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Competitive Exclusion, Harem Behaviour and Host Specificity of the Water Mite *Unionicola ypsilophora* (Hydrachnellae, Acari) Inhabiting *Anodonta cygnea* (Unionidae)

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Abstract

The co-occurring freshwater mussels *Anodonta cygnea* and *A. anatina* serve as hosts for the water mites *Unionicola ypsilophora* and *U. intermedia*, respectively. Male *U. ypsilophora* display a territorial behaviour. They fight with other males, and as a result, there is usually only one male per host. As a consequence, this intrasexual aggression results in female-defence polygyny, or a harem mating system. In contrast, *U. intermedia* shows no antagonistic behaviour between males. *A. cygnea* can serve as a host for *U. intermedia*, but this mite species apparently is excluded from the mussel by *U. ypsilophora*. In this way, *U. intermedia* is restricted by competitive exclusion to the mussel *A. anatina*.

1. Introduction

The cosmopolitan water mite genus *Unionicola* includes species whose life cycles involve a mollusc or a poriferan host. Some species are associated with a host throughout their entire post-larval life; others utilize a mollusc or sponge only to undergo metamorphosis (MITCHELL and PITCHFORD 1953, BÖTTGER 1972, HEVERS 1980; DAVIDS *et al.* 1985). Those species which are permanently associated with a molluscan host presumably feed on host tissue (BAKER 1977) or on materials entering the mussel's mantle cavity.

Host specificity is indicated for a number of European mussel-mite species, e.g., *Unionicola intermedia* (KOENIKE) and *U. ypsilophora* (BONZ) in *Anodonta anatina* (L.) and *A. cygnea* (L.), respectively (MITCHELL and PITCHFORD 1953). *U. intermedia* is occasionally found in *A. cygnea* (DAVIDS 1973). The larvae have a parasitic dependence upon chironomids (JONES 1978, HEVERS 1980). Data on the life histories of *U. intermedia* and *U. ypsilophora* are given by HEVERS (1980) and BAKER (1987). The high degree of host-specificity probably results from selective host recognition behaviour involving chemoreception (LAROCHELLE and DIMOCK 1981).

Although several invertebrate species display intraspecific aggression and territorial behaviour in an assortment of ecological contexts (MURRAY 1981), the maintenance by a male of a breeding colony of females through antagonistic interactions with conspecific males is most often associated with the social behaviour of higher vertebrates. However, some unionicolid water mites have population structures suggestive of polygynous mating systems (GORDON *et al.* 1979, DIMOCK 1985, BAKER 1987). DIMOCK (1983) has observed intraspecific aggressive behaviour among male *Unionicola formosa* (DANA and WHELPLEY) from the mussel *Anodonta imbecillis* SAY that is consistent with a harem-like mating system.

Males of several species of unionicolid mites are routinely underdispersed, sometimes occurring as a single male per host (MITCHELL 1965, DAVIDS 1973, GORDON *et al.* 1979, HEVERS 1980, DIMOCK 1985, BAKER 1987). For permanent mussel-mites, mating presumably only occurs within the host mussel's mantle cavity. Thus, the exclusive occupancy by one male of a host's mantle cavity within which reside numerous females would markedly affect that male's reproductive success.

The distribution of *Unionicola ypsilophora* and *U. intermedia* could involve interspecific competition between these species (DAVIDS 1973, HEVERS 1980). DOWNES (1986) suggested that the absence of all mite species other than *U. formosa* in *A. imbecillis* is due to aggressive behaviour by *U. formosa*. On the other hand, several unionid species may harbour up to three different mite species (JONES and BAKER 1984, DOWNES 1986). Intraspecific competition among female *Unionicola fossulata* (WOLCOTT) parasitizing several mussel species may contribute to the common occurrence of only two females and one male per mussel in this mite species (MITCHELL 1965, DOWNES 1986).

In the present study, we have analyzed intra- and interspecific behaviour of adult *U. ypsilophora* and *U. intermedia* as that behaviour affects the distribution of these two species of mites among their unionid hosts. Evidence is presented both for a harem-like mating system for *U. ypsilophora* and for the competitive exclusion of *U. intermedia* from one potential host mussel.

2. Material and Methods

Mussels were collected weekly from June 3 through September 26, 1983, and monthly from February 20 through July 24, 1984 by dipnet or by hand in "het Gein", a very slowly running stream with a silty bottom and a maximum depth of ca. 2 m., situated 10 km S.E. of Amsterdam. The following species were found: *Anodonta cygnea*, *A. anatina* and *Unio pictorum* (L.). Specimens of *A. cygnea* longer than 60 mm, and of *A. anatina* longer than 50 mm were saved. These sizes were selected because the number of mites per mussel can be influenced by the size of the mussel (DIMOCK 1985). The resident mites were extracted, counted and identified without damaging the mollusc by gently squeezing the mussel shell so that a small opening occurred, and then by flushing the mites out with water or by using a soft brush. For identification purposes the mites were anesthetized with a 4% urethane solution to immobilize them under magnification. After 5 to 10 minutes in clear water they became active again, apparently without being damaged.

For experimental purposes, the mites were kept outside the mussel no longer than one day, and were used for only one experiment. Except as specified below, in order to avoid problems with intraspecific aggression only females were used. The mussels were kept by species in tanks with a sandy bottom at a temperature of about 16 °C, and were fed with a *Chlorella* suspension.

To obtain information about the host specificity of *U. ypsilophora* and *U. intermedia* in both *Anodonta* species, 16 female mites were put into each of 3–5 mussels of each species. The individual mussels were isolated during the experiment in 1,000 ml beakers. Two and five days afterwards, the total of mites inside and outside the mussel was enumerated.

To determine whether or not interspecific interactions occur between *U. ypsilophora* and *U. intermedia*, mussels (*A. cygnea* and *A. anatina*) first were cleaned of all mites. Subsequently, 16 female mites of each species were introduced into the two mussel species. As in the previous test two and five days later the number of mites inside and outside the mussels were enumerated for each species.

To test for the occurrence of intraspecific aggression among *U. ypsilophora*, two methods were used. First, the survival of mites confined as pairs *in vitro* was determined. Twenty pairs each of male-male, male-female, and female-female combinations were established in individual vials in 5 ml of pond water. Each vial was examined daily for 21 days to monitor survivorship of the mites. The vials were placed at 16 °C in a light regime incorporating a 12-hour dark cycle. Secondly, to each of twenty *Anodonta cygnea*, two males of *U. ypsilophora* were placed two cm apart between the gills. Every two days, the mussels were examined for presence of the males.

Another question arising from literature data is the maximum density of mites a mussel can sustain. To determine whether *A. cygnea* or *A. anatina* can support more than the usual 5–10 mites/mussel that are found in the field, the number of mites was increased to a maximum of 50 females per mussel. This was done for *U. ypsilophora* as well as for *U. intermedia* in their normal host mussels.

3. Results

Unio pictorum and *Anodonta anatina* are the most common mussel species in "het Gein", the latter being less abundant. *A. cygnea* is relatively more rare, occurring at a ratio of about one in every twenty mussels.

Unionicola ypsilophora in all developmental stages was nearly exclusively found in the several hundred *Anodonta cygnea* examined. The highest number of mites found per mussel was 12. The mean number of *U. ypsilophora* per infested mussel was 3.25, at an infestation rate of 52 % for 470 mussels. There were no significant differences in the means or the infestation rate during the observation periods (February–September). The sex ratio of *U. ypsilophora* varied during the observation period from 0.1 to 0.3 males/female. Although there were no significant differences in sex ratio, the highest ratios were found in May and September. No more than one male *U. ypsilophora* per mussel was found. Adult *U. ypsilophora* were found in only two of the 765 *A. anatina* that were examined.

The highest number of *Unionicola intermedia* found per *Anodonta anatina* was 14. The mean number of mites per infested mussel was 2.9, at an infestation rate of 55 % for 765 mussels. In contrast with *U. ypsilophora*, males of *U. intermedia* were only found

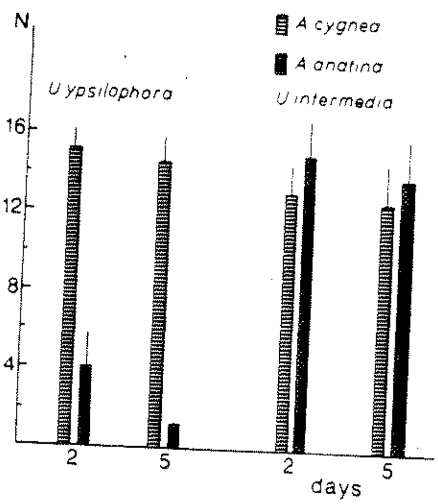

Fig. 1.

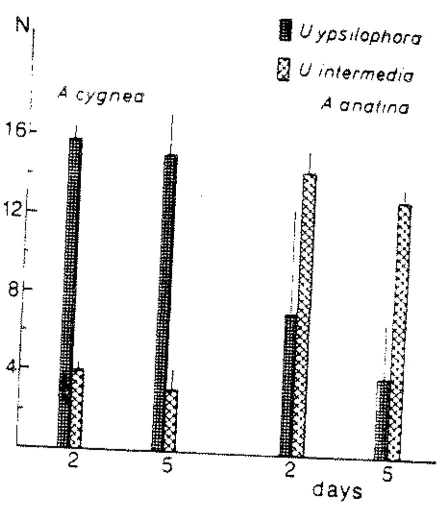

Fig. 2.

Figure 1. Preference of *U. ypsilophora* and *U. intermedia* for the mussels *A. cygnea* and *A. anatina*. The histograms depict the mean ($\pm SD$) number of mites of each species remaining after 2 and 5 days for three replicate experiments in which 16 female mites of the respective species were placed in the mantle cavity of each species of mussel.

Figure 2. Preference of *U. ypsilophora* and *U. intermedia* in double-species infestations for the mussels *A. cygnea* and *A. anatina*. The histograms depict the mean ($\pm SD$) number of mites of each species remaining after 2 and 5 days for four replicate experiments in which 32 female mites (16 of each species) were placed in the mantle cavity of each species of mussel.

from May through September. The sex ratio was highest in May (0.55 males/female), decreased to 0.2 in June and then gradually declined to 0.02 in September.

With respect to host specificity, it is clear from Figure 1 that *U. intermedia* stayed in *A. cygnea* in the absence of *U. ypsilophora*, whereas, *U. ypsilophora* left *A. anatina*. However, *U. intermedia* did not remain in *A. cygnea* when *U. ypsilophora* also was present (Fig. 2). By the end of five days, most of the female *U. ypsilophora* also had left *A. anatina* (Fig. 2), as in the previous experiment.

The survivorship of mites confined as pairs *in vitro* was highly dependent upon the combination. Male *U. ypsilophora* were aggressive toward one another, as could be seen under magnification. Within 8 days, one of the two males had died, presumably as a result of this aggressive behaviour (Fig. 3). In fact, within only three days, more than 50 % of the male pairs had been reduced to a single animal per vial. Pairs of males together in a mussel survived a few days longer (Fig. 3). However, at the end of the experiment, nineteen mites were dead and were found outside the mussels; one mite could not be accounted for. Thus, the end result was that only one male remained in each mussel. Male mites were not aggressive toward females, nor were females aggressive toward other females.

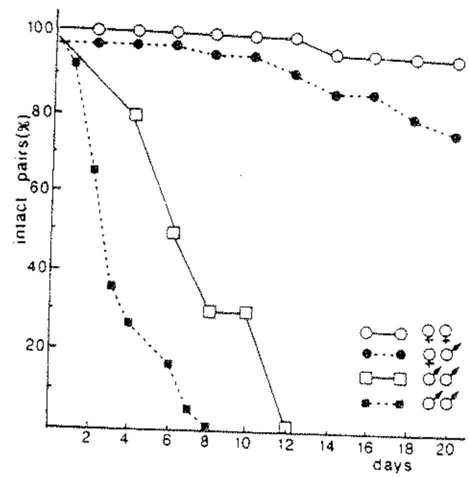

Fig. 3.

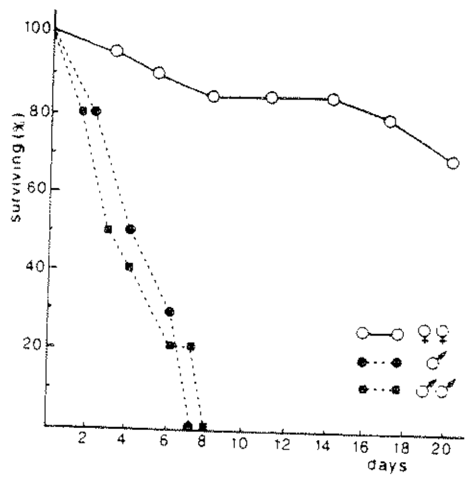

Fig. 4.

Figure 3. Survivorship curves for pairs of *U. ypsilophora* maintained *in vitro*, open squares, *in vivo*; $n=20$ pairs at time 0 for each combination. In all instances, a pair that was not intact consisted of one live and one dead animal. Experiments started in August 1983.

Figure 4. Survivorship curves for pairs of *U. intermedia* maintained *in vitro*, closed circles for single males; $n=20$ at time 0 for each combination. In all instances, a pair that was not intact consisted of one live and one dead animal. Experiments started in June 1984. See also Fig. 3.

From another experiment, it became clear that individual *U. ypsilophora* could be kept alive outside the mussel for weeks. From June onward, 30 females and 15 males were kept separately in vials. After 13 weeks, 23 were still alive. After four weeks, 50 % of the males were dead, with the last one surviving 10 weeks.

In contrast to *U. ypsilophora*, males of *U. intermedia*, whether kept singly or in pairs *in vitro*, died within 7 days; however, no aggression could be observed. Females survived significantly longer outside the mussel than did the males (Fig. 4).

To see if the density could be increased experimentally, 50 female *U. ypsilophora* and 50 female *U. intermedia* were introduced into *Anodonta cygnea* and *A. anatina*, respectively. After 4 days 47 mites were present in each mussel; and after 10 days 45 remained in *A. cygnea* and 43 in *A. anatina*. The experiments were repeated with nearly identical results.

4. Discussion

As is known from the literature, *U. ypsilophora* has a strong host preference for *A. cygnea* (HEVERS 1980). This specificity is very evident in our collection area (het Gein) where this mite is found almost exclusively in *A. cygnea* even though the population of *A. anatina* is about five times as dense. The observation that almost all adult female *U. ypsilophora* left *A. anatina* within 5 days after being placed in that mussel's mantle cavity suggests that this mite can discriminate one mussel species from another. Presumably this discrimination involves chemoreception as has been implicated for similar behaviour by *Unionicola formosa* in North America (LAROCHELLE and DIMOCK 1981). Whether or not *U. ypsilophora* exhibits species specific aggregation behaviour toward isolated pieces of mussel tissue, as does *U. formosa* (LAROCHELLE and DIMOCK 1981), has not been determined. However, it is apparent that when the host mussel is not the appropriate species, *U. ypsilophora* will leave the mussel (Figs. 1, 2).

In contrast to *U. ypsilophora*, *U. intermedia* will remain in both *A. cygnea* and *A. anatina* in the absence of *U. ypsilophora*. However, *U. intermedia* leaves *A. cygnea* if that mussel has *U. ypsilophora* in the mantle cavity (Fig. 2). This suggests that *U. intermedia* may have a broader range of host preference than *U. ypsilophora*, but may be prevented from colonizing *A. cygnea* by the presence of *U. ypsilophora*. These observations are suggestive of the occurrence of interspecific competition between these two species of mussel-mites in *A. cygnea*. However, the mechanism by which such interspecific interactions may be mediated is not known. The conclusion by DOWNES (1986) that interspecific competition between *Unionicola formosa* and other unionicolids results from interspecific aggression among adult mites is not based upon experimental evidence.

It is clear that, as a result of their aggressive behaviour, male *U. ypsilophora* have a very uniform distribution in natural circumstances. There is only a single male in a mussel in combination with one or more female mites. In an experimental situation two males survive together longer in a mussel than they do confined in a vial. This is understandable, since there is more space in a mussel, and it will take more time for the males to encounter each other. The interaction between males does not always end in the death of one of the two mites; sometimes a male may survive an encounter with another male and end up outside a mussel, but alive.

From Figures 3 and 4 it is clear that female mites can be kept in pairs for several weeks. This is in accordance with a survival time of months for female *U. ypsilophora* in the field. Unpublished data, however, indicate that female *U. intermedia* combined with female *U. ypsilophora* do not survive as well as solitary *U. intermedia*. In contrast to male *U. ypsilophora* that survive a couple of weeks as solitary males *in vitro*, male *U. intermedia* die within a week, whether or not they are paired with other males (Fig. 4), even though these experiments were done in June with a new, presumably vigorous generation of males. No aggression was observed among male *U. intermedia*, which is consistent with the fact that these males often occur at a density of more than one male/mussel (HEVERS 1980).

From the literature data combined with our findings it is clear that males of *U. ypsylophora* occur throughout the year (BAKER 1987), while the males of *U. intermedia* are confined to the summer months. Possibly, this difference in life history contributes to the lack of intraspecific aggression among male *U. intermedia*. Moreover, the mating behaviour of *U. ypsilophora* is unknown and thus a comparison between these two species of mussel-mites cannot be complete. For example, in contrast to *U. ypsilophora*, the fourth pair of legs of male *U. intermedia* are modified as gonopods for indirect copulation (HEVERS 1978).

The mean number of *U. ypsilophora* per mussel agrees with the data of BAKER (1987) for a population of *A. cygnea* in England, but the incidence of occurrence of this mite approached 100 % in BAKER's study. HEVERS (1980) has reported as many as 131 adult *U. ypsilophora* in an *A. cygnea* in Germany. It is apparent from our data that *A. cygnea* and *A. anatina* can sustain nearly 50 mites for more than a week. It is possible that the territoriality that one of us (DAVIDS 1973) attributed to female *U. ypsilophora* may occur at relatively low densities.

We do not agree with HEVERS (1980) that *U. intermedia* has a generation time of two years. Following his conclusions, that nymphal and adult periods are equal, one would expect to find more nymphs than adults in the field in the winter time, and this is not so. Like HEVERS we found most nymphs in September and most females in June.

BAKER (1987) determined that *U. ypsilophora* also has a generation time of one year in England but found that some females can live for two years. Our data are comparable, and like BAKER we found peaks in the occurrence of females in April. These data are in contrast to those for the closely related North American *U. formosa*, which apparently lives two years and has a peak abundance of females in mid-winter (DIMOCK 1985).

In the river "Gein" we found five species of unionicolid mussel-mites occurring in symbiotic associations with three species of freshwater mussels. The other three species were *Unionicola bonzi* (CLAPARÈDE) restricted to *Unio pictorum*, and two transient species, *U. aculeata* (KOENIKE) and *U. tricuspis* (KOENIKE), which only use mussels as sites for oviposition and for developmental transformation. The transformation stages of these two species were found in all three mussel species; however, *U. aculeata* seems to have a preference for *Anodonta anatina*. It is possible that this relationship of *U. aculeata* with *A. anatina* also involves competitive exclusion of *U. aculeata* from *A. cygnea* by *U. ypsilophora*. *U. tricuspis* is new to the Netherlands fauna.

HOLMES (1973) regards competitive exclusion between parasites as a common explanation for restriction to particular hosts. However, direct experimental evidence for such competitive exclusion is rare (DOBSON 1985). DOWNES (1986) has demonstrated that such interactions may occur between *Unionicola formosa* and other unionicolids, and we have now shown that *U. ypsilophora* is able to exclude *U. intermedia* from *Anodonta cygnea*. The great species diversity within the genus *Unionicola* and the variety of mussel-mite symbiosis involving this genus throughout the world may make this taxon especially amenable to studies of basic questions of population biology and evolutionary ecology.

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6. References

BAKER, R. A., 1977: Nutrition of the mite *Unionicola intermedia*, KOENIKE and its relationship to the inflammatory response induced in its molluscan host *Anodonta anatina* L.–Parasitology **75**: 301–308.

BAKER, R. A., 1987: Aspects of the life history of *Unionicola ypsilophora* (BONZ 1883).–The Naturalist **112**: 53–58.

BÖTTGER, K., 1972: Vergleichend biologisch-ökologische Studien zum Entwicklungszyklus der Süßwassermilben (Hydrachnellae, Acari). II. Der Entwicklungszyklus von *Limnesia maculata* und *Unionicola crassipes*.–Int. Revue ges. Hydrobiol. **57**: 263–319.

DAVIDS, C., 1973: The relations between mites of the genus *Unionicola* and the mussels *Anodonta* and *Unio*.–Hydrobiologia **41**: 37–44.

DAVIDS, C., R. M. COWELL and C. J. DE GROOT, 1985: The developmental cycles of two co-occurring sponge mites *Unionicola crassipes* (MÜLLER) and *Unionicola minor* (SOAR) (Acari, Hydrachnellae).–Hydrobiologia **122**: 199–205.

DIMOCK, R. V. Jr., 1983: In defense of the harem: intraspecific aggression by male water mites (Acari: Unionicolidae).–Ann. Entomol. Soc. Am. **76**: 463–465.

DIMOCK, R. V. Jr., 1985: Population dynamics of *Unionicola formosa* (Acari: Unionicolidae), a water mite with a harem.–Am. Midl. Nat. **114**: 168–179.

DOBSON, A. P., 1985: The population dynamics of competition between parasites.–Parasitology **91**: 317–347.

DOWNES, B. J., 1986: Guild structure in water mites (*Unionicola* spp.) inhabiting freshwater mussels: choice, competitive exclusion and sex.–Oecologia **70**: 457–465.

GORDON, M. J., B. K. SWAN and C. G. PATERSON, 1979: The biology of *Unionicola formosa* (DANA and WHELPLEY): a water mite parasitic in the unionid bivalve, *Anodonta cataracta* (SAY), in a New Brunswick lake.–Can. J. Zool. **57**: 1748–1756.

HEVERS, J., 1978: Zur Sexualbiologie der Gattung *Unionicola* (Hydrachnellae, Acari).–Zool. Jb. Syst. **105**: 33–64.

HEVERS, J., 1980: Biologisch-ökologische Untersuchungen zum Entwicklungszyklus der in Deutschland auftretenden *Unionicola*-Arten (Hydrachnellae, Acari).–Arch. Hydrobiol./Suppl. **57**: 324–373.

HOLMES, J. C., 1973: Site selection by parasitic helminths: interspecific interactions, site segregation, and their importance to the development of helminth communities.–Can. J. of Zool. **51**: 333–347.

JONES, R. K. H., 1978: Parasitism by *Unionicola* spp. larvae on chironomids.–Hydrobiologia **60**: 81–87.

JONES, R. K. H., and R. A. BAKER, 1984: Descriptions of unionicolid larvae from three North American unionid bivalves.–Hydrobiologia **114**: 109–113.

LAROCHELLE, P. B., and R. V. DIMOCK Jr, 1981: Behavioral aspects of host recognition by the symbiotic water mite *Unionicola formosa* (Acarina, Unionicolidae).–Oecologia **48**: 257–259.

MITCHELL, R. D., and G. W. PITCHFORD, 1953: On mites parasitizing *Anodonta* in England.–J. Conch. **23**: 365–370.

MITCHELL, R. D., 1965: Population regulation of a water mite parasitic on unionid mussels.–J. Parasitol. **51**: 990–996.

MURRAY, B. G., 1981: The origins of adaptive interspecific territorialism.–Biol. Rev. **56**: 1–22.

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