

Precopulatory mate assessment in relation to body size in the earthworm *Lumbricus terrestris*: avoidance of dangerous liaisons?

Nico K. Michiels, Andrea Hohner, and Iris C. Vorndran

Max-Planck-Institut für Behavioral Physiology, Seewiesen, Postfach 1564, D-82305 Starnberg, Germany

In the earthworm *Lumbricus terrestris* L., mating occurs on the soil surface, but partners remain anchored in their burrow and mating is preceded by repeated mutual burrow visits between neighbors. This study focuses on body size as one possible trait that earthworms may assess during these burrow visits. Size-related mate choice is predicted to result in size-assortative mating, which we found in one field sample ($n = 90$ pairs), but not in a second ($n = 102$). We discovered that when mates separate, one of them can be pulled out of its burrow. This was more likely for small individuals or those mating across wide distances. In a subsequent greenhouse experiment, we allowed focal individuals to mate with two neighbors of different sizes. Relative size affected neither mating rate nor primary preference, but focals mated sooner with the same-sized neighbor than with a differently sized one. Small focals visited large neighbors more often than small ones. We conclude that size influences mate choice as well as the outcome of mating and discuss how the “tug-of-war” that ends a mating contributes to this result. Precopulatory visits may involve assessment as well as enticement to lure the partner closer to the individual’s own burrow, in order to minimize the risk when mating with a partner that is large or far away. *Key words*: assortative mating, cost of sex, sexual conflict, simultaneous hermaphroditism, size assessment. [*Behav Ecol* 12:612–618 (2001)]

In species with separate sexes, mating success typically contributes more to male lifetime reproductive success (LRS) than to female LRS (Arnold, 1994; Bateman, 1948; but see Dewsbury 1982), and the same logic applies to simultaneous hermaphrodites (Arnold, 1994; Charnov, 1979). Hence, the basic expectation is that the male role of a hermaphrodite should be, in principle, more eager to mate than the female role. This, however, holds only for as long as the male role remains cheap. At elevated densities, promiscuity favors increased sperm investment (Greeff and Michiels, 1999). Moreover, allosperm digestion is widespread (Michiels, 1998, 1999) and will favor even larger ejaculates. As a result, allocation to sperm may become as expensive as allocation to eggs (Greeff and Michiels, 1999; Pen and Weissing, 1999). Consequently, individuals able to donate sperm may reject receptive mates when the expected gain in paternity does not outweigh the costs. Leonard (1999) comes to a similar conclusion by arguing that the male role is less preferred because it has a higher variance in success rate.

Precopulatory assessment could take several forms. First, individuals may prefer mates that reciprocate, as allosperm digestion will compensate for their own investment (Greeff and Michiels, 1999). The resultant “sperm trading” is known from sea slugs (Leonard and Lukowiak, 1984, 1991), free-living flatworms (Michiels and Bakovski, 2000; Vreys and Michiels, 1998) and possibly cestodes (Schärer and Wedekind, 1999) and may be widespread (Leonard, 1990). Second, sperm donors may prefer fecund (typically larger) mates. Size-related mate choice is known from some hermaphrodites (Tomiyama, 1996; Vreys and Michiels, 1997; Yusa, 1996; but see Baur, 1992; Peters and Michiels, 1996). Dewitt (1996) showed that in a

hermaphroditic snail in which only unilateral insemination is possible, small individuals prefer the male role when encountering a large mate (but see Wethington and Dillon, 1996). In *Aphysia*, individuals donate more sperm to large partners (Yusa, 1994). In the hermaphroditic polychaete genus *Ophryotrocha* (Premoli and Sella, 1995; Sella and Lorenzini, 2000), large individuals play the female role and their partners play the male role, but these roles alternate when sizes reverse due to heavy investment in eggs.

Oligochaetes represent a large taxon of exclusively simultaneously hermaphroditic animals with reciprocal insemination (Edwards and Bohlen, 1996). The earthworm *Lumbricus terrestris* L. lives solitarily in vertical burrows 1–3 m deep (Sims and Gerard, 1985). It forages and mates on the surface at night. During mating, partners remain anchored in their home burrow with their tail end, allowing for instant retreat. Mating costs are presumed to be high. First, mates are so tightly interlocked that withdrawal after disturbance is slow, compared to single individuals (Michiels NK et al., personal observations). Second, copulations start late, last long, and often end well after sunrise (this study). Hence, pairs are more exposed to desiccation and predators than are single individuals. Third, copulations involve physiological costs in the form of sperm and mucus production, as well as large-scale damage caused by the partner’s copulatory bristles or setae (Grove, 1925). Finally, the sperm-receiving organs (spermathecae) re-sorb sperm (Grove, 1925), which is known to raise the optimal amount of sperm an individual needs to donate (Greeff and Michiels, 1999).

Nuutinen and Butt (1997) found that neighboring *L. terrestris* regularly stick their heads into each other’s burrows. When this happens, the visited individual may follow the slowly retracting visitor to the visitor’s burrow entrance and vice versa. An irregular series of reciprocal visits like these was found to precede most copulations and was interpreted as a kind of courtship (Nuutinen and Butt, 1997).

In this study, we addressed one possible function of visiting behavior in *L. terrestris* estimation of partner size. Because burrow diameter is related to the occupant’s body weight

Address correspondence to N.K. Michiels, who is currently at the Department for Evolutionary Biology, Westfaelische Wilhelms-Universität, Huefferstrasse 1, D-48149 Muenster, Germany. E-mail: michiels@uni-muenster.de.

Received 29 March 2000; revised 3 November 2000; accepted 6 December 2000.

(Shipitalo and Butt, 1999), individuals may visit neighboring burrows to assess the occupant's size. Size may indicate health or vigor or female fecundity. Although large earthworms do not appear to produce more cocoons (Butt and Nuutinen, 1998), they tend to produce heavier cocoons (Nuutinen V, personal communication) and larger offspring (Solmsdorff K and Michiels NK, unpublished data). An allometric correlation between individual mass and clitellum size (cocoon-producing skin structure) probably explains this relationship. Fecundity increases with size in other hermaphrodites as well (Baur, 1992; DeWitt, 1996; Madec et al., 2000; Schärer et al., 2001; Trouvé et al., 1999; Vreys and Michiels, 1997; Wedekind et al., 1998; Weinzierl et al., 1999). Although size may be a sign of quality, it may also be a risk indicator, as explained below.

In the first part of the study, we investigated size-dependent mating in the field. We expected matings to be assortative by size, as favored individuals would reject suboptimal partners, leaving the latter no other choice than to accept another suboptimal partner. During trial observations preceding this study, we observed that when partners pull apart at the end of a mating, one individual is occasionally pulled out of its burrow. To determine the significance of this tug-of-war, we also estimated the likelihood of being on the surface in relation to body mass and distance between partners in the field.

In the second part of the study, we recorded sexual interactions and matings in experimental groups consisting of one focal individual and two neighbors: one of the same size as the focal individual, and one of a different size (larger or smaller). We expected to obtain indications whether size-related mate choice, if any, is inspired by risk reduction (preference for small partner when small) or a preference for fecundity (constant preference for the larger neighbor). In either case, one would predict assortative mating.

METHODS

Biology of *Lumbricus terrestris*

L. terrestris is probably the best studied earthworm (Edwards and Bohlen, 1996). Natural densities are around 30–200 individuals/m², and burrows can go down to 2 m or more (Sims and Gerard, 1985). During the active season (spring to autumn) animals are closer to the surface. Foraging on the soil surface is nocturnal (“nightcrawler”) and strongly depends on the presence of dew (“dewworm”). The mating process has been described meticulously by Grove (1925) and involves a unique mechanism of reciprocal sperm exchange: individuals oppose their genital regions (clitellum and segments 5–15) while attaining a typical S-shaped posture. Slime and specialized setae are used to tighten the bond. Matings typically take place after midnight and may last until well after sunrise (max 1.5 h later; Michiels NK et al., personal observations). At the end of a mating, individuals start to pull hard and separate with a tearing sound (Michiels NK et al., personal observations).

Choice of a field site

Individuals were collected from a public golf course near Feldafing, south-southwest of Munich. The density was visually estimated to be around 50 adult worms/m². Standard sampling methods such as chemical or electrical extraction or digging could not be used, but the short grass allowed us to see pairs on the surface from a 5 m distance before disturbing them. The homogeneity of the surface also reduced spatial structure within the population, which is essential (see below). All individuals used in this study were collected from a single lawn of approximately 30 × 100 m.

Collection in the field

After a series of trial visits, we collected two samples of mating pairs between 0300 and 0715 h on 1 May and 9 June 1998. Worm pairs were located using head-mounted torches covered with dark red foil while slowly walking in a systematic pattern across the lawn. Two people were needed to grab and hold on to one individual each. Worms were put in numbered vials. We then measured the distance between burrows (± 5 mm) and the distance to two fixed points at the edge of the lawn using a laser range finder (± 1 m; see below). Incomplete pairs of which one partner escaped or was injured were not collected, but position and burrow distance were recorded. We also noted whether one mate was not properly anchored (tail tip at burrow entrance or surfaced) when collected. Out of 309 attempts to collect a pair, 192 (62%) were successful. Burrow distance could be obtained for 302 pairs. On 9 June, we also collected all single individuals ($n = 8$) that were found lying freely on the surface in the final hours of the night (0300–0500 h), when single individuals are normally already below the surface. Swollen genital regions and mucus remnants showed that they had mated recently, and we assumed that they had been pulled out of their burrow by their partner. Such individuals were also witnessed on 1 May, but not collected. In the laboratory all animals were rinsed in tap water, dried on paper tissue, and weighed alive (± 1 mg). Measurements were finished within 6 h after collection. As a measure of size, we used weight rather than length. Length is impossible to measure reliably in living animals, whereas fixed animals are unnaturally contracted, which results in an underestimate of an animal's ability to stretch over long distances.

Spatial heterogeneity

Heterogeneity of the lawn could lead to some patches housing smaller individuals than others. This confounding effect would result in size-assortative mating in the absence of mate choice. We checked for spatial structure by determining the position of each pair on the lawn using the distance measurements described above and simple triangulation. Using a K-means cluster analysis (SPSS), we grouped pairs spatially and temporally (sampling time). The analysis was repeated twice to define 6 and 10 clusters for each sampling date (4 analyses). We then statistically compared individual size between clusters. None of the comparisons revealed significant differences (p values between .19 and .87). We therefore conclude that local size variance did not differ from overall variance within the study site, as expected for a homogeneous environment.

Effects of size in the greenhouse

After a series of trial runs, an experiment was designed such that one focal individual could choose between two partners: one of the same size, and one of a different size; the latter could either be smaller or larger, in a size ratio of 1:1.5 (Figure 1). Half of the trios had a large focal individual that was combined with one equally large and one smaller neighbor (SLL trios), whereas the other half consisted of small focal individuals paired with an equally small and a large neighbor (SSL trios). Animals were taken from a sample of 73 pairs collected on 26 April. We chose focal individuals randomly from this set. We then looked for the closest matching “identical” and “different” individual to make a trio. If this was not possible, another focal animal was taken. This procedure was repeated until twelve trios of each kind (SSL and SLL) were assembled. At the start of the experiment, equal individ-

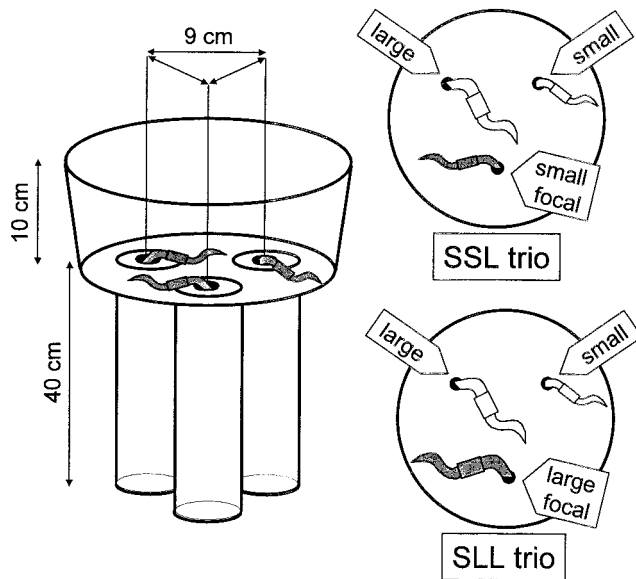


Figure 1
Schematic drawing of a trial bucket with three worms (left) and the two treatments (right). A large or small focal individual was combined with two neighbors, one of the same size and one of a different size, resulting in SSL and SLL trios. The size difference between the focal and the different sized individual was 1:1.5 (see Methods).

uals within a trio differed by only $0.299 \pm 0.298\%$, whereas unequal individuals differed by $41.7 \pm 0.98\%$. The average weight of small and large individuals was 2.32 ± 0.23 g (range 1.84–2.80 g) and 3.56 ± 0.43 g (range 2.89–4.50 g), respectively.

Trios were housed in a bucket mounted on three 40-cm PVC pipes (Figure 1). Pipes were filled with earth in which an artificial burrow of 5 mm diameter was made by means of a metal rod. The bottom of the bucket and the top of the pipes were covered with a 2-cm layer of soil mixed with decomposing leaves and some chopped vegetables (carrots, onions, and salad greens) that had been frozen to soften them. Buckets were sprayed with water vapor in the evening and morning. The greenhouse was shaded, and doors and windows were kept open to prevent overheating and to allow for cooling at night.

Sets of six buckets (3 SSL and 3 SLL trios) were put together in a single large container in an alternating pattern and recorded in infrared using a time-lapse video recorder. Four complete set-ups ran simultaneously ($4 \times 6 = 12 + 12$ trios of each type). Recording commenced shortly before dusk and ended between 0800 and 0900 h. The experiment started on 29 April and ran until 13 May (14 nights). Some individuals did not accept the burrow in which they were put, moved out, and stayed in the soil layer in the bucket or made a new burrow in a neighboring pipe. Such trios were discarded for analysis, leaving 11 SLL and 10 SSL trios.

Data collection and analysis

The experiment was designed in such a way that the focal individual could choose without interference. This, however, also allowed the two neighbors to interact with each other. We cannot exclude that this may have affected the differences between the SSL and SLL treatments. Such effects were considered during the analysis. We therefore pay more attention to within-treatment effects than between-treatment effects.

When analyzing precopulatory visits and mate choice, we only used the first mating by the focal individual, which was the first mating in the bucket in 80% of the cases. We noted number, duration, and direction of visits between the focal individual and its neighbors until its first copulation. For a general analysis of mating activity, copulation start and duration, as well as the individuals involved, were recorded for all matings throughout the observation period. Statistical analyses were done using SPSS version 8.0 for Windows. Parametric tests were used when the underlying assumptions were fulfilled, or when an adjustment procedure was available. In SPSS, a corrected t (with adjusted degrees of freedom) is calculated when variances differ in a t test. Box-plots (Figures 4 and 5) represent median \pm 1 quartile (box) and range (lines) excluding outliers. Averages are shown \pm SDs. As discussed more extensively by Vreys and Michiels (1997), traits of hermaphroditic mates cannot be correlated with a regular correlation analysis, but need to be compared using a one-way ANOVA with pair number as factor.

RESULTS

Size-assortative mating in the field?

We collected 90 and 102 intact pairs on each sampling occasion. The variance in body weight within pairs was lower than between pairs on 1 May (ANOVA $F_{89,90} = 1.45$, $p = .040$), but not on 9 June (ANOVA $F_{101,102} = 0.99$, $p = .52$), indicating assortative mating in the first, but not in the second sample. The maximum relative weight difference between individuals was 1:2.3. Differently sized partners were seen stretching or contracting their body between the genital region (segments 8–15) and the clitellum (segments 31–37). This suggests that physical incompatibility of small and large individuals cannot explain assortative mating. Average mass of mating individuals increased from 2.84 ± 0.62 g on 1 May to 3.23 ± 0.73 g on 6 June ($t_{390} = -5.6$, $p < .001$).

Distance between partners in the field

Despite the fact that animals were larger in the second sample, average burrow distance between mating partners was longer in the first sample than in the second (12.2 ± 4.8 cm and 10.1 ± 3.8 cm, respectively; $t_{278} = 4.09$, $p < .001$, including escaped pairs). The maximum distance across which individuals mated was 26.0 cm. In collected pairs the average body weight of the two mates was not related to burrow distance on 1 May ($r_p = .068$, $n = 90$, $p = .53$). Body weight was related to burrow distance, however, on 6 June ($r_p = .209$, $n = 102$, $p = .035$); large individuals mated across larger distances than small individuals in the second sample.

Completely surfaced individuals in the field

We found 14 out of 90 (1 May) and 5 out of 102 (9 June) pairs in which one partner was on or very close to the surface. This proportion was higher on 1 May ($\chi^2_1 = 6.09$, *Exact* $p = .016$). The likelihood of being on the surface was higher when mating with a partner far away (Figure 2). Smaller individuals were also more likely to be on the surface than large individuals (Figure 3). This was particularly true for individuals found singly on the surface, who were significantly smaller than the 204 paired individuals collected during the same night (2.13 ± 1.02 g versus 3.27 ± 0.68 g; $t_{7.3} = 3.13$, $p = .016$).

Greenhouse experiment: general results

Although all individuals were caught while mating 3 days earlier, the first mating was observed during the second night of

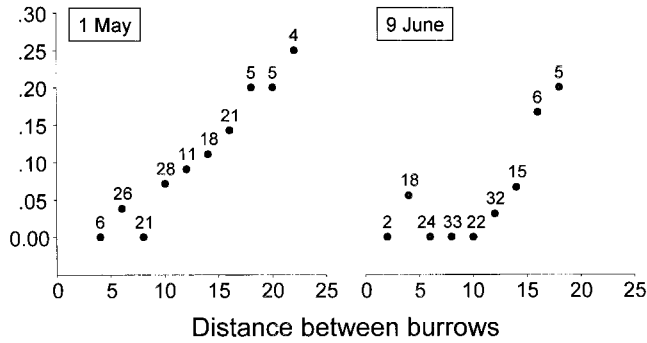


Figure 2
 Proportion of pairs in which one partner was on the surface as a function of the distance between their burrows (in 2-cm classes). X-axis values indicate the lower margin of distance interval. Numbers above points indicate number of pairs in each class. All pairs were used, including those of which one individual escaped. Distance classes with only one pair were ignored. The positive trend is significant (1 May: Spearman rank $r_s = .976$, $n = 10$, $p < .001$; 6 June: $r_s = .757$, $n = 9$, $p = .018$).

the experiment. A distribution of copulation duration of all 53 observed matings showed a bimodal pattern: short matings (minimum, median, and maximum: 2, 11, and 63 min) were considered mating attempts (7 in SSL and 7 in SLL trios). Only those longer than 2 h were considered true matings: they lasted 3.63 ± 0.57 h (range 2.6–5.5 h; $n = 39$; 19 in 10 SSL and 20 in 11 SLL trios). Matings started between 2053 and 0510 h (mean = 0022 ± 0206 h). The latest time at which a mating ended was 0845 h (sunrise around 0700 h). The total number of matings per individual varied from 0 to 3 (9, 33, 18 and 3 individuals in each category). The average rate was 1.24 ± 0.76 matings in 2 weeks or, alternatively, once every 11 days. Considering that all animals were mating when collected 3 days before the experiment, mating rate may be as high as once per 7.6 days. Small individuals mated as often as large individuals during the experiment (Mann-Whitney U test: $Z = 1.381$, $p = .167$).

Precopulatory visits in relation to relative body size

To investigate the effect of relative body size (measured as weight), we only considered behavioral interactions until the first mating of the focal individual. Trios in which the focal worm did not mate or in which one of the two neighbors was not involved in any visiting behavior until the first focal copulation were ignored. We also removed one statistical outlier in which the focal individual in an SLL trio made 107 visits in the course of 10 nights before its first copulation. The second highest number was 34. This reduced sample size to seven SSL and eight SLL trios. The first mating by focals did not suggest a preference for the larger partner: Four out of seven SSL focals mated with their larger neighbor, whereas five out of eight SLL focals mated with the equal-sized (also large) individual. The overall ratio of 9:6 does not diverge from 1:1 ($\chi^2_1 = 0.60$, *Exact* $p = .61$). This suggests the absence of a general preference for large mates, but due to small sample sizes this result should be considered with caution. Copulations occurred earlier in same-sized pairs, suggesting assortative mating. Small focals hesitated longer than large focals (Figure 4).

There was no difference between small or large focal individuals in the total number of visits to their neighbors until their first mating (SSL: 9.86 ± 6.16 ; SLL 14.5 ± 11.4 ; $t_{13} = 0.958$, $p = .35$). However, small focals made more visits to their large neighbor than to the equal-sized alternative (Fig-

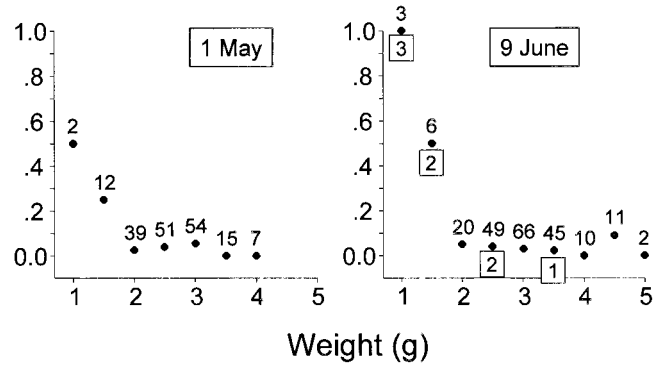


Figure 3
 Proportion of individuals on the surface when still in copula as a function of weight (0.5-g classes). Numbers above points indicate number of individuals in each class. The 9 June data include eight single individuals that were found singly on the surface, but that had finished mating shortly before (numbers in boxes). 1 May: Spearman rank $r_s = -.847$, $n = 7$, $p = .016$; 6 June: $r_s = -.736$, $n = 9$, $p = .024$.

ure 5; Wilcoxon signed-ranks test $Z = 2.03$, $p = .042$). No such difference existed in SLL trios (Wilcoxon $Z = 0.35$, $p = .73$).

A visit series that ended with a copulation consisted of 10.0 ± 9.2 visits, which is more than for series not leading to copulation (1.91 ± 0.63 ; $t_{4,1} = 3.40$, $p = .004$). Treatment had no effect, and data were therefore pooled for this analysis. Visit bouts lasted for 26.1 ± 22.4 min (range 0–72.1 min).

DISCUSSION

We found assortative mating in one field sample early in the season, not in a second taken one month later. Small size and mating with a partner across a long distance increased the likelihood that a mating individual was not anchored in its burrow, indicating that small individuals have a higher likelihood of being pulled onto the surface after the tug-of-war that ends a mating. The small size of eight postmating individuals found singly on the surface confirmed this. In the greenhouse, there were no overall indications for size-assortative

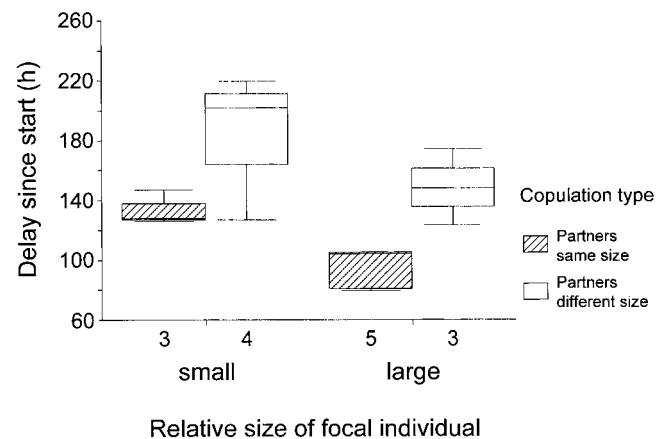


Figure 4
 Box-plot of the delay since the start of the experiment until the first copulation in which the focal individual was involved. Within each treatment (small and large focal or SSL versus SLL trio, see Figure 1), data are split for similarly and differently sized pairs (two-way ANOVA $F_{3,15} = 5.91$, $p = .012$, SSL vs. SLL: $p = .051$, similar vs. different $p = .010$, interaction $p = .78$).

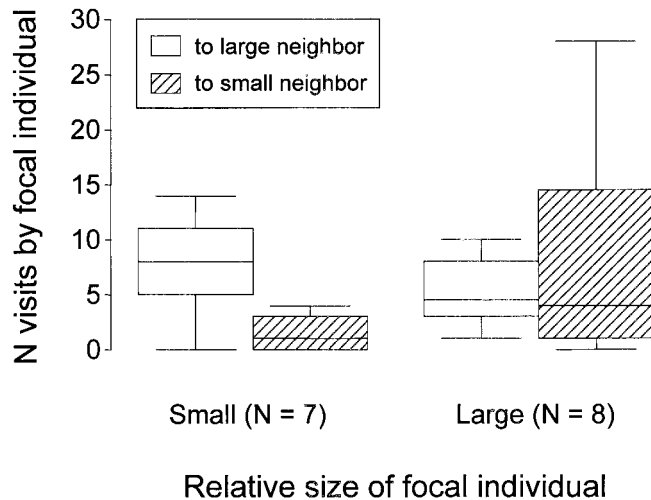


Figure 5
Box-plot of the number of visits by the focal individual to its two differently sized neighbors and small partner, which we a priori assumed to be the larger partner in both treatments.

matings, possibly in part caused by reduced sample size. Yet, pairs of same-sized individuals formed earlier than pairs of differently sized individuals, and this can lead to size-assortative mating. On the other hand, small individuals visited their large neighbor more often than their small neighbor, suggesting a high interest, but maybe also hesitation as suggested by the longer delay until the first mating. Below, we first discuss whether it is possible to find mate choice in the field at all, and then evaluate the relevance of the tug-of-war for mate choice.

Assortative mating in the field may require a synchronizing mechanism

How likely is it to find size-assortative mating in the field? Because *L. terrestris* lives in a permanent burrow, mating is only possible within the neighborhood, limiting the opportunity for choice. Figure 6 suggests that for an estimated density of 50 adults/m², there may be only little opportunity for choice, unless some external mechanism ensures synchronization of mating activity. Weather strongly affected nocturnal activity, with calm, clear, and cool nights being best (Michiels NK et al., personal observations). Prolonged periods of unfavorable weather (e.g., rainy nights) followed by weather improvement may therefore serve as a synchronizer. The lunar cycle also affects earthworm activity: preliminary data suggest very low earthworm activity around the full moon (Solmsdorf K, Michiels N, and Vorndran I, personal observations).

The tug-of-war: a unique and new mating cost

L. terrestris individuals are sometimes pulled out of their burrow by their mate. Because pairs were still mating when collected in the field, it is not possible to judge whether surfaced individuals would have found their way back to their burrow. But eight single individuals found on the surface on 9 June suggest that many may not. This adds an important trade-off to the benefits of choosiness: by increasing the radius within which potential partners are assessed, the risk is increased as well, particularly for a small individual. The tug-of-war predicts that individuals should prefer small partners, whereas size-related fecundity predicts that they should prefer a large partner. The optimal solution of this trade-off will be determined

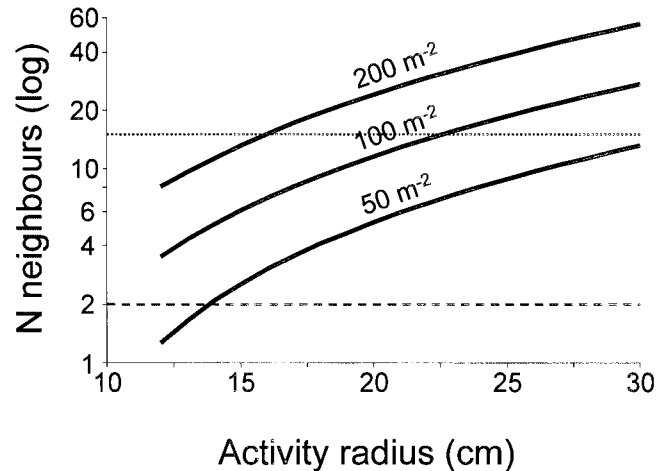


Figure 6
Is choice possible in the field? Using density and the surface of a circle with the x-axis value as radius, we calculated the number of neighbors an individual can expect to find within its home range around the burrow. Dashed line: two neighbors representing the minimum for mate choice and assuming that both are receptive. Dotted line: number of neighbors required to have two of them in a reproductive condition assuming an average mating rate of once per 7.6 days and constant mating activity on every night. Note that only adult individuals are considered.

by burrow distance: at short distances fecundity-related choice may be predominant, whereas over long distances minimizing the risk may be more important. In both cases, assortative mating is expected.

The function of multiple visits: assessment or attraction

Why do earthworms need repeated visits? If they only want to assess size, a single visit would be sufficient. Anecdotal observations and pictures of mating pairs in the field have documented that pairs often mate closer to the burrow of one of the two partners. This offers a tentative explanation for multiple visits: they may represent an attempt to mate closer to home, thus reducing the risk of having to stretch out over a long distance. The back-and-forth movements during a visit series would then represent a conflict about the exact locality where they should attain the S-position. Both mate enticement and mate assessment may therefore be at work. Visit frequency may be a measure of the reluctance to mate, as eager mates should give in early and mate close to the neighbor's home.

This view offers a tentative explanation for the difference between the two field samples. In the first, early in the season, the density of sexually active individuals was probably low, as suggested by the fact that individuals reached out farther for their mating partners in the first than in the second sample. Because risk increases with distance and individuals were smaller, choosiness should have been higher in the first sample, as was the case. There were also more nonanchored individuals in the first sample. The absence of choosiness in the second sample would then suggest that at a higher density of sexually active individuals, earthworms prefer the safety of mating close to home over the risks associated with increased choice opportunities. In the greenhouse, the large number of visits by small individuals to large partners is suggestive of the fact that small individuals have a bigger conflict with a larger neighbor over the location of the copulation. It also offers an explanation for why similarly sized pairs mated sooner than differently sized pairs.

Sexual conflict in hermaphrodites

This study adds another example to the multitude of hermaphrodite mating conflicts, in which similarity of interests between identical partners results in conflicts that may be difficult to solve (Baur, 1998; Leonard 1990, 1991, 1999; Michiels 1998; Michiels and Newman 1998). Crowley et al. (1998) describes this problem as the “complementarity dilemma.” Although their model only allows an individual to play one out of two possible roles (which limits its scope to unilaterally inseminating hermaphrodites), it may be applied to *L. terrestris*. The “my place or yours” dilemma may be regarded as a binary choice in which “my place” is the preferred role, but “your place” is acceptable when the risk is low and the benefits are high. Repeated visits may elucidate subtle differences in interests allowing mates to find a compromise, in the same way as unilaterally inseminating snails decide on who is allowed to be male (DeWitt, 1996).

Mating behavior of *Lumbricus terrestris*

Our study provides the first quantitative data on mating behavior in *Lumbricus terrestris*. Mating frequency is relatively high (once every 7–11 days). This exceeds what is needed for full fertility, as a single mating can ensure full fertility for up to 6 months (Butt and Nuutinen, 1998). The fact that mating rate is still relatively low suggests that matings are costly, an argument that is also used to explain long mating intervals in a pulmonate snail (Locher and Baur, 1999). Matings can be subdivided into short attempts and long true matings, very much in the same way as found in *Schmidtea (Dugesia) polychroa* (Peters et al., 1996). Short matings may represent failed attempts to align the genitalia or, alternatively, indicate that mate assessment continues during the first part of the mating, as is also known from *S. polychroa* (Michiels and Streng, 1998).

Conclusions

We conclude that size affects mating behavior in *Lumbricus terrestris* in an intricate way. Relative partner size, distance to putative partners, the risk of being pulled onto the surface, and size-related fecundity all appear to play key roles.

Thanks to Bruno Baur, Anders Berglund, Visa Nuutinen, Martin Storhas, Jaco Greeff, and Hinrich Schulenburg for helpful comments on earlier drafts, to Jaco Greeff, Harald Huber, and Susi Gistl for assistance in the field, and to Visa Nuutinen for advice and stimulating conversations. Special thanks to Mr. Lange from the golf course in Feldafing for allowing us to collect worms during the night (rather than worshipping the moon as suspected by some of his gardeners).

REFERENCES

- Arnold SJ, 1994. Bateman principles and the measurement of sexual selection in plants and animals. *Am Nat* 144:126–149.
- Bateman AJ, 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2: 349–368.
- Baur B, 1992. Random mating by size in the simultaneously hermaphroditic land snail *Arianta arbustorum*: experiments and an explanation. *Anim Behav* 43:511–518.
- Baur B, 1998. Sperm competition in molluscs. In: Sperm competition and sexual selection (Birkhead R, Møller AP, eds). London: Academic Press; 255–305.
- Butt KR, Nuutinen V, 1998. Reproduction of the earthworm *Lumbricus terrestris* Linné after the first mating. *Can J Zool* 76:104–109.
- Charnov EL, 1979. Simultaneous hermaphroditism and sexual selection. *Proc Natl Acad Sci USA* 76:2480–2484.
- Crowley PH, Cottrell T, Garcia T, Hatch M, Sargent RC, Stokes BJ, White JM, 1998. Solving the complementarity dilemma: evolving strategies for simultaneous hermaphroditism. *J Theor Biol* 195(1): 13–26.
- DeWitt TJ, 1996. Gender contests in a simultaneous hermaphrodite snail—a size-advantage model for behavior. *Anim Behav* 51:345–351.
- Dewsbury DA, 1982. Ejaculate cost and male choice. *Am Nat* 119(5): 601–610.
- Edwards CA, Bohlen PJ, 1996. Biology and ecology of earthworms. London: Chapman and Hall.
- Greeff JM, Michiels NK, 1999. Sperm digestion and reciprocal sperm transfer can drive hermaphrodite sex allocation to equality. *Am Nat* 153:421–430.
- Grove AJ, 1925. On the reproductive processes of the earthworm, *Lumbricus terrestris*. *Q J Microsc Sci* 69:245–291.
- Leonard JL, 1990. The hermaphrodite's dilemma. *J Theor Biol* 147: 361–372.
- Leonard JL, 1991. Sexual conflict and the mating systems of simultaneously hermaphroditic gastropods. *Am Malacol Bull* 9:45–58.
- Leonard JL, 1999. Modern portfolio theory and prudent hermaphroditism. *Invert Reprod Dev* 36:129–135.
- Leonard JL, Lukowiak K, 1984. Male-female conflict in a simultaneous hermaphrodite resolved by sperm trading. *Am Nat* 124:282–286.
- Leonard JL, Lukowiak K 1991. Sex and the simultaneous hermaphrodite: testing models of male-female conflict in a sea slug, *Navanax inermis* (Opisthobranchia). *Anim Behav* 41:255–266.
- Locher R, Baur B, 1999. Effects of intermating interval on spermatophore size and sperm number in the simultaneously hermaphroditic land snail *Arianta arbustorum*. *Ethology* 105(10):839–849.
- Madec L, Desbuquois C, Coutellec-Vetro M-A, 2000. Phenotypic plasticity in reproductive traits: importance in the life history of *Helix aspersa* (Mollusca: Helicidae) in a recently colonized habitat. *Biol J Linn Soc* 69:25–39.
- Michiels NK, 1998. Mating conflicts and sperm competition in simultaneous hermaphrodites. In: Sperm competition and sexual selection (Birkhead R, Møller AP, eds). London: Academic Press; 219–254.
- Michiels NK, 1999. Sexual adaptations to high density in hermaphrodites. *Invert Reprod Dev* 36:35–40.
- Michiels NK, Bakovski B, 2000. Sperm trading in a hermaphroditic flatworm: reluctant fathers and sexy mothers. *Anim Behav* 59:319–325.
- Michiels NK, Newman LJ, 1998. Sex and violence in hermaphrodites. *Nature* 391:647.
- Michiels NK, Streng A, 1998. Sperm exchange in a simultaneous hermaphrodite. *Behav Ecol Sociobiol* 42:171–178.
- Nuutinen V, Butt KR, 1997. The mating behavior of the earthworm *Lumbricus terrestris* (Oligochaeta; Lumbricidae). *J Zool Lond* 242: 783–798.
- Pen I, Weissing FJ, 1999. Sperm competition and sex allocation in simultaneously hermaphrodites: a new look at Charnov's invariance principle. *Evol Ecol Res* 1:517–525.
- Peters A, Michiels NK, 1996. Do simultaneous hermaphrodites choose their mates? Effects of body size in a planarian flatworm. *Freshw Biol* 36:623–630.
- Peters A, Streng A, Michiels NK, 1996. Mating behavior in a hermaphroditic flatworm with reciprocal insemination: do they assess their mates during copulation? *Ethology* 102:236–251.
- Premoli MC, Sella G, 1995. Sex economy in benthic polychaetes. *Ethol Ecol Evol* 7:27–48.
- Schärer L, Karlsson LM, Christen M, Wedekind C, in press. Size-dependent sex allocation in a simultaneous hermaphrodite parasite. *J Evol Biol*.
- Schärer L, Wedekind C, 1999. Lifetime reproduction output in a hermaphrodite cestode when reproducing alone or in pairs: a time cost of mating. *Evol Ecol* 13:381–394.
- Sella G, Lorenzi R, 2000. Partner fidelity and egg reciprocation in the simultaneously hermaphroditic polychaete worm *Ophryotrocha diadema*. *Behav Ecol* 11:260–264, 2000.
- Shipitalo MJ, Butt KR, 1999. Occupancy and geometrical properties of *Lumbricus terrestris* L. burrows affecting infiltration. *Pedobiologia* 43:782–794.
- Sims RW, Gerard BM, 1985. Earthworms. Synopses of the British fauna no. 31. London: Linnean Society.
- Tomiyaama K, 1996. Mate-choice criteria in a protandrous simultaneously hermaphroditic land snail *Achatina fulica* (Ferussac) (Stylommatophora, Achatinidae). *J Mollusc Stud* 62:101–111.
- Trouvé S, Jourdane J, Renaud F, Durand P, Morand S, 1999. Adaptive

- sex allocation in a simultaneous hermaphrodite. *Evolution* 53: 1599–1604.
- Vreys C, Michiels NK, 1997. Flatworms flatten to size up each other. *Proc R Soc Lond B* 264:1559–1564.
- Vreys C, Michiels NK, 1998. Sperm trading by volume in a hermaphrodite flatworm with mutual penis intromission. *Anim Behav* 56: 777–785.
- Wedekind C, Strahm D, Schärer L, 1998. Evidence for strategic egg production in a hermaphroditic cestode. *Parasitology* 117: 373–382.
- Weinzierl RP, Schmidt P, et al., 1999. High fecundity and low fertility in parthenogenetic planarians. *Inv Biol* 118:87–94.
- Wethington AR, Dillon RT, 1996. Gender choice and gender conflict in a non-reciprocally mating simultaneous hermaphrodite, the freshwater snail, *Physa*. *Anim Behav* 51:1107–1118.
- Yusa Y, 1994. Factors regulating sperm transfer in an hermaphroditic sea hare, *Aplysia parvula* Morch, 1863 (Gastropoda, Opisthobranchia). *J Exp Marine Biol Ecol* 181:213–221.
- Yusa Y, 1996. The effects of body size on mating features in a field population of the hermaphroditic sea hare *Aplysia kurodai* Baba, 1937 (Gastropoda, Opisthobranchia). *J Mollusc Stud* 62:381–386.