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Guild structure in water mites (*Unionicola* spp.) inhabiting freshwater mussels: choice, competitive exclusion and sex

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Summary. Unionicolid water mites inhabit freshwater unionid mussels during the nymphal and adult stages of their life-cycle. Regular sampling of mussels from two sites in St. Mark's River, Fl. established that each of four species of water mite (*Unionicola abnormipes*, *U. fossulata*, *U. serrata* and *U. formosa*) occurred mainly in one or two of the mussel species available at each site.

The role of preference for particular mussel species during host location was assessed for the first three mite species by choice experiments, in which mites were offered different mussel species simultaneously. In five out of six experiments, mites entered normally unused mussels as often as they did normally used ones. Additionally, a sexual difference in choice was found for *U. fossulata*, with males preferring one mussel species and females showing no preference. One mussel species, (*Anodonta imbecilis*), normally unused but chosen by mite species during the lab. experiments, is inhabited exclusively by the fourth mite species, *U. formosa*, in the field. An experiment showed that *U. formosa* excludes other mite species aggressively from *Anodonta imbecilis*.

The results illustrate the sometimes misleading nature of simple sampling data as an indication of host specificity or host preference in parasites. They suggest also that the population dynamics of some parasites might be more fruitfully compared to unrelated, free-living species than to other parasites.

Key **words:** Competition – Bivalvia – Host-selection – Parasites – *Unionicola*

Parasites vary greatly in the number of hosts they use. Monogeneans are often found only on a single species of fish (Kearn 1973; MacDonald 1975) while ectoparasitic arthropods may be found on a great many different species (Noble and Noble 1976). Why are some parasites so highly host specific and what factors are responsible for this restriction?

Neither question – proximate or ultimate – can be answered for the majority of parasites because available data are mainly counts of parasites found in samples of hosts taken at one or a few times or places. These data do not reveal those parasites that failed to colonize hosts nor those that died after colonization but before sampling. Additionally, high abundance is not necessarily an indication of a highly suitable host (e.g. Holmes 1976).

An analogy is the distinction, in marine benthic ecology, between initial settlement of planktonic larvae and post-settlement mortality. Counts of visible adults can not distinguish between these two events and may suggest erroneous ideas about what controls the distribution and abundance of species (see Connell (1985) for a recent review).

This distinction between initial settlement and post-settlement events is critical to distinguishing between competing hypotheses of parasite population dynamics, especially those explaining apparent high host-specificity. Holmes (1973) regards competitive exclusion between parasites as a common explanation for restriction to particular hosts. Events prior to this, such as differential mortality, differential dispersal abilities or host availability, are not considered. Moreover, the evidence is based on counts of parasites, and a reduction in the number of observed concurrent infections from that expected based on the number of individual infections with each parasitic species.

Halvorsen (1976) reviewed the experimental evidence for competitive exclusion but only two studies were not demonstrated in laboratory or domesticated animals (e.g. Wilson 1916; Paperna 1964). Other evidence comes from antagonistic interactions between larval digeneans (Li and Heyneman 1972) but overall, including more recent work (Holland 1984; Scott and Robinson 1984; Dobson 1985; Millott and Cox 1985), direct experimental evidence for competitive exclusion is rare.

An alternative view is that restriction to particular hosts is caused by highly specific methods of host location. Many parasites have only one or two individuals per host so high host specificity, together with site selectivity, increases the probability of sexual over asexual reproduction (Rohde 1979). High host specificity is a consequence of preference for particular hosts during host location regardless of the presence of other parasitic species.

A different view is that parasite populations are always fluctuating greatly because of the patchiness in time and space of host availabilities. The majority of parasites die before locating hosts so that colonization of any one host species is very low and parasite population dynamics are affected most by events prior to colonization (Price 1980). There are many ways in which hosts can vary in availability such as differential habitat selection or differential suscepti-

bility to invasion by parasites (see Whitfield 1979; Rohde 1982). Little of this evidence comes from experimental tests of such hypotheses.

Finally, parasites' occurrences in hosts may be affected most strongly by post-colonization events other than interspecific competition. These include unsuitable environments within hosts (e.g. Bober and Dick 1983), genetically less susceptible hosts (e.g. Wilson 1982) and immune or other reactions by the host (Wakelin 1976; Minchella 1985).

As yet, there are insufficient data to determine which of these models might be more correct for particular groups of parasites.

Study animals and questions

One family of water mites (Unionicolidae, Hydrachnellae, Acari) parasitizes freshwater bivalves (Unionidae, Bivalvia). The four mite species studied here were *U. abnormipes* (Wolcott), *U. serrata* (Wolcott), *U. fossulata* (Koenike) and *U. formosa* (Dana and Whelpley).

These mites have been recorded from a variety of unionid hosts (Vidrine 1980) excepting *U. formosa*, which parasitizes mainly *Anodonta imbecilis* and *Anodonta cataracta*[1] and selects *Anodonta* in preference to other mussels (LaRochelle and Dimock 1981). The number of female *U. formosa* per host varies. One male occurs in each mussel and it kills any conspecific males entering its mussel (Dimock 1983).

Life cycles are similar for all four mites (Mitchell 1955), with females laying eggs within the host's tissue. These produce larvae that leave the host (Jones and Baker 1984) but return to a mussel later to ecdyse into a nymph. Both nymphs and adults inhabit mussels and probably feed on mucous and digestive cells produced by the host (Baker 1977).

In this paper I describe the distribution and relative abundance of four mites in five mussels at two sites in St. Mark's River, Fl. I tested experimentally whether higher relative abundances in some mussels are caused by innate host preferences of mites during host location and whether absence of mite species, in one case, is caused by aggressive interspecific interactions.

Materials and methods

Study sites and sampling procedure

Mussels were collected from two study sites in the St. Mark's River, Leon County, Florida. These were the intersection of the river with Federal Highway 27 (30° 24′, 84° 7′) and downstream at Natural Bridge Historic Site (30° 17′, 84° 8′). At Route 27, water depth directly under the bridge is about 2 m maximum but varies greatly with season. The substratum is coarse sand overlain with fine silt. Current is variable with some areas beneath the bridge entirely stagnant. The mussel species collected were *Uniomerus declivis*, *Villosa villosa* and *Anodonta imbecilis*.

At Natural Bridge, the river is wider with less seasonal variability in flow and depth. The substratum is fine silt with a thick covering of decaying leaves. The water is turbid because of high amounts of suspended sediment. Mussel species collected here were *Villosa vibex* and *Elliptio icterina*.

Mussels were sampled monthly at both sites using a scoop, composed of a mesh box with a long handle, and by hand. Sampling by hand allows mussels well under the surface sediment to be collected. Mussels were placed in separate plastic Zip-Loc™ bags with a small amount of water and transported back to the lab in buckets. They were held in small containers provided with well-aerated water and sediment until examined for mites, generally within three to four days. At least seven individuals of each species were collected except in months where fast currents prevented efficient sampling.

The length and height of each bivalve was measured with calipers. Length was taken as the greatest distance from anterior to posterior. Height was measured from the top of the umbo to the ventral margin perpendicularly to the measurement used for length.

To collect mites without killing mussels, a dull knife blade was inserted between the valves and used to lever them apart slightly. A bulldog clip was inserted and used to open the valves to their fullest extent without causing internal damage or destroying the shell's margins. A cork of suitable width was jammed between the valves to keep them open. Submerged in water and with high intensity light, all mites within the mussel can be located and removed by sucking them up with a hand-held pipette or by gently flushing the mussel with water. All parts of the mussel's interior may be observed directly except for anterio-dorsal regions in larger individuals. Flushing with water was used in these individuals. Mites were identified and sexed with a Wild binocular microscope and notes taken on reproductive condition of females.

For each species of mite the data were analysed with a one-way analysis of covariance. This determined whether mite abundances differed significantly in different mussel species, and whether size of mussels had an effect on numbers present. Temporal variation was not assessed owing to very different monthly sample sizes. Separate analyses were done for nymphs.

Data were log-transformed but variances were still significantly heterogeneous in some cases. However analysis of variance may be used with heterogeneous variances

Table 1. Summary of laboratory choice experiments. The table shows the mussel in which each mite species occurs most commonly and the mussels offered simultaneously as hosts in two choice experiments

MITE SPECIES	*HOSTS USED*	*HOSTS OFFERED*	
		FIRST	SECOND
U. abnormipes	*V. villosa*	*U. declivis* *V. villosa* *V. vibex*	*V. villosa* *A. imbecilis*
U. fossulata	*V. villosa* *U. declivis*	*U. declivis* *V. villosa*	*V. vibex* *E. icterina*
U. serrata	*U. declivis*	*U. declivis* *V. villosa*	*U. declivis* *A. imbecilis*
U. formosa	*A. imbecilis*	–	–

1 There are nine species discussed in this paper. For clarity, mite species' names are written with the initial only for genus. Mussel species' names are written in full

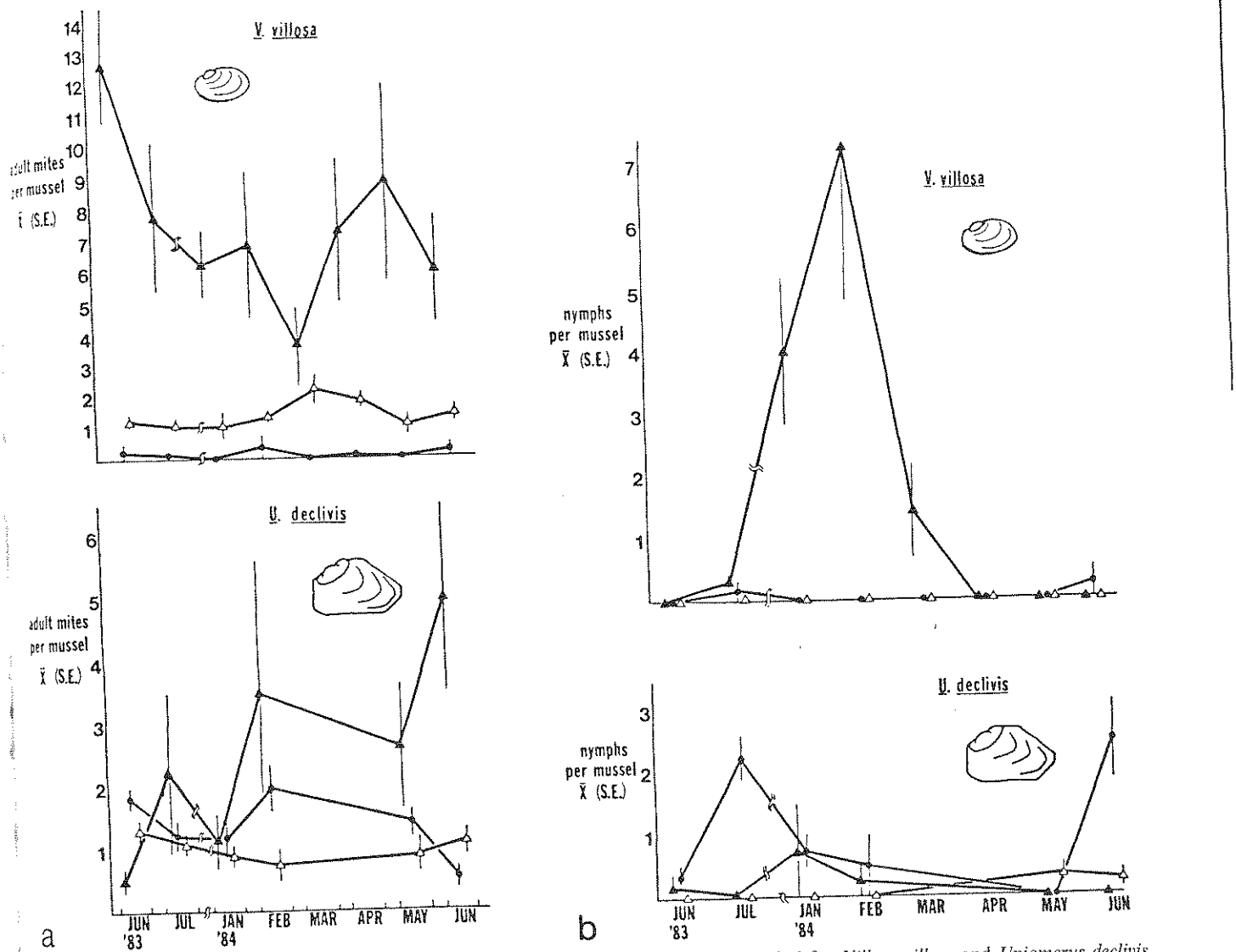

Fig. 1.a,b Mean and standard error of numbers of mites per mussel for each sampling period for *Villosa villosa* and *Uniomerus declivis*. Closed triangles = *U. abnormipes*; Open triangles = *U. fossulata*; Closed circles = *U. serrata*. Note that graphs are uncorrected for relative abundance of each mussel species. **a** adults; **b** nymphs

especially if F-values are very large and the larger variances are not from much smaller sample sizes (Winer 1971).

Relative abundance of mussel species

The numbers of mussels in 1/4 m^2 quadrats were counted at the upstream site on 29 vi 83 and 22 vii 83. Quadrats were placed randomly throughout the collecting site. Each quadrat was sampled to a depth of approximately 10 cm to collect mussels buried in the sediment.

A quadrat could not be used at the downstream site owing to dense aquatic vegetation. An estimate of relative abundance was obtained by collecting all mussels sampled with the scoop during the first 3 sampling periods.

Host choice experiments

Mussels used in these experiments were kept in water tables. They were provided with sediment from the St Mark's River, well-aerated water and fed Invertebrate Diet™ every 2 to 3 days. A partial water change was done approximately twice weekly using only well-water.

Each of the host-choice experiments followed the same general procedure. Two mussels of different species, from which all mites had been removed, were placed within circular arenas, 15.2 cm in diameter and 12.7 cm in height. An exception to this is the first experiment done on *U. abnormipes*, in which 3 mussels were offered and arenas were 20 cm in diameter. Mussels were placed diametrically opposite and facing one another. Each arena contained well-water and sand and sediment taken from the St. Mark's River. I allowed time for the mussels to begin siphoning; a single mite was placed in the centre of each arena and allowed to enter one of the mussels. Experiments were run at 20° C and with dim overhead lighting, except for the first experiment with *U. abnormipes*, in which water temperatures ranged from 25–28° C. Positions of mussels within arenas were randomized by use of a random number table. For brevity, a summary of specific experiments done for each species is given in Table 1.

Interspecific Interactions

Anodonta imbecilis were collected from the field and assigned randomly to 2 treatments. In the first treatment all *U. formosa*, (see Table 1), were removed from each mussel and a single *U. abnormipes* placed on the gills before allowing the mussel to close. In the second treatment the method of mite removal was mimicked but no *U. formosa* were removed, and a single *U. abnormipes* was placed on the gills.

Each *Anodonta imbecilis* was placed in an arena under the same conditions as the host-choice experiments and with a single uninhabited *Uniomerus declivis*. The experiment was left for 4 days before each *Anodonta imbecilis* was reopened and the presence or absence of *U. abnormipes* noted.

Results

Abundance of mites in mussels

Four of the five mussel species are parasitized by one or more mite species. The unparasitized mussel is *Elliptio icterina*. Of the 39 individuals collected only two contained mites – a single *U. abnormipes* in one and a single *U. fossulata* in the other.

Uniomerus declivis, *Villosa villosa* and *Villosa vibex* commonly contained more than a single species of mite. In *Villosa villosa*, 4% had no mites, 17% had one species, 71% had two species and 8% had three. The complementary figures for *Uniomerus declivis* are 1%, 21%, 43% and 35%. For clarity, the distribution of each mite species is discussed separately.

U. abnormipes. This species occurs at both sites in *Uniomerus declivis*, *Villosa villosa* and *Villosa vibex* (Figs. 1 and 2). Both nymphs and adults are most abundant in *Villosa villosa* (Table 2). Larger mussels have significantly greater numbers of mites – length explains 17% of the variance for adults and 4% for nymphs. Numbers of mites per host was variable and differed for *Uniomerus declivis* and *Villosa villosa* (Fig. 3). Many more *Uniomerus declivis* contained no mites of this species.

U. formosa. This mite was found only in *Anodonta imbecilis*. Because this mussel was found only directly beneath the bridge it was not collected on a regular basis. Amalgamation of small samples produces a mean of 11.7 *U. formosa* (s.d. = 11.06, $n = 45$, range = 0–50).

U. fossulata. This species occurs at the upstream site, in *Villosa villosa* and *Uniomerus declivis*, and downstream in *Villosa vibex* (Figs. 1 and 2). Slopes of the regression of number of adult mites on mussel length were heterogeneous among mussel species ($F = 5.05$, $p = 0.008$) so adults in *Villosa vibex* were analysed separately. No analysis was done for nymphs because of low numbers.

For the upstream mussel species, larger mussels do not have significantly more mites in them than do smaller ones (Table 3a) and there is no difference in numbers recorded from the two species. The maximum number of mites per mussel was three, which is significantly different from a Poisson distribution ($p < 0.05$) (Fig. 4a).

Downstream, for *Villosa vibex*, small mussels do contain this mite less often (Table 3b).

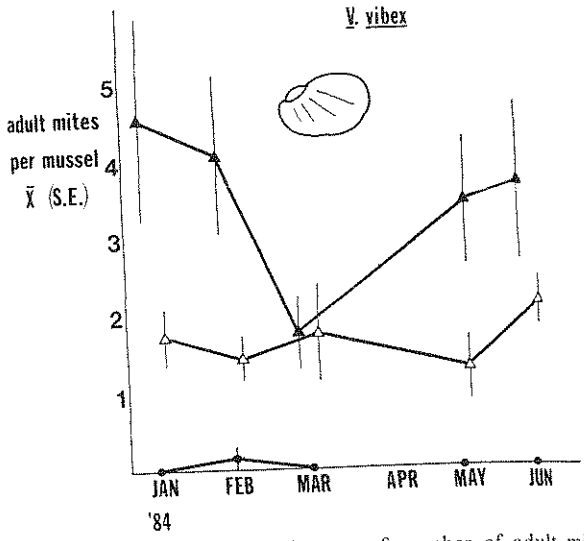

Fig. 2. Mean and standard error of number of adult mites per mussel for each sampling period for *Villosa vibex*. Symbols as for Fig. 1

Table 2. Analysis of covariance for **a** adult and **b** nymphal *U. abnormipes* found in *Uniomerus declivis*, *Villosa villosa* and *Villosa vibex*

SOURCE	*DF*	*SS*	*MS*	*F*
a ADULTS				
Mussel Length	1	5.32	5.32	49.95***
Mussel Species	2	9.67	4.83	45.37***
Error	153	16.30	0.11	
		$\beta = 0.496$		
		$R^2 = 0.17$		
b NYMPHS				
Mussel Length	1	4.66	4.66	7.37**
Mussel Species	2	21.61	10.81	17.10***
Error	153	96.71	0.63	
		$\beta = 0.214$		
		$R^2 = 0.04$		

U. serrata. Adults of this species occur upstream mainly in *Uniomerus declivis* with virtually none in *Villosa villosa* (Fig. 1). There is a significant effect caused by size of mussel but it explains only 2% of the variance (Table 4a). This species was found downstream only rarely (Fig. 2).

For nymphs there is no effect of size of mussel (Table 4b), but they show a similar pattern to adults in occurring significantly more often in *Uniomerus declivis* than in either species of *Villosa*. Again, no individuals were found in *Anodonta imbecilis*. The largest number of individuals found per host was four (Fig. 4b).

The mussel species in which each mite species occurs most commonly is repeated in Table 1.

Relative abundance of mussel species

Quadrats from both dates were combined for a total sample size of 71. The mean number of *Uniomerus declivis* was 0.89/1/4 m^2 (s.d. = 1.65, range 0–7), of *Villosa villosa* was

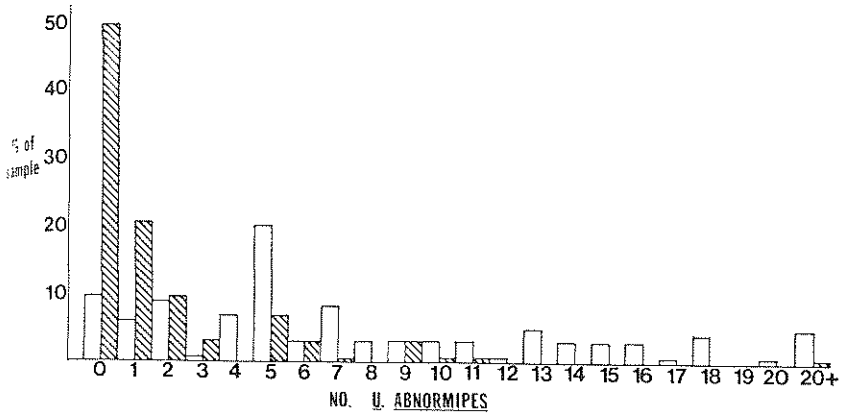

Fig. 3. Frequency distribution of numbers of adult *U. abnormipes* in *Villosa villosa* (open bars) and *Uniomerus declivis* (hatched bars) for total sample. $N = 75$ for *V. villosa* and 68 for *U. declivis*

Table 3. Analysis of covariance for adult *U. fossulata* occurring within **a** *Uniomerus declivis* and *Villosa villosa* and **b** *Villosa vibex*

SOURCE	DF	SS	MS	F
a				
Mussel Length	1	0.03	0.03	0.04 ns
Mussel Species	1	2.04	2.04	3.08 ns
Error	108	71.63	0.66	
b				
Mussel Length	1	9.23	9.23	7.54**
Error	44	53.92	1.23	
		$\beta = 0.382$		
		$R^2 = 0.15$		

Table 4. Analysis of covariance for **a** adult and **b** nymphal *U. serrata* occurring in *Uniomerus declivis* and *Villosa villosa*

SOURCE	DF	SS	MS	F
a ADULTS				
Mussel Length	1	2.33	2.33	5.28*
Mussel Species	2	24.43	12.21	27.68***
Error	153	67.53	0.44	
		$\beta = 0.183$		
		$R^2 = 0.02$		
b NYMPHS				
Mussel Length	1	0.67	0.67	1.15 ns
Mussel Species	2	20.90	10.45	17.94***
Error	153	89.13	0.58	

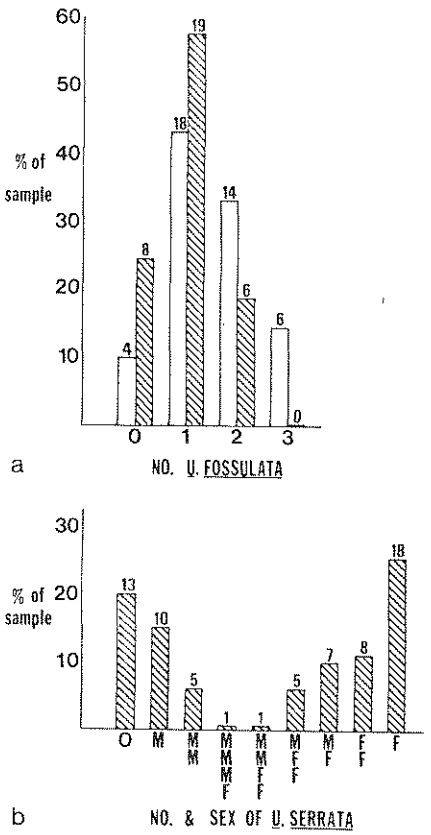

Fig. 4.a,b Frequency distribution of number of mites per mussel for **a** *U. fossulata* and **b** *U. serrata* in *Villosa villosa* (open bars) and *Uniomerus declivis* (hatched bars). Actual sample sizes are given above bars. Sex of individuals is indicated also for *U. serrata*

10/1/4 m^2 (s.d. = 0.34, range 0–2) and *Anodonta imbecilis* 06 per 1/4 m^2 (s.d. = 0.29, range 0–2).

For the downstream site, 30 *Villosa vibex* and 23 *Elliptio erina* were collected by random sampling during the Jan. Mar. '84 sampling periods, suggesting a relative abundance at this site of approximately 1:1.3.

Host choice experiments

abnormipes. Experiments were run for 24 h. This was sufficient time for almost all individuals to enter a mussel. Each replicate of the first experiment was observed until the mite had entered a mussel. This species swims well off the substratum, and enters by way of the incurrent siphon. Three mites were observed to be sucked in by the current, but the rest walked along the mantle's edge and then entered voluntarily.

The first experiment (Table 5) found no effect on choice due to sex or origin of mite. Origin is the species of mussel from which the mite had been removed originally. Such past history can influence choice of host in parasites (e.g. Boxshall 1976).

When the table is collapsed across sex and origin, no preference for any one species of mussel can be detected ($X_1^2 = 0.813$ ns).

In the second experiment (Table 6) there is again no

Table 5. Data from the first host choice experiment with *U. abnormipes* together with analysis by fitting log-linear models (Sokal and Rohlf 1981; Fingleton 1984)

ORIGIN	SEX	CHOICE			
		U. declivis	*V.villosa*	*V.vibex*	
U. declivis	M	8	5	9	22
	F	10	5	6	21
U. villosa	M	9	10	6	25
	F	7	7	9	23
		34	27	30	91

SOURCE	DF	G	DELTA G DF	G
Sex by Origin	4	3.55 ns	2	1.67 ns
Sex by Choice	4	2.11 ns	2	0.28 ns
Origin by Choice	3	1.88 ns	1	0.0005 ns
Sex by Origin by Choice	2	1.88 ns		

Simultaneous Test:
Sex by Origin = Sex by Choice = Origin by Choice = 0
$G = 3.79$ ns

Table 6. Data from second host choice experiment with *U. abnormipes*

CHOICE	SEX		
	MALE	FEMALE	
A. imbecilis	7	11	18
V. villosa	6	9	15
	13	20	33
		$G = 0.006$ ns	
		$X^2_1 = 0.273$ ns	

Table7. Data from first host choice experiment with *U. fossulata*

CHOICE	SEX		
	MALE	FEMALE	
V. villosa	4	11	15
U. declivis	23	15	38
	27	26	53
		$G = 5.07$*	
		G(adj.) = 4.89*	

difference in choice between the sexes, and no detectable difference in the numbers entering *Anodonta imbecilis* as opposed to *Villosa villosa* ($X^2_1 = 0.273$ ns).

U. fossulata. Host-choice experiments for this species were run also for 24 hours to allow the majority of mites to enter mussels. Location is achieved by walking over the substratum until a mussel is contacted, and entry achieved by walking through the incurrent siphon. Mites were sometimes unsuccessful in gaining entry when they touched the sensory tendrils surrounding the siphon causing mussels to close the valves abruptly and blow mites away. Because

Table 8. Data from **a** first and **b** second host choice experiments with *U. serrata*

CHOICE	SEX		
	MALE	FEMALE	
a			
V. villosa	8	19	27
U. declivis	15	25	40
	23	44	67
		$G = 0.45$ns	
		$X^2_1 = 2.52$ns	
b			
A. imbecilis	5	9	14
U. declivis	6	15	21
	11	24	35
		$G = 0.20$ns	
		$X^2_1 = 1.40$ns	

Table 9. Data from experiment testing for competitive interactions between *U. formosa* and *U. abnormipes*

U. formosa	*U. abnormipes*		
	In *A. imbecilis*	Not In *A. imbecilis*	
PRESENT	4	29	33
ABSENT	12	1	13
	16	30	46
		$G = 28.02$***	

successful location and entry took hours in this species, individuals were not observed until successful entry.

A significant difference was found between the choices of males and females in the first experiment (Table 7). Males chose *Uniomerus declivis* more often than they did *Villosa villosa*, while females chose these species about equally often.

No attempt was made to test for sexual differences in choice in the second experiment. Of 17 individuals used (9 females and 8 males), 13 were found in *Villosa vibex* and 4 in *Elliptio icterina*, a statistically significantly difference ($X^2_1 = 4.77$*).

U. serrata. These experiments required three days time for the majority of mites to be found within mussels. This species is similar to *U. fossulata* in that movement was mainly by walking over the substratum and mites were sometimes blown away by mussels. Again, exact times to locate and enter mussels are unknown.

No differences between the sexes in choice was found for the first experiment (Table 8a), and no statistically significant preference found for *Uniomerus declivis*. It is possible that significantly more mites might enter *Uniomerus declivis* with a larger sample size, but it would still be a rather weak preference.

Because this result was so different from the distribution of this mite in the field, the experiment was repeated using nymphs to see whether they determine the location of adults. Of 22 replicates, 13 were found in *Villosa villosa* and

in *Uniomerus declivis*, which is an insignificant difference ($\chi^2_1 = 0.727$ ns).

In the final experiment, no effect of sex on choice was detected, and mites entered *Anodonta imbecilis* about as often as they did *Uniomerus declivis* (Table 8b).

Interspecific interactions

The presence of *U. formosa* had a very strong effect on whether *U. abnormipes* were relocated within *Anodonta imbecilis* (Table 9). Of the 29 *U. abnormipes* not in *Anodonta imbecilis* when *U. formosa* were present, 8 were relocated within the *Uniomerus declivis* provided. The remaining 21 mites could not be relocated despite intensive searching of the arenas.

Discussion

I found higher relative abundances of mites in one or two mussel species of those available. These higher relative abundance patterns can be divided into three general types:

(1) A total absence of particular mites: *Elliptio icterina* was unparasitized, and *Anodonta imbecilis* was parasitized exclusively by *U. formosa*, which in turn lived nowhere else.

(2) Mites found in highest abundance in an uncommon mussel: *U. abnormipes* were found in highest abundance in the less common mussel, *Villosa villosa*.

(3) Those mites occurring in about the same relative abundance as those of their hosts: *U. fossulata* and *U. serrata*.

The samples revealed also that the density of mites per mussel differed for each mite species and sometimes in different hosts. *U. abnormipes* attains high numbers per host and does so mostly in *Villosa villosa*. *U. fossulata* have no more than three mites per host. Recent data (Downes, unpub. data) confirm that this represents a maximum of two females and one male per mussel as has been reported elsewhere (Mitchell 1965). *U. serrata* also have relatively low numbers per host.

Of the three patterns described, the first can be explained by the preferences and aggressive interaction between mite species. The lack of mites in *Elliptio icterina* is clearly because this is an unsuitable host. Although the relevant choice experiment was not done for *U. abnormipes*, the dispersal ability of this mite (Downes, in prep.) together with the overlapping distributions and roughly equivalent abundances of the two mussels, make it likely that this mite can locate *Elliptio icterina* in the field. Since *U. fossulata* will respond to mantle-water taken from *Elliptio icterina* (Downes, in prep.) it is probably attracted to this mussel but conditions within it are somehow unsuitable.

Absence of mite species other than *U. formosa* in *A. imbecilis* is almost certainly due to aggressive behaviour by *U. formosa*. Although this experiment was done only for *U. abnormipes*, some data from another river system suggest *U. formosa* may be aggressive generally. Lake Talquin, an artificial lake produced by the damming of the Ocklochonee River in Florida, had large numbers of *Anodonta imbecilis* and closely related *Anodonta peggyae* before it was drained in 1983. Samples taken in February 1983 and April 1983 showed both mussel species were parasitized by *U. formosa* and another much smaller species, *U. wolcotti*. High numbers of *U. formosa* within a mussel were never found with high numbers of *U. wolcotti*, and *vice versa* (Fig. 5). The evidence to date suggest that *U. formosa* at least were excluding *U. wolcotti* at higher densities. It is unknown whether many *U. wolcotti* are able to exclude *U. formosa*. Draining of the lake caused greater than 90% mortality of mussels before experiments could be done.

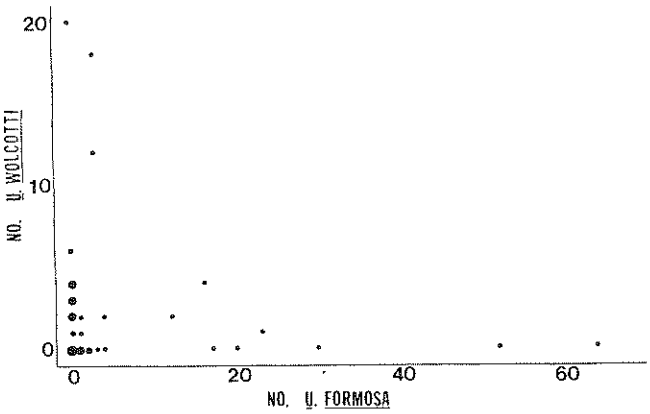

Fig. 5. Number of *U. formosa* and *U. wolcotti* in each *Anodonta imbecilis* and *Anodonta peggyae* collected from Lake Talquin. Size of dot indicates relative number of points at those coordinates. N = 55

For the remaining patterns one possibility not yet discussed is that the distribution of adults is determined primarily by selectivity of nymphs, which then remain in the same host even after metamorphosis. This can be rejected for *U. serrata* since nymphs are demonstrably not selective. However, adults of all three species do move and select hosts in the field (Downes, unpub. data) so choice experiments should detect preference for particular mussel species.

An interesting possibility is that interactions between *U. abnormipes* and *U. serrata* result in reduced numbers of the former in *Uniomerus declivis* and none of the latter in *Villosa villosa*. Hypothetically, the interactions might occur because of potential overlap in egg-laying site. Each water mite species lays its eggs in specific tissues of the mussel. *U. abnormipes* and *U. serrata* both lay their eggs in the mantle (Mitchell 1955; Vidrine 1983). Also, the location of *U. serrata* females inside mussels in the first host choice experiment differed for each mussel species. Fourteen of 15 females in *Villosa villosa* were located on the edge of the mantle whereas only 5 of 13 individuals were found there in *Uniomerus declivis*. The remaining females were located on the labial palps. This is a significant difference ($G = 10.49$, $p < 0.001$). This suggests that females might use *Villosa villosa* just as places in which to lay eggs, but that *Uniomerus declivis* is used for other functions such as location of mates.

Other possibilities are that mussel species differ in habitat selection or behaviour and that this alters their relative availability to mites. Any differences in habitat selected by mussel species are certainly subtle. One possibility is that mussels may select sites by how fast the water current is directly over the substratum, since the presence of logs or rocks can make a large difference to local current velocities (Vogel 1981). Mites may also be affected by slight differences in current velocity.

Behaviourally, mussels could exclude mites by spending less time siphoning, since a mussel that has its valves shut is unavailable to mites. However, since all mites enter mus-

sels the same way, any difference in siphoning time ought to affect all mite species. One possibility is a temporal synchronicity where a mite species searches only for hosts at a time when only a particular mussel species siphons. There was no evidence of this during choice experiments because all mussel species began siphoning generally within 15–20 min of being placed in arenas.

Finally, the occurrence of *U. serrata* in *Uniomerus declivis* only might be explicable just on the basis of relative abundance of mussels. However, a more recent estimate of mussel densities suggests that *Villosa villosa* is more abundant than first thought (density = 0.50/1/4 m^2, 11 vi 1985). The almost total absence of *U. serrata* from this mussel is unlikely to be simply because of the lower numbers of hosts available.

In this system, interactions between conspecifics seem potentially to be important too. The sexual difference in choice found for *U. fossulata*, together with a sexual difference in host location behaviour (Downes, unpublished work) suggest that the behaviour of males during host location might depend more upon the presence of females than just the presence of mussels *per se*. Also, more mites can be found in larger mussels. There are two possible explanations for this. First, larger mussels may be easier to locate. Possibly, larger mussels have a stronger excurrent stream that is more easily detected by mites. Second, mites may reside in mussels only up to a maximum density so that larger mussels can accommodate more mites.

Both factors may be operating. Both *U. fossulata* (Table 4b) and *U. serrata* (Table 5a) occur less in small mussels in some circumstances. The proportion of the variance explained is very small showing that it is a relatively weak effect. *U. abnormipes* are affected by the size of mussels during both nymphal and adult stages but the variance explained is less for nymphs than it is for adults. If it is assumed that nymphs and adults search for mussels equally effectively, the greater R^2 value for adults may reflect interactions between individuals within the same mussel. Maximum numbers per host are not set and occasionally reach large values (Fig. 3).

Overall, these results illustrate how interpreting host preference or host specificity from sampling data can be misleading. A better understanding of the causes and consequences of variation in host specificity will be hard to reach in the absence of experiments.

Additionally, the population dynamics of the parasites in this system are probably more akin to those of some free-living animals using highly patchy resources. The high percentage of mussels parasitized, the common joint occurrence of different mite species in one host and the high rates of recruitment to mussels are all unusual characteristics. Other parasites often occur on only a small proportion of the host population and mixed infections tend to be uncommon. In general, comparisons of population dynamics of parasites across widely different life cycles and taxonomic groups are probably not very useful, and seem mainly responsible for the perceived differences in viewpoints discussed earlier.

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