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Abstract: Seasonal reproductive patterns for the 11 terrestrial isopod species found in Wisconsin are presented. The pattern of the most widespread species, *Trachelipus rathkei*, is examined in detail through a series of paired north/south samplings which reveal a seasonal lag in the percent of females which were gravid in populations from the northern part of the state. A difference in sex ratio between north and south samples is reported.

Introduction

Since beginning our Wisconsin terrestrial isopod studies a decade ago, we have increased the number of species known to occur in the state from 6 (Jass & Klausmeier 1987) to 11 (Jass & Klausmeier 1996). Besides adding species to the state list, we have also recorded information on their Wisconsin distributions and life histories.

Because there is no key available which covers all of the species which occur in the state, we have constructed a key for the identification of the 11 terrestrial isopods we have found in outdoor habitats. Our key is geared to distinguishing among adults, because, while immatures superficially resemble tiny adults, they may differ from them in various body proportions.

The reproductive process of terrestrial isopods as it pertains to gravid females has been summarized by Sutton (1980). After mating, the female produces eggs which are carried in a ventral, water-filled marsupium where they undergo a maturation process. The egg is a yolky mass covered with two membranes. In a little over two weeks, limb buds and the first signs of segmentation appear. After three weeks, the embryo has enlarged to the point where the more rigid exterior membrane breaks open, leaving only the interior elastic one to enclose an embryo shaped much like the adult and having pigmented eyes. Movements at this stage subsequently break away the second

membrane but the young isopod stays in the marsupium for at least several more days (Sutton 1980).

In addition to noting the seasonal cycle of these stages for Wisconsin isopods, we made a more detailed comparison of populations from different parts of Wisconsin for the most widespread species, *Trachelipus rathkei*. We gathered data throughout the 1996 growing season on the percent of females which were gravid and noted the sex ratio in our monthly samples.

In an earlier study of the life cycle of a Wisconsin population of *Porcellio spinicornis* (Jass et al. 1991), we found the sex ratio to be skewed toward females (60.9% female and 39.1% male). Similar proportions have been reported in the literature for several other common terrestrial isopod species (Geiser 1934, Howard 1940, Hatchett 1947). We have gathered no Wisconsin data on the sex ratios at birth. However, Hatchett (1947) found, when studying Michigan terrestrial isopod species in the lab, that although populations of very young individuals may be composed of equal numbers of males and females, females predominate by the time reproductive maturity is reached. We therefore included the comparison of sex ratios in our study of northern and southern populations of Wisconsin *Trachelipus rathkei*.

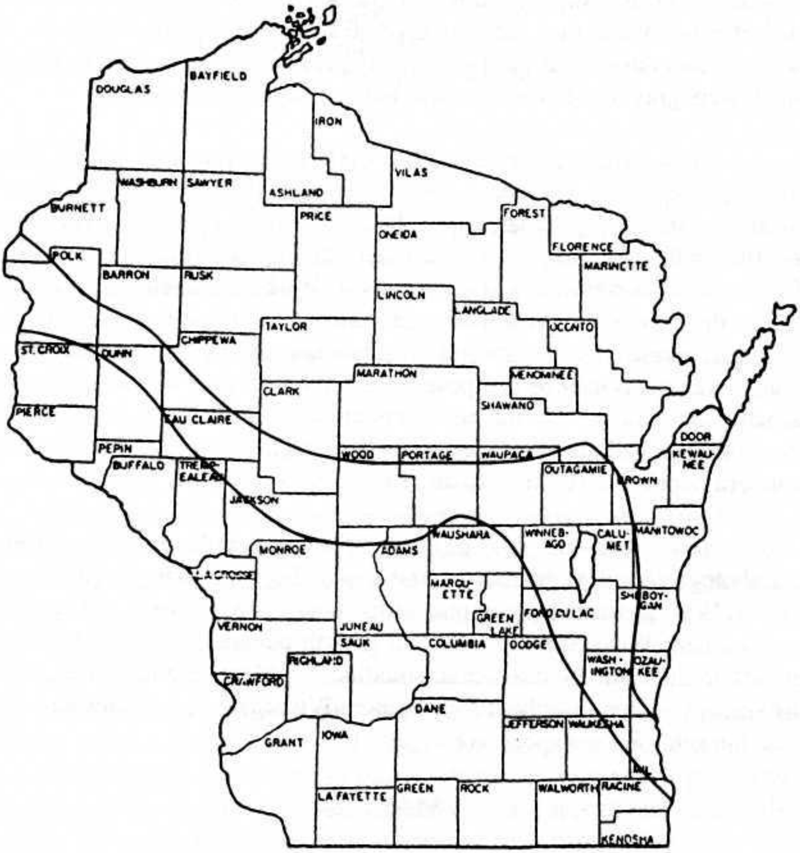
Most wide-ranging species consist of populations that differ in morphological and physiological traits, including seasonal growth patterns. Curtis (1959) described geographic differences between plants from northern and southern Wisconsin in "seasonal growth patterns or in adaptations for growth in different environmental situations." More recently, phenological differences between northern and southern Wisconsin populations have been found in some animal species (Parejoko 1987).

Methods

In 1995 we travelled throughout the state to gather distribution data. While we have previously noted by month the presence of females with eggs or young for these isopods (Jass & Klausmeier 1996), in this report the percent of gravid females is traced through the growing season for a more detailed comparison of their life histories.

Curtis (1959) defined a tension zone where geology, climate and ecological factors combine to divide the state into northern and southern sectors (Map 1). We studied the life history of *Trachelipus rathkei* in more detail by

Map 1. Wisconsin's northern and southern sectors divided by the tension zone (Curtis 1959) and the 1996 counties of collection for paired samples for comparison of *Trachelipus rathkei* populations.



	SOUTH	NORTH
May	Dane County	Sheboygan County
Jun	Waushara County	Marinette County
Jul	Monroe County	Bayfield County
Aug	Milwaukee County	Shawano County
Sep	Rock County	Ozaukee County
Oct	Pepin County	Burnett County

collecting samples from north and south of the tension zone in Wisconsin (Curtis 1959) in order to compare the reproductive phenology in populations of this widespread species. From May through October 1996, we visited a selection of paired sites from north and south of the boundaries of this zone and collected a minimum of 30 *Trachelipus rathkei* individuals at each locality. All collections were preserved in 70% ethanol. Each sample was examined in the laboratory under a dissecting microscope and separated into males, females (nongravid), females with eggs and females with young.

Results

Based on our continuing statewide collecting program for all Wisconsin species, we have attempted to determine the distributions of the terrestrial isopods found in the state. Table 1 presents all records from the MPM collection through the 1996 collecting season and shows marked divisions into restricted, moderately restricted, and widespread species. The extent to which these county records indicate zoogeographical boundaries for certain of the species is still open to question.

Table 1. Terrestrial isopods ranked in order based on the percent of Wisconsin's 72 counties from which they have been recorded.

Relative Distribution in Wisconsin	Species (number of counties)
Restricted Less than 3% of counties	*Armadillidium nasatum* (2) *Miktoniscus medcofi* (2) *Oniscus asellus* (2)
Moderately Restricted 7-28% of counties	*Trichoniscus pusillus* (5) *Armadillidium vulgare* (12) *Porcellionides pruinosus* (16) *Hyloniscus riparius* (20)
Widespread 88-100% of counties	*Porcellio scaber* (63) *Cylisticus convexus* (72) *Porcellio spinicornis* (72) *Trachelipus rathkei* (72)

We developed a key for Wisconsin adult terrestrial isopods (Table 2). Two terms from the key may be unfamiliar: uropods and pseudotrachaeae. Uropods are the posteriormost extensions of the body. In the genus *Armadillidium* these are blunt rather than extended, allowing these species to roll up into a perfect sphere--a feature where morphology and behavior make identification easy. The pseudotrachea is an internal mass of tiny air channels which opens directly to the outside air through a small pore. Pseudotracheae are located on the ventral side of the abdomen and appear as paired white patches.

Generally June and July are the peak months for terrestrial isopod reproduction in Wisconsin (Table 3). However, none of the *Hyloniscus riparius* females we collected in June were gravid (Table 3). For both *Hyloniscus riparius* and its fellow trichoniscid *Trichoniscus pusillus*, we did find gravid females in the August-October period.

Of the three widespread species which we have found in every county of the state--*Cylisticus convexus*, *Porcellio spinicornis* and *Trachelipus rathkei*--only *T.rathkei* has a reproductive period that spans several months (Table 3). While it shares the June-July peak with other species, 13% of *Trachelipus rathkei* females collected in August 1995 were also carrying eggs or young. This more extended breeding season may be one of the reasons why *T.rathkei* has been able to occupy more habitats in the state than other species (Jass & Klausmeier 1996).

Table 4 shows the percent of *Trachelipus rathkei* females which were gravid by month of collection from our 1996 paired north/south samples and indicates a tendency for samples from the northern part of the state to have a time lag in their reproductive seasonality when compared to those from the south. A comparison of the July samples shows a significantly higher proportion of females gravid in the sample from north of the tension zone (X^2=4.12, $p<0.05$, d.f.=1) (SAS 1985). Although there was a general trend for the bearing of eggs and young to be delayed in the north (Table 4), only the July difference was significant.

Table 2. Key to the adult terrestrial isopods of Wisconsin

1 Body length 12-16 mm, eye of many ocelli--4
1' Body length 5-6 mm, eye of one or three ocelli-------------------------------------2

2 Eye of one ocellus---3
2' Eye of three ocelli, color reddish--------------------------------*Trichoniscus pusillus*

3 Body surface dull with many tiny bumps, color pale-----------*Miktoniscus medcofi*
3' Body surface shiny, color dark wine-red-------------------------*Hyloniscus riparius*

4 Uropods extending beyond the terminal abdominal segment------------------------6
4' Uropods not extending beyond the terminal abdominal segment--------------------5

5 Very distinct process on forehead which projects well above the head between the antennae---*Armadillidium nasatum*
5' Forehead without distinct process projecting well above the head between the antennae---*Armadillidium vulgare*

6 Three-segmented antennal flagellum, no pseudotracheae------------*Oniscus asellus*
6' Two-segmented antennal flagellum, pseudotracheae distinct-----------------------7

7 Antennal joints banded with white, frosty narrow body with abruptly narrow abdomen, 2 pair distinct pseudotracheae, moves quickly----*Porcellionides pruinosus*
7' Antennal joints not prominently banded with white----------------------------------8

8 Dorsal surface of body smooth and strongly convexed, capable of rolling into a ball, 5 pair distinct pseudotracheae--------------------------------------*Cylisticus convexus*
8' Dorsal surface not as above, incapable of rolling into a ball-------------------------9

9 Five pair of pseudotracheae, posterior margin of first thoracic segment curved, 7th leg of male with prominent keel-like expansion on dorsal border of third segment from distal end--*Trachelipus rathkei*
9' Two pair of pseudotracheae, posterior margin of first thoracic segment straight, no keel-like expansion on male 7th leg---10

10 Double longitudinal row of yellow patches on dorsum, head and abdomen darker than thorax, ventral abdomen dark, tubercles slight-----------*Porcellio spinicornis*
10' Not as above, color often but not always gray, distinct tubercles very prominent on dorsal surface including head--*Porcellio scaber*

Table 3. Percent gravid females in different months for Wisconsin isopod populations collected in 1995 except where otherwise noted (dash = no data).

Species Family ($n_{Total\ Female}$)	M	J	J	A	S	O
Hyloniscus riparius, Trichoniscidae (20)	-	0	-	80	-	-
Miktoniscus medcofi, Trichoniscidae (1)	-	-	-	-	-	0
Trichoniscus pusillus, Trichoniscidae (21)	-	-	-	-	-	10
Oniscus asellus, Oniscidae (4)	-	-	-	-	-	0
Armadillidium nasatum, Armadillidiidae (3, 1993)	-	-	0	0	0	-
Armadillidium vulgare, Armadillidiidae (12, 1996)	0	60	100	-	0	-
Cylisticus convexus, Cylisticidae (90)	0	69	14	0	0	0
Porcellio scaber, Porcellionidae (59)-	79	100	-	0	0	
Porcellio spinicornis, Porcellionidae (129)	0	79	31	0	0	0
Porcellionides pruinosus, Porcellionidae (5) -	67	-	-	-	0	
Trachelipus rathkei, Trachelipidae (147)	0	74	46	13	0	0

Table 4. Percent of females gravid (=females with eggs+females with young) and percent of the gravid females that had young rather than eggs in Wisconsin *Trachelipus rathkei* in 1996.

	SOUTH		NORTH	
	Gravid ($n_{Total\ Female}$)	With young	Gravid ($n_{Total\ Female}$)	With young
May	58.1 (43)	00.0	40.0 (15)	00.0
Jun	76.9 (26)	45.0	62.5 (16)	00.0
Jul	74.4 (39)	37.9	91.9 (37)	29.4
Aug	03.7 (27)	100	04.3 (23)	100
Sep	00.0 (31)	--	00.0 (25)	--
Oct	00.0 (19)	--	00.0 (31)	--

Separating the paired sample females into those with eggs and those with young gives a more finely tuned picture of the development process. We used the point at which the enlarging embryo breaks out of its outer membrane and has developed pigmented eyes to distinguish between females with eggs and females with young. Gravid females in the May samples carried eggs only. The lag between north and south is statistically significant for June (X^2=6.43, $p<0.05$, d.f.=1), (SAS 1985). In that month 45% of the gravid females from the southern sample carried young, whereas none of the gravid females from the northern population carried embryos that had developed past the egg stage at that time. In the August samples, gravid females were no longer carrying eggs, only young.

The sex ratios in our 1996 samples of *Trachelipus rathkei* are presented in Table 5. These data seem to indicate a fairly consistent difference between the ratios in northern and southern samples. In general, southern samples were at least two-thirds females (except for the October end-of-the-season sample), while those from the north were more evenly divided between the sexes. Chi-square testing on pooled north/south totals shows this difference to be statistically significant (x^2=13.96, $p<0.001$, d.f.=1) (SAS 1985).

Table 5. Sex ratio in Wisconsin *Trachelipus rathkei* populations in 1996.

	SOUTH			NORTH		
	Male	Female	(n/n)	Male	Female	(n/n)
May	24.6%	75.4%	(14/43)	61.5%	39.5%	(24/15)
Jun	33.3%	66.7%	(13/26)	50.0%	50.0%	(16/16)
Jul	17.0%	83.0%	(8/39)	14.0%	86.0%	(6/37)
Aug	25.0%	75.0%	(9/27)	54.0%	46.0%	(27/23)
Sep	24.4%	76.6%	(10/31)	53.7%	46.3%	(29/25)
Oct	55.8%	44.2%	(24/19)	39.2%	60.8%	(20/31)
TOTAL			(78/185)			(122/147)

The differing proportion of females was also statistically significant for the May samples (X^2=13.24, p<0.001, d.f.=1), (SAS 1985). North/south sex ratio differences in June and July samples were not statistically significant. Sampling in August again showed sex ratios in north and south samples with proportions similar to those found earlier in the year. For both August and September these north/south differences were statistically significant with chi-square values of 7.23 and 8.28 respectively (p<0.01, d.f.=1), (SAS 1985). October north/south ratios were not significantly different.

Discussion

A majority of individuals of Wisconsin terrestrial isopod species live one year or less. Several studies suggest that each sex experiences a die-off after the completion of its phase in the reproductive cycle. McQueen (1976), in a southern Ontario study based on mark-recapture data, found that less than 3% of individuals in his study population survived to the August of their second summer. In both our north and south July samples, males fell to less than 20% of the totals. A die-off of most older males soon after the mating period would explain this large decrease.

Hatchett (1947) compared the results of his Michigan fieldwork with laboratory cultures that he kept of *Cylisticus convexus*, a species where females were also consistently predominant. From this comparison he determined that the mid-summer drop in numbers of females (although they remained a

majority) was due to a die-off of some females during the molt following the early summer period of gravidity and subsequent release of young from the marsupium, a phenomenon which he had observed in the laboratory.

Souty-Grosset et al. (1988) reared females of different geographic origins under varying photoperiods and found that long days stimulated reproduction in all. But, whatever the conditions, females from higher latitude localities began to breed later than ones from lower latitudes. The ability of the females to remain in a reproductive state after a first brood was also related to their latitude of origin, showing a correlation with those climates where milder conditions favor a longer breeding season.

These phenomena might also be occurring in Wisconsin populations of *Trachelipus rathkei* and provide at least a partial explanation of some of the observed differences. Phenological differences in reproduction can be followed in a month-to-month comparison of our gravidity data. Only 40% of the northern females were gravid in May in comparison to over 58% of the southern females. It was June before more than half (62.5%) of northern females were gravid. After the June peak of 76.9% gravid in the south, the percentage there reversed to show a downward trend in July (74.4%). The peak in the north arrived a month later than it did in the south, with the percentage there still rising in July to a high of 91.9.

The reproductive peak in the north was not only later but also more strongly pulsed. Southern *Trachelipus rathkei* females carried young in three of our monthly samples, while those from the north did so only in two. The early start received by the southern population is most telling in the comparison of June figures for percent with young. None of the northern females carried young while a full 45% of the gravid southern females did. If, as was the case for the species studied by Souty-Grosset et al. (1988), *Trachelipus rathkei* females begin to breed earlier and remain in a reproductive state for longer in southern Wisconsin populations than they do in northern ones (as our gravidity data seem to indicate), this may reveal some of the factors which operate to restrict northward expansion of even a species as widespread as this one. Although *Trachelipus rathkei* does seem to have life cycle parameters which might favor northerly expansion (such as a longer breeding season than other Wisconsin species), the smaller proportion of females in *T. rathkei* populations north of the tension zone is indicative of the population's diminished reproductive ability, in comparison to southern populations.

Sutton (1980) treated the climatic influences affecting the repopulation and distribution of terrestrial isopods across Great Britain after the retreat of Ice Age glaciers. He identified the short, cool summers of parts of Great Britain as being a primary limiting factor for less hardy species. Dangerfield and Telford (1990) hypothesized that selection for favorable environmental conditions for offspring survival dominates this phenomenon. Adults of surface-active, temperate species detect environmental variables such as daylength to cue reproduction. Soil dwelling species are buffered from environmental extremes and may have breeding seasons which extend into autumn. Perhaps this explains our finding that the trichoniscids *Hyloniscus riparius* and *Trichoniscus pusillus* were unique in having an August-October period of gravidity in Wisconsin. Differences in habitat preference, climate of origin, and physiological factors no doubt all influence the variability in the reproductive cycle, setting different northern limits for the various terrestrial isopod species.

Vitagliano et al. (1996) studied sex ratios in two different geographical populations of the isopod *Asellus aquaticus* and found that while one population always had a sex ratio skewed for more females, the other consistently produced more males. To verify a geographic difference in sex ratio in Wisconsin *Trachelipus rathkei* populations, and to differentiate among the various possible causes of these differences, would require a more intensive experimental study to sort out environmental and genetic determining factors (e.g. Ganter & Hanton 1984).

Some of those species which do not have a broad distribution in the state do seem to have a southern concentration for their Wisconsin county records to date. For example, of the 9 new county records of *Armadillidium vulgare* we added in 1996, 8 were from localities south of 44°N. Species like *A. vulgare* display this kind of correlation (Souty-Grosset et al. 1988) and, when they are found further north, seem to be confined fairly strictly to synanthropic habitats. The fact that its reproductive cycle characteristics persisted even after several laboratory generations led Souty-Grosset et al. (1988) to study the component of genetic control in the reproductive response of *Armadillidium vulgare* to photoperiod and temperature.

We hypothesize that differences in life cycle parameters such as those we have presented here cause certain species of terrestrial isopods to have distributions which are more limited in terms of northerly expansion and to have stronger ties to the sheltered situation of human structures. Terrestrial isopod species which have escaped the direct effects of climate by association with the artificial environments of manmade structures are sometimes termed

synanthropes. Sutton (1980) suggested the possibility that a number of those species initially confined to synanthropic sites might gradually become acclimatized and spread out into the countryside in what he termed a process of naturalization. The extra shelter offered by manmade habitats may be especially important in any situation where species are thought to have originated from relatively recent introductions, such as is assumed to be the case for Wisconsin as well as the rest of North America.

Sutton (1980) discussed the expansion of terrestrial isopods into Great Britain following the retreat of Ice Age glaciers in terms of a time span of approximately 10,000 years but in Wisconsin these non-native species, introduced following European settlement, have had less than a tenth of that time to reach their present distributions in the state. This no doubt accounts for the comparatively limited numbers of species and their restricted distributions here.

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