Published in final edited form as:

Mar Freshw Behav Physiol. 2013 December 1; 46(6): 419–430. doi:10.1080/10236244.2013.834110.

Sexual Reproductive Biology of a Colonial Rotifer *Sinantherina socialis* (Rotifera: Monogononta): Do mating strategies vary between colonial and solitary rotifer species?

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Abstract

In many aquatic invertebrates including monogonont rotifers, sex provides genetic variation and dormant stages that allows dispersal in time and space. While the reproductive biology of some solitary monogonont rotifer species is known, little is known concerning mating behaviors in colonial rotifers. Coloniality poses unique challenges to the typical mating behavior of solitary rotifers. For instance, most species engage in circling behavior, where the male swims in close proximity to the female. In colonial forms, access to a particular female may be hindered by nearby colony mates. Here we provide descriptions of (1) male morphology, (2) mating behavior, and (3) types of eggs of the widespread colonial rotifer *Sinantherina socialis*, and discuss modifications in mating strategies as a consequence of coloniality. Two important differences from mating patterns documented in solitary rotifers were found in *S. socialis*. First, duration of circling phase of mating is protracted for males encountering small colonies of females as compared to solitary females. Males encountering single females removed from their colonies behave similarly to those of solitary species. Second, duration of copulation in *S. socialis* is the shortest reported for any rotifer species. Endogamy might occur in this species as sons copulate with their sisters and mothers, at least under laboratory conditions. Examples of behaviour in linked video clips.

Keywords

invertebrate reproduction; colonial rotifer; *Sinantherina socialis*; male morphology; mating; behaviour; video analysis

Introduction

Sexual reproduction provides genetic variation that allows populations to adapt to changing environments (Williams 1975) and in some species such as cyclical parthenogenetic monogonont rotifers its product is a diapausing embryo. This embryo remains in a state of

suspended animation until conditions favorable for hatching occur, thus allowing the population to persist under adverse environments. The diapausing embryo (or resting egg) can also serve as a means of dispersal (Wallace et al., 2006). Thus mating and the formation of a viable resting egg is a vital component of fitness in monogonont rotifers.

With about 2,030 species (Segers 2007) and a diversity of life history patterns (Wallace & Ricci 2002), substantial differences in mating behavior may occur among species in the phylum Rotifera. The three classes of Rotifera provide a clear example of the diversity of reproductive strategies within the phylum: The Seisonaceae is a strictly sexual ectoparasitic group; the Bdelloidea are strictly parthenogenetic; and the Monogononta (including *Sinantherina*), contains species where parthenogenesis and sexuality co-occur (Wallace et al., 2006). Although monogonont rotifer mating behavior was first described more than 40 years ago, few studies have provided detailed information on specific components of the mating sequence (Gilbert 1963; Velázquez-Rojas et al. 2002). The basic steps comprising mating behavior in the solitary monogonont rotifer *Brachionus plicatilis* were described by Snell & Hawkinson (1983). These steps are: encounter (the random contact between the male corona and the female), circling (where a mating attempt is initiated and the male circles around the female while keeping contact with her), coronal localization (after circling the male finds the corona or other site to start copulation), sperm transfer (or copulation), and dissociation (Wallace et al. 2006).

Aloia & Moretti (1973) were the first to point out differences between rotifer species (*Brachionus* versus *Asplanchna*) in the site of initial mating attempt and copulation, activity of males, and penile attachment versus penetration. In addition, the “typical” pattern described for brachionid rotifers (Wallace et al. 2006) has been challenged by Velázquez-Rojas et al. (2002) due to the absence of the coronal localization step in *Platyias quadricornis*. Finally, some non-brachionid species (*Epiphanes ukera*, *Euchlanis dilatata*, *Lecane quadridentata*) have specialized mating behaviors (Rico-Martínez & Snell 1997; Schröder 2003; Schröder & Walsh, 2010). For instance, *E. ukera* males guard developing female embryos and initiate mating behavior immediately after the female emerges from the egg (Schröder, 2003).

Mating behavior has been described to some extent in 6 families, 10 genera and about 23 monogonont rotifer species (Velázquez-Rojas et al. 2002; Schröder 2003; Schröder & Walsh, 2010). However, mating behavior has not been characterized in colonial species although there is some information regarding their general reproductive biology. For instance, *Sinantherina socialis* (Linnaeus 1756; Flosculariidae) is one of the few species that has been found to be amphoteric (Champ & Pourriot 1977). Amphoteric females are those capable of producing both diploid and haploid eggs (and therefore producing both females and male neonates) in separate or mixed broods (Gilbert & Williamson 1983). Wesenburg-Lund (1923) described the male of *S. socialis* but did not make any reference to the mating behavior of this species. Champ & Pourriot (1977) mentioned the presence of males and amphoteric females in a population of *S. socialis* in the Loire River in France. Here we describe several aspects of the sexual reproductive biology of the colonial rotifer *Sinantherina socialis*, describe the male, verify that the species is amphoretic, and discuss

differences in mating behavior observed in males interacting with solitary versus colonial females in the context of the general monogonont mating series described above.

Materials and methods

Rotifer culture

Sinantherina socialis was collected from Tule tank in Big Bend National Park TX, USA. (GPS coordinates 29° 14.547 N, 103° 26.635 W). *S. socialis* was grown in filtered Río Bravo water (collected in El Paso, TX) diluted to 0.880 mScm⁻² with filtered spring water (Ozarka®, 0.45 µm Millipore® filters). Rotifers were fed the green algae *Chlorella vulgaris* (strain UTEX 30) and *Chlamydomonas reinhardtii* (strain UTEX 90) grown on proteose and soil extract media respectively (Starr & Zeikus 1993). Thirty colonies were originally collected from the sampling site. Rotifers were grown in the laboratory for one month previous to any experiments and/or observations. Rotifers were grown at room temperature (about 22°C).

Mating behavior test

Cross-mating assays were done according to Snell & Hawkinson (1983) with some modifications. Briefly, this assay involves placing one neonate female larva and one neonate male larva (both < 18 hours old), into 50 µ L of spring water. The number of male mating attempts and completed copulations occurring in a five-minute period was then recorded in each of five replicates using different males and females. A mating attempt was recorded if a male circled around a female maintaining contact with his corona. A copulation was recorded when a male attached his penis to a female. We also observed and recorded data from five mating tests involving one male and one small-size colony (about 12 females). Each tests consisted of virgin males and colonies. We used *t*-tests (Statistica version 7.0) to compare the different characteristics of the sexual reproductive behavior whenever these data were comparable. We also videotaped complete sequences of the mating behavior of this species (*n* = 11) and recorded: a) duration of copulation, b) sites of mating behavior initiation, c) sites of copulation, and d) swimming speed. Additionally, we photographed several steps of the mating behavior, the sexual egg, and the male and female of *S. socialis*. Videotaping of single individuals and colonies was performed with a Sony Power HAD color videocamera placing specimens in standard microscope slides (7.5 × 2.5 cm) in the same culture medium.

Swimming speed estimation

Swimming speed was estimated by videotaping ten female larvae and ten male larvae at 25× magnification for several minutes. The video was then replayed with a clear acetate sheet taped to the monitor and the swimming path of a rotifer was traced for ten seconds. A cartometer was then used to measure the length of the path. Swimming speed differences between females and males in terms of mm/s and body-lengths/s were compared using *t*-tests (*n* = 10). Here swimming speed was determined in a two-dimensional plane, however, this method was shown to give comparable results with other more sophisticated techniques for measuring swimming speed that consider three-dimensional space (see Rico-Martínez & Snell 1997).

Morphology of females, males and eggs

All measurements were made after at least three generations of laboratory culture under controlled conditions and a standard amount of food. Morphometric characterization of females, males and the three types of eggs known in this species: a) male unfertilized sexual egg, b) female asexual egg, and c) female fertilized sexual egg, were performed by direct observations. We measured maximum length (ML), and maximum width (MW) of the body, and maximum length and maximum width of the egg. Animals were transferred to a standard microscope slide with the same culture medium and then videotaped. All measurements were taken from 20 healthy animals from the videotape (animals were not preserved). We conducted two-tailed t-tests to compare females and males, and the production of the three types of eggs found in this species. For most comparisons, the number of replicates equaled 20.

Experiments to determine the percentage of amphoteric females

In a controlled experiment, we follow a set of 12 females from birth and recorded formation and size of colonies. We also noted, whether or not there were simultaneously males and females present within a colony to determine the percentage of colonies that are amphoteric. The duration of the experiment was ten days and conditions were the same as for original culture, except that each female was placed in an individual well of a 24-well polystyrene plate (Falcon, USA) and was placed in an incubator at 25°C.

Results

Description of the male of *Sinantherina socialis*

The body consists of three regions: a) a retractile head where the ciliated corona is located, b) a cylindrical trunk with a vestigial digestive system lacking a mastax and a primitive reproductive system with a single testis with two prostate glands and a short penis, and c) a foot (Fig. 1, Videos 1 & 2). There is clearly sexual dimorphism in this species. A pool of 20 randomly selected females is 3 to 8 times larger than a pool of 20 randomly selected males (Fig. 2; Table 3; t-test, $p < 0.001$; $n = 20$ for both maximum length (ML) and maximum width (MW) comparisons).

Mating behavior

In addition to the 5-minute tests, we observed and videotaped more than 25 complete episodes (total observation time was about twenty hours over a three week period) of mating behavior in *Sinantherina socialis*. In 80% of these episodes we observed the coronal as the preferred site for a mating attempt (also called mating initiation site or mating behavior initiation site) and in 63.6% the corona is the preferred site of copulation (Table 1). Figure 3 shows representative copulations. In five-minute tests, the percentage of encounters becoming mating attempts was 48.7 ± 16.8 for males mating with individual females ($n = 5$; Table 2). This fits the range (15 to 70%) of most of the species studied so far (Rico-Martínez & Snell 1997). However, we found significant differences in the percentages of encounters becoming mating attempts between solitary versus colonial rotifers. Males attempted to mate with colonies in 32.0% of encounters versus 48.7% ($n = 5$; $p < 0.05$) of encounters

with single individuals (Table 2). One copulation event was recorded during the five-minute mating tests (Table 2). However we recorded 5 copulations in our videotape observations (Video 3).

The mean duration of copulation observed (16.6 ± 7.0 s; see Table 1) is the shortest recorded for a rotifer (25 to 607 s) (Rico-Martínez & Snell 1997). We found significant differences in the tests performed with one male mating with one female versus one male mating with one small-size colony (5-15 individuals). The most remarkable difference is in the duration of the circling step. It takes a few seconds (6.2 ± 3.6 s) for a male to circle an individual female. However, it can take several minutes (330.5 ± 260.7 s) to circle around a mid-size colony (16-40 individuals). This difference was statistically significant ($t = 2.63$, $p = 0.05$, $df = 4$).

We also made observations of the number of diapausing eggs carried by an individual and the frequencies of individuals within a colony carrying diapausing eggs. We observed individuals carrying up to 5 resting eggs (Videos 4 & 5). We found that in colonies with 11, 12 and 32 individuals, 33%, 25% and 27% of the females respectively were carrying diapausing eggs.

Swimming speed

Female larvae swam faster than male larvae in terms of absolute speed ($t = 3.19$, $p = 0.01$, $df = 9$; in mm/s), but in terms of body lengths/s *S. socialis* males swam 1.7 times faster ($t = 2.80$, $p = 0.02$, $df = 9$; see Table 1). In general the swimming speed of this species falls in the range (0.18 to 1.04 mm/s) reported for other male rotifers (Rico-Martínez & Snell 1997).

Size of eggs, females and males

For comparison of the sizes of females, males, and of the three types of eggs in this species, see Table 3. Figure 4 shows the resting egg of this species. The fertilized sexual egg (diapausing egg) of *S. socialis* is similar in size (153 μ m in length) to the other fertilized sexual eggs of other rotifer species. However, this resting egg is more rounded than those of the brachionid rotifers. The diapausing egg of *S. socialis* is significantly longer ($t = 4.51$, $p < 0.001$, $df = 19$) and wider ($t = 12.22$, $p < 0.001$, $df = 19$) than the parthenogenetic egg. Although there are significant differences in the maximum width of the resting egg with the sexual unfertilized egg ($t = 15.0$, $p < 0.001$, $df = 2$) as expected, there is no significant difference in length with the sexual unfertilized egg ($t = 1.73$, $p = 0.225$, $df = 2$).

Presence of amphoteric females

In the set of 12 females we followed from birth, we found that 9 (75%) produced only female offspring while 3 (25%) were amphoteric after four days. All 12 females produced small-size colonies (5-15 individuals) within 10 days. No resting eggs were recorded during this period for the amphoteric females.

Discussion

This is the first detailed description of the mating behavior of a colonial, amphoteric and sessile rotifer. In many aspects the mating behavior of *S. socialis* is similar to that of other monogonont rotifer species. The female assumes a passive role throughout the process, the circling step is present, males are smaller than females, and faster swimmers, and the initiation of mating behavior and copulation occurs mainly at corona. However, several deviations from the typical pattern are observed in *S. socialis*. The most remarkable difference is the duration of the circling step. This step usually takes only a few seconds in most species (Rico-Martínez & Snell 1997). However, for *S. socialis* males attempting to mate with females in a mid-size colony of 16 to 40 individuals, this step can take more than 5 minutes (Table 1). We also found significant differences in the percentage of encounters developing into mating attempts when a male encounter a solitary female (larva or artificially detached from colony), versus a small colony of 12 individuals. Another important difference is the body size ratio between males and females. By using the mean ML values reported in Table 3, a 3.1 to 1 ratio between body size in females and males is expected. Due to the wide size range of *S. socialis* females, the males (who have a much less size variation) can mate with females of their own size (1:1 ratio) as well as with females up to 8 times larger (see Fig. 3). Similar variation in the size range of females was reported by Garcia (2004). The range of variation in the female/male size ratio recorded here is substantial larger than seen previously in rotifers (see Rico-Martínez & Snell 1997; Melone, 2001).

In studying the mating behavior of a colonial rotifer there are several questions that naturally emerge. One is the possible interference caused by the colonial feeding behavior. We observed that in many cases males were carried away from large colonies (> 40 individuals), because of the current produced by colonies engaged in filter feeding. Obviously this effect is not seen when a male mates with an individual female. It is difficult to test the potential role of this interference for the entire mating behavior process because many unknown factors are involved (differences in age, fertility, endogamy, etc.). A second question regards the incidence of endogamy (R. L. Wallace, pers. comm., 2004). We made anecdotal observations of males attempting to mate with their sisters. In a more controlled experiment, we follow a set of 12 females from birth and we found that 9 produced only females, and 3 were amphoteric after four days. All 12 females produced small-size colonies (5-15 individuals) within 10 days. This observation substantiates Garcia (2004) findings of colonies being formed from single individuals. For the 3 amphoteric females, we observed attempted mating and copulation between brother and sisters, and perhaps with the mother. However, no diapausing eggs were produced when the experiment was terminated at 10 day. These data corroborate the findings of amphoteric females in this species by Bogoslavsky (1958) and Champ & Pourriot (1977). The presence of amphoteric females in rotifers seems to be restricted to very few species, as this report represents the only recording in more than 31 years. This is only the fifth species where amphoteric females have been documented. The other four species are: *Asplanchna herricki*, *A. priodonta*, and *Conochiloides coenobasis* (Gilbert, 1974), and the ovoviviparous rotifer *Trochospaera solstitialis* in which males never leave their mother (McCullough & Lee, 1980).

Optimal sexual reproductive patterns in rotifers may be explained by hypotheses as defined by three factors: a) habitat deterioration, b) male-female encounter, and c) resource demand (Serra et al., 2004). The resource demand hypothesis best fits the conditions found in the Chihuahuan Desert where our *S. socialis* population was originally collected. This hypothesis suggests that when favorable conditions occur they induce high population densities and sexual reproduction of rotifers. Our population was collected from temporary habitat, a former cattle tank, that fills during seasonal rain events and may persist for days to months. High chlorophyll concentrations (Walsh, unpub. data) indicate that food availability for rotifers is high and may promote rapid population development. In addition these desert aquatic systems are known to select for rapid population development and high rates of sexual reproduction in rotifers (Schröder et al 2007).

What are the implications of the presence of colonial individuals, amphoteric females, and the longest circling step with the shortest copulation time? A long circling step, such as that employed by male *S. socialis* may be a potential mechanism to decrease inbreeding in temporary habitats with high population densities. This behavior would facilitate identification of appropriate mates. In *S. socialis* the protracted circling state is followed by very rapid copulation. male uses this long circling step to find adequate mates, but once they find adequate mates the copulation is fast. It is likely that this combination of characteristics result in higher fertilization rates; thus, ensuring a rich supply of resting eggs to survive the dry season of this rotifer population inhabiting the Chihuahuan Desert. This strategy is also consistent with our observation of the lack of diapausing eggs production, in spite of attempted matings and copulations, between brothers and, sisters or mothers.

Schröder (2003) demonstrated that *Epiphanes senta* (now *E. ukera*) shows precopulatory guarding behavior. He argued that mating behavior is far more complex than previously thought and that more intricate patterns will be unveiled as studies become more comprehensive. A similar suggestion was made by Velázquez-Rojas *et al.* (2002). Our present contribution supports this view, and adds new information to the modern theoretical framework of sexual reproductive behavior in rotifers that has been slowly developing since the early work of Gilbert (1963). Our results provide the first mating behavior observations for a colonial, amphoteric and sessile species, and contribute detailed mating behavior information for an additional rotifer species. To assess the importance of our observations, additional information on similar species is needed to confirm whether they represent the “typical” behavior for colonial rotifers, or alternatively an adaptation found in rotifers inhabiting temporary habitats (e.g. Chihuahuan desert ponds under selection for rapid production of diapausing stages). However, these findings are an important first step increasing our knowledge of the complexities of the sexual reproductive behavior in colonial rotifers.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

The authors thank Dr. Robert Lee Wallace of Ripon College, Wisconsin, for his comments and suggestions as well as two anonymous reviewers. Rotifers were collected under permit BIBE-2001-SCI-0058 to E. J. Walsh at Big Bend National Park. We thank the Universidad Autónoma de Aguascalientes and NIH NCRR S06GM80012-30 for funding.

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Figure 1.
A micrograph of the male *S. socialis*. Bar = 40 μ m.

Figure 2.
An amphoteric female *S. socialis* carrying one parthenogenetic egg and two unfertilized sexual eggs. Bar = 200 μm .

Figure 3.
Copulation of a *S. socialis* male with a conspecific female at the corona. Bar = 100 μ m.

Figure 4.

A) The *S. socialis* parthenogenetic egg. B) resting egg. Bar = 25. μ m.

Table 1

Summary of the sexual reproductive behavior of *Sinantherina socialis*. These data were obtained from videotape observations, and the results of the mating tests. Results are the mean $\pm$ one SD.

Characteristic	Value
Site of initial mating attempts (n = 10)	Corona (8) Lateral anterior 1/3 part of body (2)
Site of copulation (n = 11)	Corona (7) 1/3 lateral anterior part of body (1) 2/3 lateral posterior part of body (2) Mid-lateral part of body (1)
Duration of copulation (n = 5)	16.6 $\pm$ 7.0 s
Duration of circling (with one female) (n = 5)	6.2 $\pm$ 3.6 s
Duration of circling (midsize colonies) (n = 6)	330.5 $\pm$ 260.7 s
Female Swimming speed (n = 10)	0.5 $\pm$ 0.2 mm/s
Male Swimming speed (n = 10)	0.3 $\pm$ 0.1 mm/s
Female Swimming speed (n = 10)	1.4 $\pm$ 0.6 body-lengths/s
Male Swimming speed (n = 10)	0.8 $\pm$ 0.4 body-lengths/s

Table 2

Summary of mating behavior tests with *Sinantherina socialis* males with individual females and small-size colonies (5-15 individuals). Results are the mean $\pm$ one SD. Differences in % mating attempts and % copulations between individual and colonial mating tests were significant (two-tailed t-test, $p < 0.05$).

Mating test	Encounters	% Mating Attempts	% Copulations
Individual n = 5	29	48.7 $\pm$ 16.8	20.0 $\pm$ 44.7
Colonial n = 5	31	32.0 $\pm$ 1.8	0 $\pm$ 0

Table 3

Morphological characterization of individuals (females and males) and the three types of eggs of *Sinantherina socialis* (n = 20 except when stated otherwise. Results are the mean $\pm$ one SD).

Individuals	Maximum Length (Mean $\pm$ SD)	Maximum Width (Mean $\pm$ SD)
Females	628.9 $\pm$ 317.5	120.4 $\pm$ 49.7
Males	200.8 $\pm$ 19.0	69.0 $\pm$ 11.4
Parthenogenetic eggs	130.6 $\pm$ 15.9	91.5 $\pm$ 18.2
Sexual eggs	153.0 $\pm$ 10.1	125.9 $\pm$ 10.8
Sexual unfertilized eggs (n = 3)	145.0 $\pm$ 5.0	80.0 $\pm$ 0.0