Population Dynamics of Unionicola formosa (Acari: Unionicolidae), a Water Mite with a Harem

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ABSTRACT: The population dynamics of the water mite *Unionicola formosa*, a symbiont of the freshwater mussel *Anodonta imbecillus*, were monitored for 2 years in a North Carolina farm pond. Since the density (number/mussel) of females was correlated with host-size, but males were uniformly isolated at 1/host, the sex ratio approached 80:1 (female: male) among large mussels. This "harem" distribution persisted throughout the year.

Female mites were most abundant in winter and experienced ~50% mortality by early summer. Nymphs were present throughout the year. Size-frequency data for females, coupled with the pattern of occurrence of nymphs, suggested that recruitment into the adult population began in May as overwintering nymphs transformed to adults, and continued into late summer and autumn. Egg production occurred throughout the year, but oviposition and the development of eggs were seasonal, with larvae emerging from the host from late spring to early autumn. Adult *U. formosa* probably live at least 2 years.

INTRODUCTION

The life cycle of freshwater mites is complex and includes the egg, prelarva, lar protonymph (postlarval resting stage I), deutonymph (nymph), tritonymph (postlar resting stage II) and the adult (Böttger, 1977; Hevers, 1980). Five genera of the w mite family Unionicolidae commonly occur in association with freshwater sponges, g trophods and/or mussels (Mitchell and Pitchford, 1953). The cosmopolitan genus *Unionicola* includes species whose life histories involve a mollusc or portferan, either temporarily as a site for oviposition and for the postlarval resting stages (Hevers, 1980), or permanently in associations which include parasitism of the molluscan host by nymphs and adults (Baker, 1977). The larvae of free-living, predatory species, as well as those symbiotic species, probably all have a brief (3- to 8-day) parasitic dependence upon c ronomid dipterans (Davids, 1977; Booth and Learner, 1978; Jones, 1978; Heve 1978a, 1980).

*Unionicola formosa* (Dana and Whedlepley) occurs throughout much of North Amer in symbiotic associations with several genera of anodontine mussels (Bivalvia: Unio dae) (Vidrine, 1980). Field observations (Dobson, 1966; Roberts, 1977; Vidrine, 198 and experimental behavioral studies (LaRochelle and Dimock, 1981; del Portillo a Dimock, 1982) indicate that in the southeastern U.S. the mussel *Anodonta imbecillus* is the preferred host of this mite. Although the spectrum of interactions between *U. formosa* and its molluscan hosts is not fully known, females oviposit in the host's gills, presumably the larvae and nymphs embed in host tissue prior to their ontogenic transformations. The nature of any nutritional dependence of this mite upon its host has not been fully resolved (LaRochelle, 1979); however, the mantle cavity of the clearly constitutes a microcosm for the mite and is the focal point for much of the bi ology of this species.

The ecology of the Unionicolidae is less well-known than that of other taxa marine and freshwater mites (e.g., Davids, 1973a, 1977; Kitron, 1980; Lanciani, 198 Riessen, 1982; Viets, 1982). Seasonal distributional data for species associated w molluscan hosts are available only for *Najaicola ingens* (Koenike) from New Hampsh

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(Humes and Russell, 1951), and for *Unionicola formosa* in association with *Anodonta catans* Say in eastern Canada (Gordon et al., 1979). Mitchell (1955, 1965) described the life histories of four species of *Unionicola* from the mussel *Lampsilis silicoides* (Barnes) in Michigan, but provided little quantitative information. Davids (1973b) discussed the distribution of several unionicolids in the Netherlands and included anecdotal references to seasonal events. Hevers (1980) described the life histories of the German species of *Unionicola*, but included few quantitative seasonal data.

I have previously shown that male *Unionicola formosa* are territorial and exhibit intense intrasexual aggression that is consistent with a female-defense polygynous mating system, *i.e.*, a harem (Dimock, 1983). In this paper I describe a 2-year study of the population dynamics of *U. formosa* in association with *Anodonta imbecillis* in a North Carolina farm pond. The data document the persistence of a highly female-biased sex ratio for this mite. The distribution of *U. formosa* in *A. imbecillis* is shown to differ in seven important respects from that in *A. cataracta* in Canada (Gordon et al., 1979), thus under-scoring the necessity for additional comprehensive field investigation to elucidate the ecology of the Unionicolidae.

**Materials and Methods**

The study area was a 6-ha farm pond (Honeycutt's pond) in Cabarrus Co., North Carolina, that had been undisturbed for at least 20 years. The mussel populations were not quantified, but the pond supported large numbers of *Anodonta imbecillis* and *A. cataracta* that were readily collected by hand or with a clam rake. Although the sampling protocol was not strictly random, mussels from several sites around the pond were included in each collection. All mussels were placed individually in polyethylene bags in a mudpot and removed from the substratum and were subsequently thoroughly examined in the laboratory.

Since preliminary observation indicated that the abundance of *Unionicola formosa* and *Anodonta imbecillis* was correlated with the size of a mussel, I collected and measured (1.0 mm with vernier calipers) 100 mussels (24-83 mm total length) in March and April 1979 and counted their adult mites. From those data and an impression of the abundance of various size-classes of *A. imbecillis* in the pond, I confined all subsequent collection to mussels of 60.0-69.9 mm. Fifteen mussels were collected between the 6th and 12th day of each month from May 1979 to April 1981 and were examined for the present of adult female, adult male, sexually immature nymphs and postlarval resting stages of *U. formosa*. Each month from May 1980 to June 1981 I also examined at least 15 *A. cataracta* of various sizes for the presence of this mite.

The size-frequency distribution of 650 adult female mites (50/month, July 1980-July 1981) was determined by measuring the length of the idiosoma with an ocular micrometer. The annual pattern of egg production by *Unionicola formosa* was quantified by dissecting the eggs from 15 females/month (May 1980-May 1981); 10 eggs/month were also measured with an ocular micrometer. The density of mite eggs and of prelarvae: the gills of *Anodonta imbecillis* was monitored by examining the left inner demibranch mussels (3/month; May 1980-May 1981) that had each harbored an average of 25.2 female mites when they were collected. Only inner demibranchs were examined because *A. imbecillis* is hermaphroditic (Kati, 1983) and employs the outer demibranchs as a supa for its glochidia. Since mite eggs may not otherwise be readily discernible, all gill eggs were fixed and cleared in xylene.

All data were examined for normality and homoscedasticity before statistical analysis following the procedures of Zar (1974). Correlation between variables was dete mined by Spearman's rank correlation. The significance of differences among other parameters was assessed either by Student's *t* test or one-way analysis of variance (ANOVA) and Student-Newman-Keuls multiple range test (SNK), if appropriate.
91.5% of *A. imbecillis* harbored at least one male mite, fully 86% of the mussels had only a single male in the mantle cavity (see also Dimock, 1983, Fig. 1). The prevalence of male mites among the mussels ranged from 86-100%, but exhibited no obvious seasonal pattern.

The density of males did not differ significantly throughout the 2-year study (P > 0.05, ANOVA, SNK). However, seasonal differences in the relatively rare occurrence (23 of 360 mussels) of > 1 male/mussel were apparent, especially when one considers the presence of multiple males in at least two of the 15 mussels collected each month, a condition that only occurred in the autumn or early winter (Fig. 4). The two mussels that harbored three male mites were collected in November (1979) and October (1980). When two males were present within a single mussel, one usually was substar.

![Diagram showing the distribution of male mites in mussels over 12 months and their total length.](image)

**Fig. 3.** — The distribution of the body lengths (idiosoma, mm) of female *Unionicola form* over 13 months. Entries on the abscissa are the minimum size (mm) for each size class, except for < 1.00 and > 1.49. Arrows indicate the size class of the mean for each distribution. Sample size = 50/month; 650 for the total sample (July 1980-July 1981).
tially smaller (perhaps younger?) than the other; on the two occasions in which they were 3/mussel, two were of similar size and much smaller than the third.

The occurrence of nympha Unionicola formosa among Anodonta imbecillis also markedly seasonal (Fig. 5), with both a summer and a winter maximum in their abundance each year. Nymphs were present every month ($\bar{x} = 2.67 \pm 0.14$ se, range:0-mussel) but their prevalence varied from 33-100%. The minima in both the prevalence and the density of nymphs generally occurred in the same months (Fig. 5). The variance/mean ratio for nymphs differed from that of both female and male U. form in that in 12 of the 24 months (mostly in the summer and autumn) the $S^2/\bar{x}$, indicating a random distribution of nymphs among the mussels, whereas, in the other 12 months, the nymphs were overdispersed (i.e., $S^2/\bar{x} > 1$). There was no correlation between the monthly $S^2/\bar{x}$ ratios and the monthly mean density of nympha U. formosa.

Trionymphs of Unionicola formosa were occasionally observed attached to the gill Anodonta imbecillis, or more frequently to the mantle, either near the exhalant siphon region or on the posterior-dorsal aspect of the mantle cavity. Although this transitional stage was never numerous ($\bar{x} = 0.13$/mussel), the density and prevalence of trionymphs among the mussels were seasonal, with maxima usually occurring either simultaneously with, or 1-2 months after, the bimodal annual maxima in the density nymphs (Fig. 5).

The number of eggs per female Unionicola formosa and the occurrence of mite e and prelarvae in the gills of the mussels varied seasonally (Fig. 6). Prelarvae were abundant in May, and their numbers declined steadily over the summer as they emerge from the mussels as free-swimming larvae. The development and emergence of larvae essentially stopped by mid-September (Fig. 6). As mite eggs matured into prelarvae in the host gill, the number of eggs/gill decreased exponentially (May-August). However, as prelarvae became rare at the end of summer (i.e., when eggs ceased to

![Diagram](image-url)  

Fig. 4. — Pattern of occurrence of multiple males of Unionicola formosa among Anodonta imbecillis. Points are the number of mussels (of 15 sampled each month) with two or more males.
velop), the number of eggs in the gills increased until November and then remained virtually constant until subsequently increasing again in early spring (Fig. 6).

The seasonal pattern in the number of eggs/female mite is clear (Fig. 6) and was in several respects complementary to that of eggs and prelarvae in mussel gill. Gravid females were present throughout the year. However, from January-March essentially 100% of the females had eggs (maximum = 30/female), while in July >50% had no eggs and the maximum number of eggs/female was two. The size of mite eggs dissected from females was constant throughout the year (~240 μm x 160 μm).

Of the 204 Anodonta cataracta from Honeycutt's pond that were systematically examined from May 1980-June 1981, 34 (~17%) harbored Unionicola formosa. Only 2 female and 19 male mites were recovered from these mussels, with only four having >1 mite. The males were uniformly distributed at 1/mussel. No eggs were present in the gills of these mussels, and no other stages in the life cycle of the mite were observed.

On 17 September 1982 I collected 20 Anodonta cataracta from another farm pond (Fisher's pond), ~1 km from the primary study site, and 100% harbored Unionicola formosa. The mean density of females was 16.2 ± 3.3 % (range: 0-52) mites/mussel whereas males were present at x = 0.95/mussel. I found one nymph of U. formosa, and mite eggs and prelarvae were present in the gills of the mussels. Fewer than 1% of ~2000 mussels that I removed from Fisher's pond as it was being drained were A. imbecillius. I also collected 20 A. cataracta on 17 September from Honeycutt's pond and, in contrast to Fisher's pond, found only a single female U. formosa and no other evidence of this mite.

![Graph](image)

**Fig. 5.** — Distribution of the nymphs (solid circles, dashed line) and tritonymphs (open circles, solid line) of Unionicola formosa among Anodonta imbecillius. Points are the percentage of mussels/month having >0 nymphs or tritonymphs (prevalence), and the mean number of respective developmental stage/mussel. Error bars are the SE (one direction). For entries with out error bars, the symbol is larger than the error bar.
DISCUSSION

Females are more numerous than males in many invertebrate taxa (Hamilt 1967), but the existence of female-harem or female-defense polygyny (Emlen a Oring, 1977; Alcock, 1980) among invertebrates has been described only rar (Wilson, 1975; Jenner, 1978; Dimock, 1983). Thus, the press study constitutes one of the few quantitative demonstrations of the long-term pers ence of a female-biased sex ratio among invertebrates. However, the mating system Unionicola formosa may be typical of many unionicolids, which commonly have sex rat of two or more females/male. For example, Hevers (1980) observed as many as 66 male:three male U. intermedia (Koenike) in one Anodonta anatina (Linnaeus) and eight male:one male U. bonzi (Claparedel) in a single Unio pictorium (Linnaeus) in Germany. contrast, Mitchell (1965) never found more than two females and one male U. fossu (Koenike) in Lambsilis siliquoides, while the unionicolid Najadicola ingens commonly oc curs at 2/mussel (one female:one male) in A. cataracta and Elliptio complanata (Lightfo but in a ratio of up to eight females:four males in L. radiata (Gmelin) (Hurns a Jarmnback, 1950). Thus, if successful mating among mussel-mites only occurs with

![Graph of distribution of the density of eggs/female Unionicola formosa, and the density mite eggs/cm² of gill and of prelarvae/cm² of gill of Anodonta imbecillis. Points are the means; error bars ±SE.](image)

Fig. 6. -- Distribution of the density of eggs/female *Unionicola formosa*, and the density mite eggs/cm² of gill and of prelarvae/cm² of gill of *Anodonta imbecillis*. Points are the means; error bars ± SE.
the host's mantle cavity, as has been shown for *U. intermedia* (Hevers, 1978b), harer
defense polygyny may be widespread among the Unionicolidae.

Both the abundance and the sex ratio of mussel-mites may also be influenced by e

gographic location, host-size and season. For example, Hevers (1980) observed as ma
as 131 adult *Unionicola pispilophora* (Bonz) in a single *Anodonta cygnea* (Linnaeus) in Ge

many, while Davids (1973b) found only five adults of that mite in the same mussel

the Netherlands. I have observed 78 female:one male *U. formosa* in *A. imbecillus* and 52

in *A. cataracta* in North Carolina, while Gordon *et al.* (1979) reported a maximum of

adult mites in *A. cataracta* in Canada (average sex ratio = 1.6:1, female:male).

Vidrine (1980) suggested that mussels from large populations in lentic systems ha
bores more *Unionicola formosa* than mussels from lotic areas in which the density of mus
sels was low. However, no association between the population biology of the host a
that of symbiotic mites has yet been established. Since *Anodonta cataracta* from Hone

cutt's pond, where *A. imbecillus* was also abundant, harbored essentially no *U. formos*
while the same mussel from Fisher's pond, where *A. imbecillus* was very rare, hosted

considerable population of this mite, the factors affecting the distribution of this m:
apparently are complex.

In contrast to my observations and those of Gordon *et al.* (1979) on host size-relat
parameters of the population biology of *Unionicola formosa*, Humes and Jamback (195
showed that the prevalence of *Naupicola inquis* was inversely related to the size of *Ellip
complanata* and *Anodonta cataracta*, whereas Mitchell (1965) found no correlation betw
host size and any parameter of the population biology of *U. fossulata*. The fact that t
abundance of female *U. formosa* increased with host size and was not asymptotic with
the range of mussels encountered in Honeycutt's pond (Fig. 1) suggests that the ma
mum number of mites in *A. imbecillus* is a function of a size-related feature of the ho

Although the occurrence of mite-induced host mortality in this symbiotic relations:
has not been investigated, it is unlikely that mussels larger than those observed, wh
might also have harbored more mites, were missing as a consequence of mite-induc
mortality, since *A. imbecillus* rarely exceeds 90 mm in length (Johnson, 1970). Of cou:
however, individual mussels of any size but with higher than observed mite densi:
could have disappeared before the mussel population was sampled. The uniform dist
bution of one male *U. formosa* per mussel results in a highly host size-dependent sex r
atio which approximates 1:1 in mussels ~35 mm long and becomes skewed to 70-80
(female:male) in the largest *A. imbecillus*.

Mitchell (1965) contends that the limited availability of sites for oviposition within
mussel is instrumental in the regulation of mussel-mite abundance and in the evoluti
of sympathy within the Unionicolidae. However, intraspecific differences in suitabi
as hosts by mussels of various size classes, as well as interspecific variation in the eff
of mussels on the host-oriented behavior of mites (LaRochelle and Dimock, 1981; P
Portillo and Dimock, 1982; Werner, 1983), could also result in differential recruitmen
If *Unionicola formosa* lives for several years, larger (older) mussels may simply acu
more mites as a consequence of increased exposure to the invasive stage(s) of this mi
Also, no data are available to evaluate the effect of the size of the resident population
mites on recruitment of additional mites into a mussel.

Although Gordon *et al.* (1979) detected no seasonal differences in the distribution
adult *Unionicola formosa* among *Anodonta cataracta* in Canada, seasonal variation char
cterized much of the population biology of this mite in *A. imbecillus*. Adult females we
most numerous in the winter and least so in late spring and summer (Fig. 2), but se
sonality in the distribution of males was only evident in the infrequent occurrence
multiple males being present in several mussels. The seasonal occurrence of such su
numerary males paralleled the autumn-winter increase in the abundance of fema
(Figs. 2 and 4). The temporary seasonal increase in the density of males was quickly st
ored to one male/mussel, probably through intrasexual aggression (Dimock, 1988). H
However, the possibility that the sex of a transforming mite, and hence the abundan
of males, is in some way influenced by the distribution of adult mites has not been
vestigated.
Patterns in the abundance of adult mites are consistent with the major periods of
crutment into the adult population following the maxima of nymphal and tritonymp
abundance (Fig. 5), although a low level of recruitment may occur throughout much
the year. The continuous presence of nymphs and the winter increase in their pre-
ience indicate that some *Unionicola forma* overwinter as nymphs, as has previously be
suggested for this and other unionicolids (Gordon *et al.*, 1979; Hevers, 1980). The sc
city of tritonymphs among *Anodonta imbecilis* may reflect high nymphal or tritonymp
mortality, although tritonymphs could have been more numerous among other s
classes of mussels.
The size-frequency distribution of female *Unionicola forma* provides additional e
cidence for seasonal changes in the population structure of this mite. The relatively h
density of small females in May probably reflects the recruitment of new adults fr
the overwintering nymphs, while the relatively numerous small females in October z
December (Fig. 3) represent new recruits from the nymphs that were most abundant
late summer and early winter (Fig. 5). The loss of some large females in the populat
during the summer-autumn recruitment indicates that mortality occurs among the
males even while their overall abundance increases from summer to winter (Fig. 2).
The maximal mean size of female mites occurred in midwinter, concomitantly w
the peak density of eggs/female (Fig. 6). However, since swelling of the idiosoma m
have occurred even among relatively young females as eggs accumulated in late win
(Fig. 6), it is impossible to determine whether or not the large females present in
winter included surviving large females from the previous summer that were still p
ducing eggs. The reduction in the size of females that occurred into the spring proba
resulted from the death of some of the largest (oldest?) females as well as a reduction
the size of the previously distended idiosoma as oviposition ensued (Fig. 6). In additi
the spring recruitment of overwintering nymphs would contribute to the reduction
mean body size. There was not, however, a wholesale seasonal replacement of one s
class by another that might have indicated the termination of a generation which, as
posedly, occurs in July among *Unionicola forma* in Canada (Gordon *et al.*, 1979) and
*foissulata* in Michigan (Mitchell, 1965).
The dynamics of oviposition and larval development by *Unionicola forma* (Fig.
reveal that this mite is similar to other species in the genus in that larvae emerge fr
the host mussel between May and October (Mitchell, 1955, 1965; Paterson and M
the early spring following the annual maximum in the number of eggs/female, at w
time 100% of the females are also gravid. As oviposition continues during the spri
the number of eggs/female decreases until the summer minimum of \(\frac{1}{2}\) egg/s fem
occurs and 50% of the females are gravid. Females then either cease ovipositing or
so at such a rate that the development of eggs to larvae is sufficiently rapid to result i
continuous decline in the density of eggs in the host's gill (Fig. 6).
As the water temperature decreases in late summer, the development of eggs cea
and the number/gill increases. Oviposition apparently stops from about January
March or April, during which time eggs accumulate in the females either as a con
quence of the cessation of oviposition or from increased egg synthesis in midwinter.
Since no annual difference in the size of mite eggs occurred, egg synthesis may proce
at a low but continuous rate year-round.
Comparable seasonal data on egg production and oviposition are not available
many other unionicolids. Mitchell (1955) first reported that *Unionicola fossulata* egg
spear in early spring and oviposition occurs through early June with gravid females
ing present but not ovipositing in the autumn, but later (Mitchell, 1965) suggested t
egg production is continuous and eggs accumulate in the host's gill from August un
late June. Gordon *et al.* (1979) made an exhaustive attempt to quantify egg producti
by *U. formosa* in Canada, and variously attributed production of 100,000 + eggs to between 80 and –325 female mites. Their efforts are confounded, however, by the fact that *U. formosa* apparently only oviposits in the gills of its anodontine hosts (Vidrine 1980), while their observations concerned eggs in the mantle and foot of four species mussels, only one of which actually harbored *U. formosa*.

Larval *Unionicola formosa* presumably have a brief parasitic dependence upon chironomid dipters, as is now well-established for other members of the genus (Heve 1978a, 1980). However, the question of parasitism of insects by the larvae of this m remains open, since I have not investigated it and Paterson and MacLeod (1979) attend, curiously without providing quantitative evidence, that larval *U. formosa* can morphose to the nymph without involving either an insect or a mussel. Mites which emerge as larvae early in the season probably reach sexual maturity by their first winter. Those which emerge late in the larval season overwinter as nymphs and transfe to adults the following spring. However, eggs and adults also overwinter. Since approximately 50% of the adult population (at least of females) dies each year, adult *U. formosa* probably live at least 2 years.

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