A STUDY OF MILLIPEDE SEXUAL SELECTION

BENJAMIN W. WRIGHT AND ANA I. BAPTISTA

Abstract. Nyssodesmus python (millipedes) exhibit a post-copulation riding behavior, suggesting the possibility of strong sexual selection (Heisler 1983). We hypothesized that sexual selection would be based on male size. Alternatively, millipedes may mate at random on a "first come first serve" basis. Experiments were designed to test for male and female size dominance. We found no size dominance in males or females nor any evidence for non-random mating success in males.

Key Words: Nyssodesmus python, *size dominance*

INTRODUCTION

Nyssodesmus python are millipedes common in the forest floor of abandoned cacao plantations at La Selva Biological Station, Costa Rica. Males exhibit a post-copulation riding behavior that may represent a response to extreme sexual selection (Heisler 1983). We hypothesized that sexual selection, either through female preference or male-male interference, would lead to size dominance in reproductive success. Alternatively, because millipedes tend to be highly dispersed and slow moving one might expect them to exhibit a "first come, first serve" behavior in which millipedes mate with the first individual they encounter.

We predicted that if size-based sexual selection occurs, then larger males and females would secure more copulations than smaller millipedes. In addition to this, solitary millipedes should be smaller than those that are mated. Sexual selection could also be based on criteria other than size. In this case, we would expect that (1) a recently mated male to be more likely to secure future copulations than a size-matched male without recent mating success and (2) different female millipedes should consistently choose the same mate from size-matched pairs of males.

METHODS

We collected millipedes on 15-16 February 1998 along the Senderos Tres Ríos near La Selva Biological Station, Costa Rica. Millipedes were separated into four categories: solitary males, solitary females, mated males, mated females, and kept separate until experiments. Four experiments with 12 replicates were set up in 48 chambers (16 x 33 x 12 cm). In the first experiment, two mated males, one small and one large, were put with one female to test for sexual selection based on male size dominance. The second experiment placed two recently mated males of the same size with one female. After copulation occurred, the successful male was marked with liquid paper and the female was replaced to test the repeatability of preference. The third experiment contained a large and small female along with one recently mated male to test for female size dominance. The fourth experiment tested for female preferences between a solitary male and a recently mated male of the same size.

Large and small males and females were chosen by sorting them all by mass and pairing the largest with the smallest millipedes. Millipedes of similar size were chosen to minimize differences in size. We used a paired t-test to confirm differences or similarities in mass among paired millipedes. Copulations were observed ~ 6 hours after setup. Those experiments that did not have copulations were checked again three hours later. Reproductive success was tested with chi square analyses.

RESULTS

As intended, experiments 1 and 3 included male pairs that differed in size and experiments 2 and 4 included male pairs that were size –matched (Table 1). Both male and female millipedes were equally likely to copulate with large or small mates (Table 2, experiments 1 and 3). Experiment 2 showed that males that successfully copulated on the first trial did not have a better chance of copulating with a new female than previously unsuccessful males. Experiment 4 further supported this by showing that solitary and mated males did not differ in their ability to secure copulation. Males that were collected from the field as solitary individuals were significantly loarger than males that were collected from the field while paired with a female (Table 3).

DISCUSSION

Our results refute the hypothesis that strong sexual selection exists in *Nyssodesmus python*. Millipedes showed no preference in mate size for either males or females. The fact that mated males surveyed weighed less then solitary males is probably due to post copulation riding rather then a reproductive advantage for smaller males. The males ride females for up to five days after copulation, during which they presumably do not eat and are in a negative energy balance. In all experiments, millipedes seemed to choose their mates indiscriminately. Recently mated males had no better chance to secure a copulation than males that had not recently mated and males that obtained copulations in one trial had no chance to succeed in a subsequent trial. These results suggest that female millipedes mate with whatever male avails (first come first serve).

There is at least one remaining mechanism by which sexual selection could operate in this system. Post-copulation riding might incur a cost to the male. If some males are able to ride on a female longer and thus more effectively maintain sperm precedence they may attain greater reproductive success. For example, larger males may have the greater energetic reserves required to remain with a female longer.

LITERATURE CITED

Heisler, Q.S. *Nyssodesmus python.* pp 747-748 *in* D. H. Janzen, ed. Costa Rican Natural History. University of Chicago Press, Chicago, IL. U.S.A.

TABLE 1. Comparison of millipede pairs in experiments.

Experiment	Range of Difference (g)	Mean Difference ± SE (g)	t statistic	P value
1	0.99 - 2.48	1.48 ± 0.12	12.47	<0.001
2	0.01 - 0.09	0.06 ± 0.01	-1.56	0.15
3	3.80 - 1.35	2.66 ± 2.00	13.60	<0.001
4	0 - 0.29	0.08 ± 0.02	-1.65	0.13

TABLE 2. Copulation results (P>0.05 indicates lack of sexual selection, df = 1).

Experiment	Ratio of copulations	X^2 value	P value
1	7:5 (large:small)	0.33	> 0.05
2	5:7 (successful:unsuccessful)	0.33	> 0.05
3	7:5 (large:small)	0.33	> 0.05
4	6:6 (mated:solitary)	0.00	0.995

TABLE 3. Mass of solitary and recently mated millipedes (n = 103 mated males, 71 mated females, 23 solitary males, and 8 solitary females).

Sex	Mean mass of solitary ± SE	Mean mass of mated ± SE	t statistic	P
Male	4.81 ± 0.12	4.50 ± 0.06	2.4	0.018
Female	6.05 ± 0.35	5.94 ± 0.12	0.3	0.76