *M. calcifontis* 1 (1.7%)/1 (1.5%), 1.0, *Micropsectra* spp. ♀ 1 (1.7%)/1 (1.5%), 1.0, Tanytarsini indet. 1 (1.7%)/1 (1.5%), 1.0.

Host species were found among the chironomid subfamilies Orthocladiinae and Chironominae (Table 1). The seasonal patterns of *Atractides fonticolus* differ at both collecting sites. At E1 larvae were found from April 6th to October 19th

(Fig. 2). The data on larvae from July 13th is missing and thus there is no distinct maximum of abundance for the first period of the sample season. In the second half of the season a more distinct peak was present at end of September and beginning of October. At E7 larvae were present from April 6th to August 24th (Fig. 2). A peak is not clear but it is remarkable that in E7 *A. fonticolus* did not appear again in autumn as in E1.

Figure 2. Phenology of attached and detached larvae of water mites from different springs in Luxembourg: top: *Lebertia glabra* (E7), *Arrenurus fontinalis* (E3) and *Hygrobates norvegicus* (E3), center: *Lebertia sefvei* (E3, E5, total), bottom: *Atractides fonticolus* (E1, E7, total).

Remarks: No data on the host spectrum of *Atractides fonticolus* has been previously reported. Our results show that *A. fonticolus* has no distinct host specificity, although *Brillia bifida* was the most important host at E1 and *Corynoneura lobata* at E7, respectively.

<center>*Atractides pennatus* (K.Viets, 1920)</center>

E7: *Tvetenia calvescens* 6/6.

The larvae of *A. pennatus* were collected from May 18th to June 29th.

Remarks: The larvae of this taxon were ascribed to *Atractides pennatus* since this is the only species of this genus found in Luxembourg springs until now apart from *A. fonticolus* (see Gerecke et al., 2005. Martin, 2006). A host for *A. pennatus* was previously unknown.

<center>Feltriidae K.Viets, 1926
Feltria rouxi Walter, 1907</center>

E6: *Orthocladius rubicundus* 1/1.

The only larva of *Feltria rouxi* found was in the sample of November 3rd.

Remarks: Feltria rouxi was the only species of the genus found in Luxembourg springs (see Gerecke et al., 2005). That was the reason why Martin (2006) attributed this specimen to *F. rouxi*. For *F. rouxi* chironomid species within the chironomid subfamily Orthocladiinae were reported as hosts by Martin (1998; 2000). Efford (1962; 1963; 1965; 1966) found a high specificity for *Stempellinella flavidula* (subfamily Chironominae).

<center>Pionidae Thor, 1900
Pseudofeltria scourfieldi Soar, 1904</center>

E4: 1 detached larva, E6: Orthocladiinae indet. (♀) 1/4.

At E4, the detached larva was found July 13th, the specimen at site E6 was collected on November 3rd.

Remarks: Martin (2000) reported chironomids as hosts; Smith & Oliver (1976) had already reported the genera *Parametriocnemus* (Orthocladiinae) and *Micropsectra* (Chironominae, Tanytarsini) as hosts for *Pseudofeltria* sp. Thus, this new data supports previous observations.

<center>Pionidae indet. (cf. *Tiphys* Koch, 1836 sp.?)</center>

E7: *Micropsectra notescens* 1/1.

The attached larva of *Tiphys* sp.(?) was collected on June 29th.

Remarks: Martin (2006) attributed this specimen to a pionid larva and near to the genus *Tiphys*. Smith & Oliver (1976) reported chironomids of the subfamilies Orthocladiinae and Chironominae as hosts for *Tiphys* spp.

<center>Aturidae Thor, 1900
Axonopsinae K.Viets, 1929
Ljania bipapillata Thor, 1898</center>

E1: 51/151 3.0, *Brillia bifida* 24 (47.1%)/95 (62.9%), 4.0 (1–21), *Parametriocnemus stylatus* 22 (43.1%)/49 (32.5%), 2.2 (1–8), *Orthocladius oblidens* 4 (7.8%)/6 (4.0%), 1.5 (1–3), *Micropsectra attenuata* 1 (2.0%)/1 (0.7%), 1.0, E3: *Rheocricotopus effusus* 7/8, E5: 153/351 2), 2.3, *B. bifida* 23 (15.0%)/166 (47.3%), 7.2 (1–21), *Stempellinella flavidula* 76 (49.7%)/91 (26.0%), 1.2 (1–3), *P. stylatus* 16 (10.5%)/34 (9.7%), 2.1 (1–6), *R. fuscipes* ♂♂ 11 (7.2%)/20 (5.7%), 1.8 (1–5), *O. oblidens* 16 (10.4%)/21 (5.9%), 1.3 (1–6), *R. atripes* ♂ 1 (0.7%)/8 (2.3%), 8.0, *Orthocladius* sp. 4 (2.6%)/4 (1.1%), 1.0, *Microtendipes tarsalis* 2 (1.3%)/3 (0.9%), 1.5 (1–2), *Rheocricotopus* spp. ♀♀ 3 (2.0%)/3 (0.9%), 1.0, *M. junci* ♂♂ 2 (1.3%)/2 (0.6%), 1.0, *Micropsectra* sp. ♀ 1 (0.7%)/ 1 (0.3%), 1.0, *M. longicrista* 1 (0.7%)/1 (0.3%), 1.0, *R. effusus* 1 (0.7%)/1 (0.3%), 1.0, E7: *P. stylatus* 5/5, *Stempellinella* spp. ♀♀ 3/3, *St. flavidula* 2/2, *Corynoneura* sp. ♀ 1/1, *M. schrankelae* 1/1, Tanytarsini indet. ♀ 1/1.

Different chironomids from the two subfamilies Orthocladiinae and Chironominae were recorded as host species (Table 1). The parasitised hosts at E3 were collected on May 5th and May 18th. At E7 larvae were collected from April to September with the exception of July. The phenology of *Ljania bipapillata* from the two sample sites with numerous larvae was similar (Fig. 3). At E5 mite larvae were present from April 6th to November 3rd in two periods: April to June, and July to November. At E1 larvae were also collected in two distinct periods (April 6th to May 18th and July 27th to October 5th) separated by a lack of larvae from June to the end of July. Only data for July 13th were lacking for that site (see material and methods) and also after that time only a few individuals were collected at E1 (Fig. 3). At E5, the most important host species was *Brillia bifida* parasitised by almost half of the *L. bipapilata* larvae. More than 60% of *L. bipapillata* larvae at E1 were attached to *Brillia bifida*.
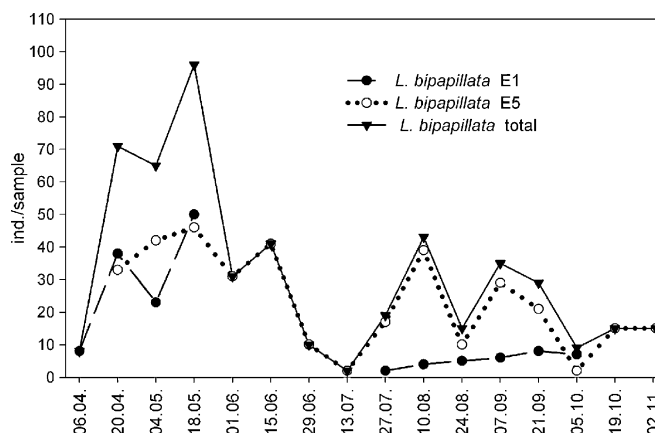
Figure 3. Phenology of attached and detached larvae of *Ljania bipapillata* from sites E1, E5 and totally.

Remarks: Numerous hosts are reported for *Ljania bipapillata* (Efford, 1963; 1966; Ullrich, 1978; Smith, 1984; Martin, 1998; 2000), all being chironomids of the subfamilies Chironominae, Orthocladiinae and Diamesinae. The preference for *Brillia bifida* as host was not only shown in the present study but also in the studies of Martin (1998) and Ullrich (1978). In contrast to these data, *Stempellinella flavidula* was reported by Efford (1963; 1966) as the most important host species for *Ljania bipapillata*.

Mideopsidae Koenike, 1910
Mideopsis willmanni (K.Viets, 1920)

E4: *Micropsectra* sp. ♀ 1/1.

The host specimen with the attached larva of *Mideopsis willmanni* was collected on October 19th.

Remarks: No host species have hitherto been reported. Smith & Oliver (1976) reported different subfamilies of chironomids as hosts for the genus *Mideopsis*.

Arrenuridae Thor, 1900
Arrenurus fontinalis K.Viets, 1920

E1: *Dixa submaculata* 1/1, E3: 15/55 (9), 3.7, *D. dilatata* 7 (46.7%)/22 (40.0%), 3.1 (1–6), *D. submaculata* 8 (53.3%)/33 (60.0%), 4.1 (1–12), E4: *D. submaculata* 1/8.

At E1 and E4 larvae were present on July 7th and August 8th. At E3, *Arrenurus fontinalis* larvae appeared from June 29th to August 10th with a clear maximum of abundance on July 13th (Fig. 2).

Remarks: Martin (2000) reported *Dixa* cf. *dilatata* as a host of *Arrenurus fontinalis*. Meanwhile, larval Dixidae were also found as host for *A. fontinalis* (P. Martin, unpublished data, R. Gerecke, pers. comm.).

Evidence for host preference?

With a few exceptions no difference in the intensity of parasitism was found between the species compared. Four water mites show a different intensity in attachment to different host species: Larvae of *Atractides fonticolus* were attached at a higher intensity to *Brillia bifida* than to *Corynoneura lobata* (**; χ^2-value 12,6279, $p = 0,0055$). The intensity of parasitism by *Ljania bipapillata* larvae was higher for *B. bifida* compared to *Stempellinella flavidula* (***; χ^2-value 60,9973, $p = 0,000$) and *Parametriocnemus stylatus* (**; χ^2-value 11,9466, $p = 0,0076$). Comparing the intensity for the attachment of *L. bipapillata* for *St. flavidula* and *P. stylatus*, a higher intensity for the latter was found (***; χ^2-value 20,8754, $p = 0,0001$).

Are host species parasitised at different intensities by different mites?

In these tests no statistically significant differences in the intensities were found with one exception: *Brillia bifida* was found to be more heavily

parasitised by larvae of *Ljania bipapillata* at E5 than larvae of the same species at E1 (*; χ^2-value 8,39205, $p = 0,0386$).

Is there a preference for a male or female host?

There was no significant difference in the number of larvae attached to males or females, respectively, and no significance of a higher intensity of parasitism in one host sex.

Discussion

Host spectrum and host specificity

The present study confirms the findings of Smith (1991) for different genera of spring living that as a rule, spring living water mites also have a parasitic larval stage. In addition, here for the first time the existence of a parasitic larval stage could be demonstrated in nearly all species of individual springs. The loss of parasitism in water mites, which seems to be a rare phenomenon in general (Smith, 1998), seems also to be an exception for spring-dwelling mites. For the species of the present study, no such case could be observed in the laboratory (Martin, 2006).

As in most studies on the host spectrum of water mites from different habitats (e.g. Martin, 1998 for streams, Smukalla & Meyer, 1988 for lakes), the present investigation showed that chironomids were also the most important hosts in springs (92.4% of the infested host individuals). This underlines the prominence of this insect family which is general valid for water mites (Smith & Oliver, 1986). For ten mite species hosts were previously unknown on species level (*Thyas palustris*, *Sperchon insignis*, *S. longissimus*, *Bandakia concreta*, *Lebertia holsatica*, *L. sefvei*, *Hygrobates norvegicus*, *Atractides fonticolus*, *A. pennatus*, *Mideopsis willmanni*). For an additional nine species the known host spectrum has been confirmed and/or supplemented (*Thyopsis cancellata*, *Sperchonopsis verrucosa*, *Sperchon squamosus*, *S. thienemanni*, *Lebertia glabra*, *Feltria rouxi*, *Pseudofeltria scourfieldi*, *Ljania bipapillata*, *Arrenurus fontinalis*). Regarding the host spectrum on a taxonomic higher level, the parasitism of the

studied mites fits the known observations on their families and genera, respectively (Smith & Oliver, 1986; Smith et al., 2001).

In Stur et al. (2005), for the chironomids of the presently investigated springs the degree of parasitism was reported from the hosts' perspective. Only 7.8% of the emerged chironomids (only males were considered) were parasitised by the mites but for some host species (e.g. *Brillia bifida* or *Rheocricotopus fuscipes*) the prevalence reached >50%. But the range of prevalence depends on various spatiotemporal variables. Also the considerations on the "host specificity" which were discussed here have to be as a first attempt to approach the phenomenon by field data.

Host specificity is e.g. defined as "the extent to which a parasite taxon is restricted in the number of host species" (Poulin, 1998). For most water mites, host specificity is not well investigated at all. Most studies derive the host specificity from field observations and only rarely acceptance or rejections of hosts have been investigated in the laboratory, only exceptionally with dipteran hosts (e.g. Smith & McIver, 1984 for Culicidae). The known host spectrum often reflects a more or less accidental insight into the full and/or true host spectrum. With a few exceptions (see Böttger & Martin, 2003 for a widespread *Arrenurus* species), water mite hosts are only known from one, or few, sample sites. Already Mitchell (1957) noted that "many instances of apparent host specificity could be the result of only one potential host being available in the habitat." Thus host specificity must be regarded at least on two different levels (not to mention spatiotemporal gathering on microhabitat level). Is there a host specificity in the respective habitat or site? Also what about host specificity for the species in general? The last question has to remain unsolved for most of the here observed species since data for the species from different sites are scarce.

In the present study four species (*Thyas palustris*, *Thyopsis cancellata*, *Sperchon insignis* and *Arrenurus fontinalis*) parasitise other than chironomid hosts (Limoniidae, Simuliidae, Dixidae). At the moment, these species seem to be restricted to these host families and seem to reject chironomids as hosts.

For the chironomid parasites the results are less clear. Although in some cases the host spectrum is

similar in general, preferred host species could be different. For example, *Sperchon thienemanni* and *Ljania bipapillata* have several host species together at site E5, but seem to prefer different host species (most *S. thienemanni* were attached to *Stempellinella flavidula*, and most *L. bipapillata* to *Brillia bifida*). Not so clear is the pattern at E1 where the four most abundant mite species have a similar host spectrum: *Atractides fonticolus* and *Ljania bipapillata* larvae were most frequently found as parasites of *Brillia bifida*, *S. thienemanni* was most frequently attached to *Tvetenia calvescens* and *S. longissimus* to *Micropsectra* sp. The presented field data indicate that host preferences differ between the mite species. However, because of the correlative nature of our field data we cannot control for the impact of host availability in time and space and also not for the relative density of mite species in relation to host species.

As a "host specialist" highly host-specific parasites could be seen which are restricted to one host species and the specificity declines as the number of suitable host species increases. The other end of such a parasite spectrum, a parasite that accepts a high number of host species in similar intensities, is called a "host generalist". A clear distinction is rarely possible. If only one single host species was present, a high host specificity could be presumed and the species would appear to be a host specialist. But the findings could also only reflect a specific feature of the habitat, e.g. a generally low host species diversity. Conversely, typical host generalists that have a wide host spectrum (e.g. *Ljania bipapillata* in the present study) could obviously prefer one host species and only exceptionally attach to other hosts.

Among water mites, parasites of chironomids often have a broader host spectrum than parasites of other, less speciose host taxa. But also within chironomid parasites, local host specialists have been recorded. Efford (1963) found a high host specificity of *Feltria rouxi* to one single host species (*Stempellinella flavidula*) in a small lowland stream in England. But from the data presented here and the studies of Martin (2000), *F. rouxi* is now known as a parasite of at least five species. Thus, host spectra (and specificity) can vary from one to another site to a very large extent. In some studies a calculation of the host specificity was attempted

(e.g. Rohde, 1980; Poulin, 1998). Extrapolating to the present results seems to be questionable due to the relatively few observations for one collecting site. However, if the degree of known host species is cautiously estimated, and the distribution to the respective host species prorated, one could roughly arrange some of the species. In Table 2 the number of host species is given and the number of species to which more than 80% of the mite parasites were attached. If only parasites with a single host as host specialists are considered we find solely the rare mite species *Sperchon insignis* parasitising exclusively *Simulium crenobium*. Larvae of *Thyas palustris* and *Lebertia glabra* were also predominately parasites of one host species. For *L. glabra* our findings fit the observations of Efford (1966) who regarded this species as host-specific. At the other end of the spectrum *Ljania bipapillata* (E5), *Sperchon thienemanni*, *Atractides fonticolus* and *Hygrobates norvegicus* had between seven and 10 host species and 80% of the parasites were attached to at least three different species. Thus, these species may be regarded as host generalists. But the example of *Ljania bipapillata* in E1 (a total of four host species and only two preferred host species) shows that the degree of host specificity can vary between sites.

Another aspect of host specificity was raised by Gerecke & Di Sabatino (1996) and addresses the reasons for the high numbers of water mite species strictly limited to spring habitats. These authors suggested that these mites would prefer such hosts, which are also exclusively restricted to spring habitats. Only with such a host preference, could the mites assure a return to their habitat. More euryoecious host species would only accidentally come back to habitats well-suited for e.g. the development of their parasitic mites. In the present study, nearly all mites were demonstrably crenobiont or crenophilous (see Gerecke et al., 2005 and Table 1); exceptions are *Thyopsis cancellata*, *Sperchonopsis verrucosa*, *Sperchon clupeifer*, *Feltria rouxi* and the undetermined larva of Pionidae. Recent studies revealed that spring preference of animals can vary slightly between different geographic areas (Gerecke et al., 2005). A categorisation of the host species was attempted; for chironomids such a ranking was already done by Stur et al. (2005). More than one third of the hosts species belonged to crenophilous species for only

Table 2. Number of host species, host specificity and preferences of the water mites for spring-preferring host species

	Site	Host species	Host species to which >80% of mites were attached	% attached to crenophilous hosts	% attached to non-crenophilous hosts
Sperchon insignis	E7	1	1	100.0	0.0
Arrenurus fontinalis	E3	2	2	100.0	0.0
Lebertia glabra	E7	2	1	96.3	3.7
Sperchon squamosus	E3	3	2	45.7	54.3
Sperchon thienemanni	E1	10	3	39.5	60.5
Atractides fonticolus	E1	7	5	35.3	64.7
Lebertia sefvei	E3	2	2	29.3	70.7
Sperchon squamosus	E2	2	2	26.3	73.7
Atractides fonticolus	E3	7	3	24.1	75.9
Hygrobates norvegicus	E3	7	3	20.6	79.4
Sperchon thienemanni	E5	8	3	16.9	83.1
Lebertia sefvei	E5	3	3	6.3	93.8
Ljania bipapillata	E5	10	3	2.6	97.4
Sperchon longissimus	E1	3	2	2.1	97.9
Ljania bipapillata	E1	4	2	2.0	98.0
Thyas palustris	E3	3	1	0.0	100.0

The abundant mite species were listed for each collection site separately.

six mite species in the Luxembourg springs (Table 2). All hosts of *Sperchon insignis* and *Arrenurus fontinalis* are spring-preferring species. Although these results are only preliminary it is, however, not as simple as the assumption that all crenophilous water mites prefer spring-restricted hosts. Similar results were found by Martin et al. (2002) for alpine springs where also only single species seem to prefer crenophilous hosts. In conclusion, the close relationship to springs attributed by the dependency on spring-bound hosts, could only be observed for a few water mite species. Thus, dependency on crenobiontic hosts is not well suited to be an argument for the crenobiosis of the water mites.

Intensity of parasitism

As a rule, negative consequences of parasitism for the hosts depend on the intensity of parasitism. This has also been demonstrated for water mites and their hosts (Smith, 1988; Weiberg & Edwards, 1997). The decrease e.g. in host's fecundity or longevity in some cases could be compensated for by the production of fewer but fitter offspring (Rolff, 1999), however, it is an open question whether this is the rule. For larval water mites, some general parasitological assumptions have been made based on reviews on parasite-host associations e.g. by Smith & Oliver (1986), Davids (1997), Rolff (2001), Smith et al. (2001). Plesiotypic water mites with terrestrial larvae often produce a lot of offspring but this does not inevitably result in high loads of mites attached to the host. The losses during searching for hosts are quite higher for these larvae than they are for the aquatic larvae of the more derived mites, which often pass through a preparasitic attendance near their later hosts and thus can effort to produce less offspring (Smith & Oliver, 1986). Moreover, the load of the mites attached to a host depends on the host's size and thus on its carrying capacity. Thoracic parasites often show a lower intensity than abdominal parasites do (see Smith & Oliver, 1986; Martin & Stur, 2005). Our presented results for the most abundant species reflect these findings

Table 3. Mean and maximum intensity of parasitism by the water mites

	Mean intensity	Maximum intensity
Thyas palustris	10.8	41
Sperchon longissimus	1.7	6
Sperchon squamosus	1.8	5
Sperchon thienemanni	1.4	4
Lebertia glabra	1.4	3
Lebertia sefvei	1.4	3
Sperchon insignis	1.2	2
Hygrobates norvegicus	1.2	3
Atractides fonticolus	1.4	3
Ljania bipapillata	2.7	21
Arrenurus fontinalis	3.7	12

If a mite species was abundant at more than one site, the results were summarised. Top: species attached to host's thorax, bottom: species attached to host's abdomen.

to a large extent (Table 3). The hydryphantid mite *Thyas palustris*, which belongs to the more plesiotypic mites of the present study and prefer host's thorax as attachment site (see Martin & Stur, 2005), shows both the highest mean intensity (10.8 larvae/host) and the highest maximum intensity (41 larvae/host). The *Sperchon* and *Lebertia* species prefer their host's thorax as attachment sites whereas the other species mostly attach to the host's abdomen (Martin & Stur, 2005). Differences were not great between the *Lebertia* species on thoracic sites and *Hygrobates norvegicus* and *Atractides fonticolus* on abdominal sites. All *Sperchon* species show a higher mean and maximum intensity than the aforementioned species. However, the abdominal attaching *Ljania bipapillata* and *Arrenurus fontinalis* had the expected higher intensity than the *Sperchon* and *Lebertia* species.

The intensity of parasitising water mite larvae often varies between different host species, and a higher intensity in one of two host species could reflect a higher host preference or specificity. Such differences were only seldom significant in this study. In one case one mite species (*Atractides fonticolus*) showed a higher intensity for one host species but only if comparing host species from different sites. This finding indicates a relative high preference for *Brillia bifida*. The results for *Ljania*

bipapillata were more positive since all compared host species came from the same sample site. Larvae of *L. bipapillata* showed a decreasing intensity of parasitism from *Brillia bifida* to *Parametriocnemus stylatus* to *Stempellinella flavidula*.

A preliminary attempt to show different host specificity by field data was to look for different intensity of parasitism of the same host species parasitised by different mite species. These comparisons showed no significant results. Perhaps each host species has a certain number of potential attachment sites, more or less independent of the parasite species. But the intensity of parasitism of *Ljania bipapillata* mites attached to *Brillia bifida* at two different spring sites (E1, E5) varied. This may be seen as an indication that the intensity of parasitism depends on the number of available hosts. For this reason, the interpretation of observed intensity variability should be done cautiously since it might be sample site dependent.

Preferences for host sexes

For a water mite larva the parasitism of a female host could be advantageous because only female hosts reliably return to or near the water for ovipositioning and thus enable the mites a return to water for entering next developmental stages. In general, investigations on sex biased parasitism in water mites show inconsistent results (Smith, 1988). But at least in some cases virtual sex biased parasitism was shown, e.g. for odonates (Lajeunesse et al., 2004) and also for some dipterans (Culicidae: Lanciani, 1988). Our results for chironomid hosts (anyhow the are based only relatively few numbers of individuals) show no evidence for sex biased parasitism by water mites, neither in host sex preference nor in parasite intensities (number of mite larvae per host) of parasitised males and females, respectively. In conclusion, either the mites have not evolved the ability to distinguish host sexes or there is no constraint to such a behaviour because it is no disadvantage to parasitise male hosts. Or, if the likelihood of encountering a female within a reasonable amount of time is low, the mites could not afford to reject male hosts. At least for spring dwelling chironomids no sex biased differences in adult behaviour are known and thus it is

improbable that the parasitised hosts depart far away from their water of origin. However, our results fit the general statement of Smith (1999) that parasite-host associations of water mites, which are characterised by preparasitic attendance usually lack any gender-bias.

Life cycles and seasonality

Water mites often show different seasonality in the occurrence of the parasitic larvae. This was interpreted as a temporal niche separation and thus as a strategy for host partitioning (Lanciani, 1970). Both for standing and running waters such strategies are naturally embedded in differences in the life histories (e.g. Meyer & Schwoerbel, 1981 for a lake, Martin, 1998 for two streams). For lotic water mites life cycles are known only for some stream living water mites and also in these cases larvae show different seasonal patterns (Efford, 1963; 1965; 1966; Ullrich, 1978; Martin, 1998). In the present study, seasonal differences in parasitism between species can be shown for spring dwelling water mites for the first time. There are springtime species occurring early in the year (*Sperchonopsis verrucosa*, *Sperchon squamosus*, *Hygrobates norvegicus*) and species which parasitise in the summer (*Thyas palustris*, *Sperchon longissimus*, *Lebertia glabra*, *Arrenurus fontinalis*). Another group of species shows two peaks of occurrence, one in the springtime and one in late summer and/or autumn (*Sperchon thienemanni*, *Lebertia sefvei*, *Atractides fonticolus*, *Ljania bipapillata*). As previously shown for a stream population of *S. thienemanni*, the second peak reflects a second egg laying event by the females (Martin, 1998). These general seasonal differences for the species are also reflected by the different collecting sites or the emergence traps, respectively. Some species show a consecutive occurrence. Considering only the abundant species, just in E1 the different seasonality has the potential to enable a host partitioning in the mite species *Sperchon longissimus*, *S. thienemanni*, *A. fonticolus* and *Ljania bipapillata*, all parasites of chironomids. But for those species obviously there are also some differences in preferences for specific host species and thus also at that site varying phenology cannot be seen as a sufficient agent for host partitioning.

It is not known how the different appearances of the larvae are connected with the life histories of the water mite species occurring. As found for species in lakes and streams, most of the spring-living species probably also overwinter as deutonymphs or adults. Rearing of water mite larvae from spring habitats in the laboratory is difficult (P. Martin, unpubl. observations), and it is thus unclear whether or not some species are able to overwinter as fully developed larvae in their clutch envelopes as for instance seen in the stream living species *Atractides nodipalpis* (Martin, 1998). The complete life histories of spring-dwelling water mite species can best be analysed when parallel benthic and emergence samples are taken throughout the year.

Conclusions and perspectives

As a rule, springs are seen as habitats often with low species diversity and relatively simple species interactions, and are thus well-suited as outdoor laboratories (Williams & Williams, 1998). On the other hand, in springs, water mites and chironomids and other dipterans are nevertheless relatively species-rich, both in species numbers and in abundances (Lindegaard, 1995; Fischer & Schnabel, 1995; Di Sabatino et al., 2003). In future spring investigations, where emergence collections in individual sites also to be made, parasite-host associations deserve more attention.

Our previous results on parasite-host associations from the Luxembourg springs are ambiguous with respect to host partitioning. There are prerequisites for host partitioning in attachment sites (Martin & Stur, 2005), host spectrum and specificity as well as in different phenologies (this study) but indications for a realised resource partitioning are scarce. The prevalence of parasitism is generally low (e.g. 35% of the chironomid species and 5% of the individuals; see Stur et al., 2005) and thus the interspecific competition is low at the observed sites.

In conclusion, due to their relative low diversity, single springs are excellent habitats to make progress in the fields of larval morphology and host spectra of water mites but not for an investigation of host partitioning strategies. Conversely, the proved evidence of low interspecific competition for larval water mites in spring habitats could be at least one of the reasons for the high number of water mite

species, which are strictly confined to springs. Food resources are also probably not limited for the mites in springs since most of them prey on the abundant chironomid larvae (Martin, 2005).

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