# Population Dynamics of Unionicola formosa (Acari: Unionicolidae), a Water Mite with a Harem[1]

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ABSTRACT: The population dynamics of the water mite *Unionicola formosa,* a symbiont of the freshwater mussel *Anodonta imbecillis,* 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 wa mite family Unionicolidae commonly occur in association with freshwater sponges, g tropods and/or mussels (Mitchell and Pitchford, 1953). The cosmopolitan genus *Unic cola* includes species whose life histories involve a mollusc or poriferan, either tempor ily as a site for oviposition and for the postlarval resting stages (Hevers, 1980), or m permanently in associations which include parasitism of the molluscan host by nym 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 Whelpley) 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, 19 and experimental behavioral studies (LaRochelle and Dimock, 1981; del Portillo a Dimock, 1982) indicate that in the southeastern U.S. the mussel *Anodonta imbecillis* S is the preferred host of this mite. Although the spectrum of interactions between *U. mosa* and its molluscan hosts is not fully known, females oviposit in the host's gills, a presumably the larvae and nymphs embed in host tissue prior to their ontogene transformations. The nature of any nutritional dependence of this mite upon its ho has not been fully resolved (LaRochelle, 1979); however, the mantle cavity of the h clearly constitutes a microcosm for the mite and is the focal point for much of the bi ogy of this species.

The ecology of the Unionicolidae is less well-known than that of some other taxa marine and freshwater mites (*e.g.*, Davids, 1973a, 1977; Kitron, 1980; Lanciani, 19 Riessen, 1982; Viets, 1982). Seasonal distributional data for species associated w molluscan hosts are available only for *Najadicola ingens* (Koenike) from New Hampsh

[1]Contribution No. 214 from the Tallahassee, Sopchoppy and Gulf Coast Marine Biolog Association.

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

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

## MATERIALS AND METHODS

The study area was a 6-ha farm pond (Honeycutt's pond) in Cabarrus Co., Nort Carolina, that had been undisturbed for at least 20 years. The mussel populations wer not quantified, but the pond supported large numbers of *Anodonta imbecillis* and *A. ca taracta* that were readily collected by hand or with a clam rake. Although the samplir protocol was not strictly random, mussels from several sites around the pond were ir cluded in each collection. All mussels were placed individually in polyethylene bags im mediately upon removal from the substratum and were subsequently thoroughly exam ined in the laboratory.

Since preliminary observation indicated that the abundance of *Unionicola formosa* i *Anodonta imbecillis* was correlated with the size of a mussel, I collected and measured (t 0.1 mm with vernier calipers) 100 mussels (24-83 mm total length) in March and Apr 1979 and counted their adult mites. From those data and an impression of the abun dance of various size-classes of *A. imbecillis* in the pond, I confined all subsequent colle tion to mussels of 60.0-69.9 mm. Fifteen mussels were collected between the 6th ar 12th day of each month from May 1979-April 1981 and were examined for the presen of adult female, adult male, sexually immature nymphs and postlarval resting stage (*i.e.*, tritonymphs) of *U. formosa.* Each month from May 1980-June 1981 I also surveye 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-Ju 1981) was determined by measuring the length of the idiosoma with an ocular microm eter. The annual pattern of egg production by *Unionicola formosa* was quantified by di secting the eggs from 15 females/month (May 1980-May 1981); 10 eggs/month we 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 f male mites when they were collected. Only inner demibranchs were examined becau *A. imbecillis* is hermaphroditic (Kat, 1983) and employs the outer demibranchs as ma supia for its glochidia. Since mite eggs may not otherwise be readily discernible, all gil were fixed and cleared in xylene.

All data were examined for normality and homoscedasticity before statistical anal sis following the procedures of Zar (1974). Correlation between variables was dete mined by Spearman's rank correlation. The significance of differences among other p rameters was assessed either by Student's $t$ test or one-way analysis of varian (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 ha only a single male in the mantle cavity (*see also* Dimock, 1983, Fig. 1). The prevalenc of male mites among the mussels ranged from 86-100%, but exhibited no obvious sea sonal pattern.

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

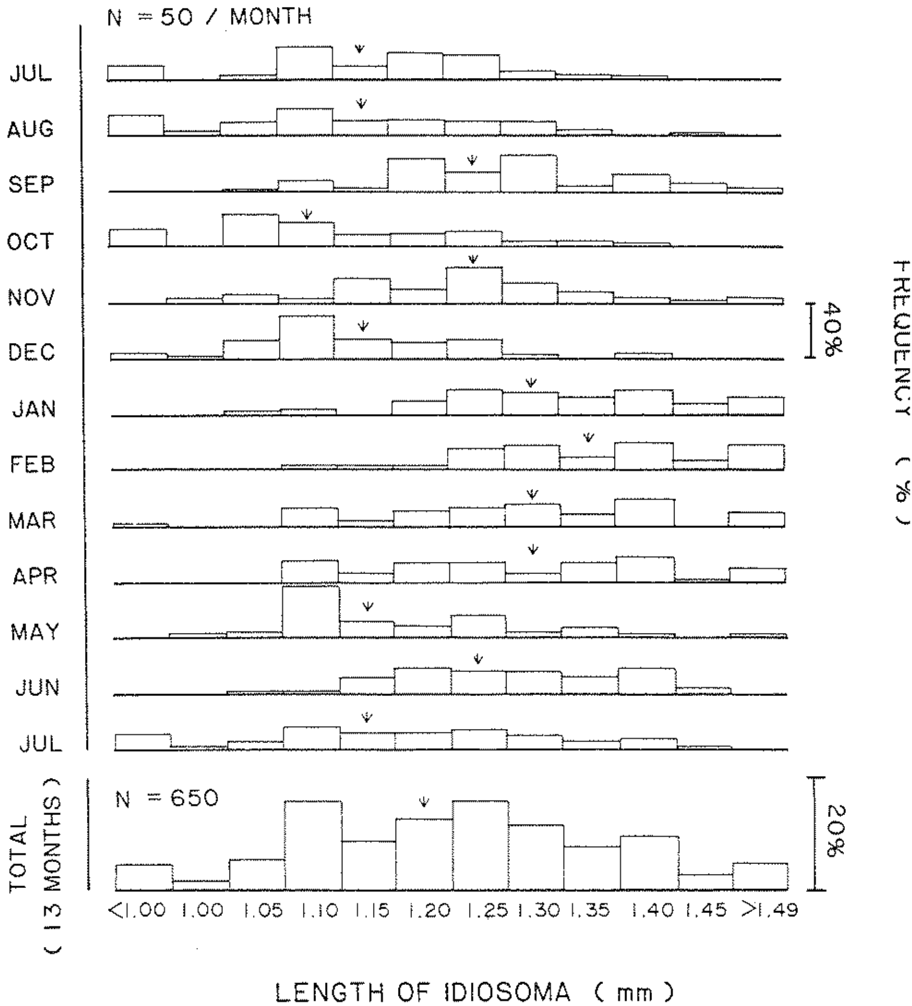


Fig. 3.—The distribution of the body lengths (idiosoma, mm) of female *Unionicola form* over 13 months. Entries on the abscissa are the minimum size (mm) for each size class, exce for <1.00 and >1.49. Arrows indicate the size class of the mean for each distribution. Samp size = 50/month; 650 for the total sample (July 1980-July 1981)

tially smaller (perhaps younger?) than the other; on the two occasions in which th were 3/mussel, two were of similar size and much smaller than the third.

The occurrence of nymphal *Unionicola formosa* among *Anodonta imbecillis* also markedly seasonal (Fig. 5), with both a summer and a winter maximum in their ab dance each year. Nymphs were present every month ($\overline{x} = 2.67 \pm 0.14$ SE, range:0- mussel) but their prevalence varied from 33-100%. The minima in both the prevale and the density of nymphs generally occurred in the same months (Fig. 5). T 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 $S^2/\overline{x}$ = indicating a random distribution of nymphs among the mussels, whereas, in the ot 12 months, the nymphs were overdispersed (*i.e.*, $S^2/\overline{x} > 1$). There was no correlation tween the monthly $S^2/\overline{x}$ ratios and the monthly mean density of nymphal *U. formosa.*

Tritonymphs of *Unionicola formosa* were occasionally observed attached to the gill *Anodonta imbecillis,* or more frequently to the mantle, either near the exhalant sipho region or on the posterior-dorsal aspect of the mantle cavity. Although this transforr tional stage was never numerous ($\overline{x} = 0.13$/mussel), the density and prevalence of tonymphs among the mussels were seasonal, with maxima usually occurring either multaneously 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 ab dant in May, and their numbers declined steadily over the summer as they emer from the mussels as free-swimming larvae. The development and emergence of lar mites essentially stopped by mid-September (Fig. 6). As mite eggs matured into pre vae in the host gill, the number of eggs/gill decreased exponentially (May-Augu However, as prelarvae became rare at the end of summer (*i.e.*, when eggs ceased to

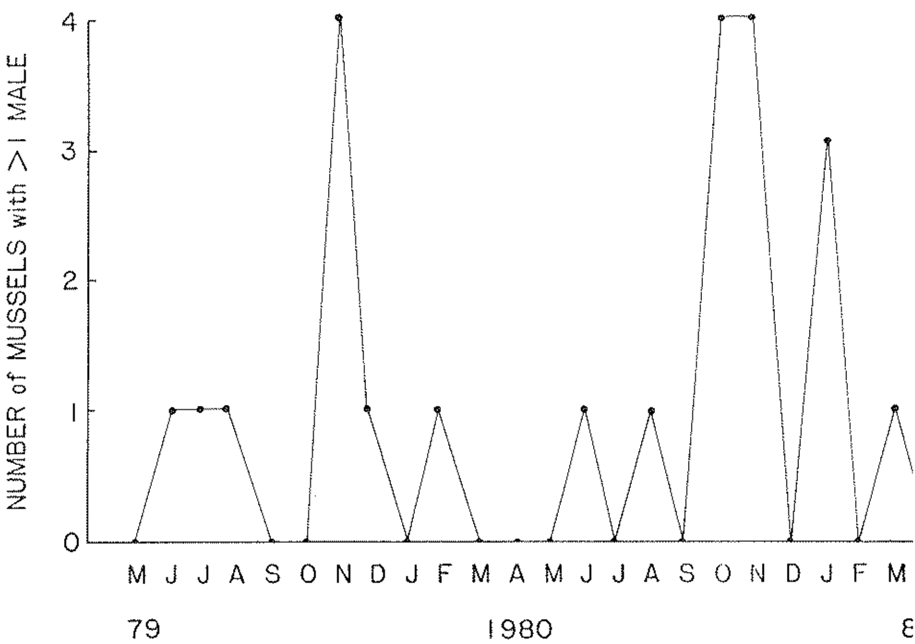


Fig. 4. — Pattern of occurrence of multiple males of *Unionicola formosa* among *Anodonta i cillis.* Points are the number of mussels (of 15 sampled each month) with two or more r mites

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 ($\sim$240 mμ x 160 mμ).

Of the 204 *Anodonta cataracta* from Honeycutt's pond that were systematically examined from May 1980-June 1981, 34 ($\sim$17%) harbored *Unionicola formosa*. Only 20 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), $\sim$1 km from the primary study site, and 100% harbored *Unionicola formosa*. The mean density of females was 16.2 ± 3.3 SE (range:0-52) mites/mussel whereas males were present at $\bar{x}$ = 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 $\sim$2000 mussels that I removed from Fisher's pond as it was being drained were *A. imbecillis*. 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.

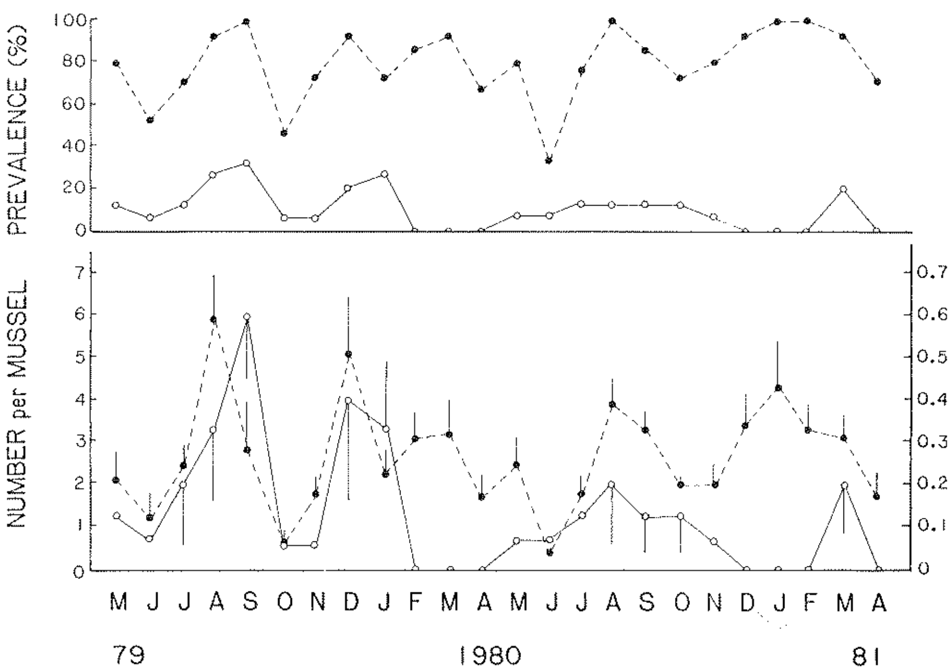


Fig. 5.—Distribution of the nymphs (solid circles, dashed line) and tritonymphs (open circles, solid line) of *Unionicola formosa* among *Anodonta imbecillis*. Points are the percentage of 1: mussels/month having >0 nymphs or tritonymphs (prevalence), and the mean number of the respective developmental stage/mussel. Error bars are the SE (one direction). For entries without 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; Kirkendall, 1983). Thus, the pres‹ 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* (Claparede) in a single *Unio pictorum* (Linnaeus) in Germany. contrast, Mitchell (1965) never found more than two females and one male *U. fossu* (Koenike) in *Lampsilis siliquoidea*, while the unionicolid *Najadicola ingens* commonly 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) (Humes a Jamnback, 1950). Thus, if successful mating among mussel-mites only occurs witl

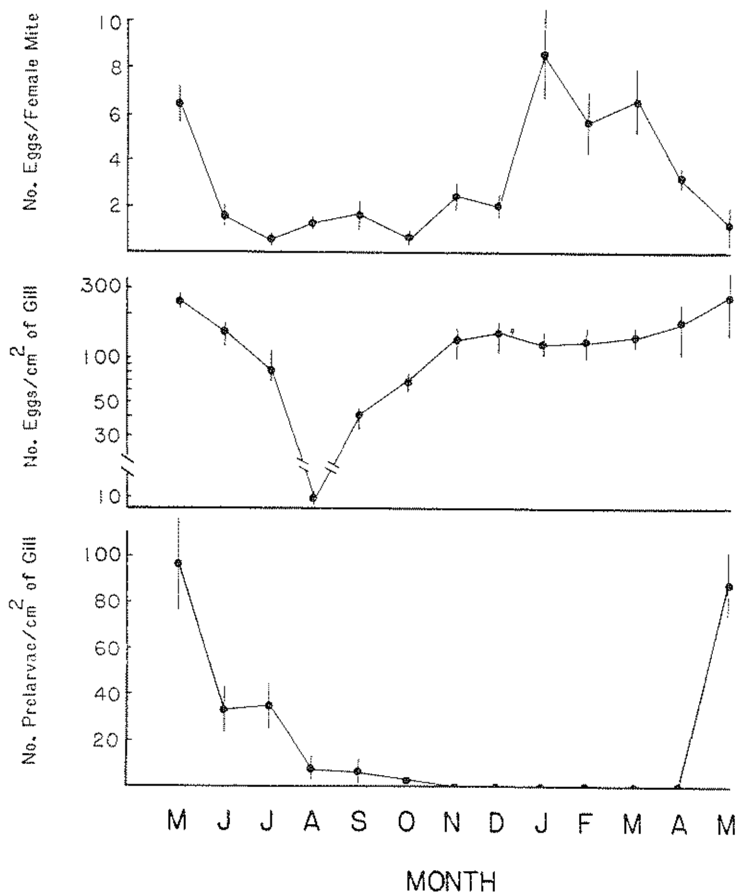


Fig. 6.—Distribution of the density of eggs/female *Unionicola formosa*, and the density mite eggs/cm² of gill and of prelarvae/cm² of gill of *Anodonta imbecillis*. Points are the means; ror bars ± SE

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 g ographic location, host-size and season. For example, Hevers (1980) observed as mai as 131 adult *Unionicola ypsilophora* (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. imbecillis* 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 bored more *Unionicola formosa* than mussels from lotic areas in which the density of mu sels was low. However, no association between the population biology of the host ai that of symbiotic mites has yet been established. Since *Anodonta cataracta* from Hone cutt's pond, where *A. imbecillis* was also abundant, harbored essentially no *U. formo:* while the same mussel from Fisher's pond, where *A. imbecillis* 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 Jamnback (195 showed that the prevalence of *Najadicola ingens* was inversely related to the size of *Ellip complanata* and *Anodonta cataracta,* whereas Mitchell (1965) found no correlation betwe 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. imbecillis* is a function of a size-related feature of the ho Although the occurrence of mite-induced host mortality in this symbiotic relationsh has not been investigated, it is unlikely that mussels larger than those observed, whi might also have harbored more mites, were missing as a consequence of mite-induc mortality, since *A. imbecillis* rarely exceeds 90 mm in length (Johnson, 1970). Of cours however, individual mussels of any size but with higher than observed mite densit 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 ı tio which approximates 1:1 in mussels ~35 mm long and becomes skewed to 70-8( (female:male) in the largest *A. imbecillis.*

Mitchell (1965) contends that the limited availability of sites for oviposition withir mussel is instrumental in the regulation of mussel-mite abundance and in the evoluti of sympatry within the Unionicolidae. However, intraspecific differences in suitabil as hosts by mussels of various size classes, as well as interspecific variation in the effe of mussels on the host-oriented behavior of mites (LaRochelle and Dimock, 1981; ( Portillo and Dimock, 1982; Werner, 1983), could also result in differential recruitmei If *Unionicola formosa* lives for several years, larger (older) mussels may simply acqu 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 chara terized much of the population biology of this mite in *A. imbecillis.* 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 supe 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 ı stored to one male/mussel, probably through intrasexual aggression (Dimock, 198: 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 cruitment 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 lence indicate that some *Unionicola formosa* 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 imbecillis* 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 formosa* provides additional e dence 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 a 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, su posedly, occurs in July among *Unionicola formosa* in Canada (Gordon *et al.*, 1979) and *fossulata* in Michigan (Mitchell, 1965).

The dynamics of oviposition and larval development by *Unionicola formosa* (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 Leod, 1979; Gordon *et al.*, 1979; Hevers, 1978a, 1980). Maximal oviposition occurs the early spring following the annual maximum in the number of eggs/female, at wh time 100% of the females are also gravid. As oviposition continues during the sprin the number of eggs/female decreases until the summer minimum of ~2 eggs/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 midwin Since no annual difference in the size of mite eggs occurred, egg synthesis may proc 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* eggs pear 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 u late June. Gordon *et al.* (1979) made an exhaustive attempt to quantify egg product by *U. formosa* in Canada, and variously attributed production of 100,000 + eggs to l tween 80 and ~325 female mites. Their efforts are confounded, however, by the f that *U. formosa* apparently only oviposits in the gills of its anodontine hosts (Vidrin 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 chirc omid dipterans, 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) cc tend, curiously without providing quantitative evidence, that larval *U. formosa* can me morphose to the nymph without involving either an insect or a mussel. Mites wh emerge as larvae early in the season probably reach sexual maturity by their first w ter. Those which emerge late in the larval season overwinter as nymphs and transfo to adults the following spring. However, eggs and adults also overwinter. Since appro mately 50% of the adult population (at least of females) dies each year, adult *U. form* probably live at least 2 years.

*Acknowledgments.* — I am grateful for the ideas and assistance that Andy Roberts, Pete LaI chelle, Hernando del Portillo, Bill Werner, Sammy Turnipseed and John Foil generously p vided. Peter LaRochelle, University of Colorado Museum, kindly verified the identity of mussels, and Dr. Malcolm Vidrine, Jefferson Davis Parish Mosquito Abatement Progra Jennings, La., confirmed the identity of the mites. Mr. and Mrs. James Honeycutt, Mt. Ple ant, N.C., graciously allowed me to tamper with their farm pond, as did Jim Fisher. The ma uscript benefitted from the suggestions of Drs. Bob Browne, Jerry Esch and Peter Weigl. T study was supported in part by a grant from the Wake Forest University Research and Publi tion Fund.

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SUBMITTED 23 APRIL 1984 ACCEPTED 7 JUNE 1