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ORIGINAL PAPER

Assortative mating with respect to size in the simultaneously hermaphroditic land snail *Bradybaena pellucida*

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Abstract There is ample evidence that body size is tightly linked with quality and fecundity of individuals in simultaneously hermaphroditic species. Especially in simultaneous hermaphrodites with reciprocal intromission, it has been thought that assortative mating with respect to body size occurs. Contrary to this expectation, studies on size-assortative mating in such simultaneous hermaphrodites have shown inconsistent mating patterns. It is important to gain an understanding of mating patterns with regard to body size in various hermaphroditic species as a first step for considering the causes for such species differences. In the present study, we examined the relationship between body size and fecundity in the simultaneously hermaphroditic land snail *Bradybaena pellucida*. We also tested size-assortative mating patterns in this species under a laboratory condition. The results of the experiments showed that life-span fecundity was positively correlated with body size and that the snails tended to choose mating partners of similar body size. As we had predicted, size also affected the mating pattern and assortative mating in simultaneous hermaphrodites with reciprocal intromission. This size-assortative mating pattern seems to result from sexual selection processes, not from mechanical constraints and habitat heterogeneity between large and small individuals.

Keywords Land snails · Mate choice · Simultaneous hermaphrodites · Size-assortative mating · *Bradybaena pellucida*

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Introduction

In many vertebrate and invertebrate species, animals choose mating partners of better quality in order to increase reproductive success. Various phenotypic traits are known as indicators in such mate choice. Body size is one of the most important indicators of sexual selection. Assortative mating with respect to body size (i.e., the tendency of individuals of similar body size to mate together) is widespread in nature (e.g., Arnqvist et al. 1996; Bollache and Cézilly 2004). Although several hypotheses such as mechanical constraints (e.g., Han et al. 2010), habitat heterogeneity (e.g., Ferrer and Penteriani 2003), and temporal isolation (e.g., Ennos and Dodson 1987) have been proposed to explain such assortative mating patterns, mate choice based on body size has been considered to be an important underlying mechanism (Arak 1983; Ridley 1983; Crespi 1989; Hoefler 2007; Baldauf et al. 2009; Jiang et al. 2013).

As in many species with separate sexes, sexual selection plays an important role in simultaneous hermaphrodites, which produce both male and female gametes at the same time (e.g., Charnov 1979; Koene et al. 2005; Kimura et al. 2013; Leonard 2013). There is ample evidence that the body size of an individual is tightly linked with its fitness; thus, a larger individual produces more eggs in such hermaphroditic species (e.g., Peters and Michiels 1996; Schärer et al. 2001; Koene et al. 2007; Yu and Wang 2013). Therefore, a mate preference for larger individuals is expected. In hermaphroditic species with reciprocal intromission (i.e., an individual plays male and female functions in a single mating event), this preference ultimately results in the formation of mating pairs between larger individuals and subsequent pairing between remaining smaller individuals (Ridley 1983). Contrary to this expectation, studies on size-assortative mating in simultaneous hermaphrodites with reciprocal intromission have shown inconsistent mating patterns. Some studies found

positive size assortment (Tomiyama 1996; Michiels et al. 2001), whereas other studies found no evidence for such mating patterns (Baur 1992; Peters and Michiels 1996). The ubiquitous of size-assortative mating seems to be lower than expected in simultaneous hermaphrodites. To consider the pervasiveness of the expectation, it is important to understand mating patterns with regard to body size in various hermaphroditic species.

In the present study, we examined the relationship between body size and fecundity in the simultaneously hermaphroditic land snail *Bradybaena pellucida* (Gastropoda, Pulmonata, Bradybaenidae). We also tested the size-assortative mating pattern in this species under a laboratory condition.

Materials and methods

Study species

For this study, we chose the simultaneously hermaphroditic land snail *B. pellucida*. Over the course of a 1-year life cycle, *B. pellucida* grows determinately to an adult shell size of approximately 10–17 mm. In a single mating event, two adult snails simultaneously reciprocally intromit their penises and exchange sperm. Similar to many other land snail species, adults *B. pellucida* experience multiple mating events with different partners and lay eggs several times.

Juvenile snails of *B. pellucida* were collected in the summer of 2012 in Hamamatsu, Japan, and were kept individually in plastic pots (180 ml) at 22 °C and at approximately 65 % relative humidity. Although it was not controlled for, all snails were maintained under the same photoperiod condition. The snails were fed oatmeal with a powder mixture consisting of proteins and calcium ad libitum, and the housing containers were cleaned every 2 weeks. After sexual maturation under the laboratory culture, the adult individuals were used in oviposition and mating experiments.

Body size and fecundity

Twenty-five pairs of adult snails were selected randomly. Each pair was placed in a small pot (180 ml) and provided the opportunity to mate. After the pairs successfully mated, the individuals were separated and cultured in pots with the same conditions as described above. In addition, a bed of moist soil was added to each pot for the snails to lay eggs. Once laid, the eggs were cultured in separate pots containing moist soil to avoid desiccation until their hatch. We recorded the number of hatched eggs for each of the snails until they died. Our preliminary investigation found no intra-clutch egg cannibalism (i.e., hatchlings never consume eggs from their mother clutch) in our study species. Photographs of the shell were taken with a Nikon COOLPIX P7000 camera. The shell diameter and height of all individuals were measured with ImageJ software (National Institutes of Health, Bethesda, MD, USA). Shell volume (shell diameter^2 × shell height) was used as an indicator of body size. We used a Pearson's correlation coefficient to assess the relationship between body size and life-span fecundity.

Body size and pairing

From 600 *B. pellucida* snails (997.11–3582.57 mm^3), we randomly selected 30 groups of 20 snails. Each group was placed in a small container (approximately 2000 ml) and provided the opportunity to mate. The pair of snails that achieved successful mating first was recorded for each group. If two pairs started to mate at the same time in a single group, both were recorded. Eventually, 44 mating pairs were attained. To test whether snails mate with an individual having similar body size, we calculated the intraclass correlation coefficient r_i as performed by Vreys and Michiels (1997). Although it is not possible to examine the correlation between male and female sizes because of the sexual system in *B. pellucida* (i.e., simultaneous hermaphroditism), similarity in size of two mating snails can be evaluated by considering the proportion of the variance between mating pairs in the total variance. To examine whether pairs of large and small *B. pellucida* are physically limited when mating, we conducted an additional experiment using the residual 512 individuals. The five largest individuals (3324.52–3582.57 mm^3) among the 512 snails were given the opportunity to mate with one of the five smallest individuals (997.11–1137.34 mm^3), and all observations of mating occurrence were recorded.

All analyses in this study were conducted in R 2.15.1 (R Development Core Team 2012).

Results

Life-span fecundity was examined for 50 individuals (25 pairs) of *B. pellucida*. The number of eggs ranged from 7 to 114. The life-span fecundity was weakly but significantly correlated with the body size, as shown in Fig. 1 (Pearson's correlation coefficient: r=0.35, p=0.014). In the pairing experiment, 88 individuals chose a mating partner and successfully mated (i.e., 44 pairs). A significant positive correlation was found between the body sizes of mates (r_i=0.50, p<0.001) (Fig. 2). In the following mating experiment using the five largest and smallest individuals, all five pairs successfully started mating and exchanged sperm.

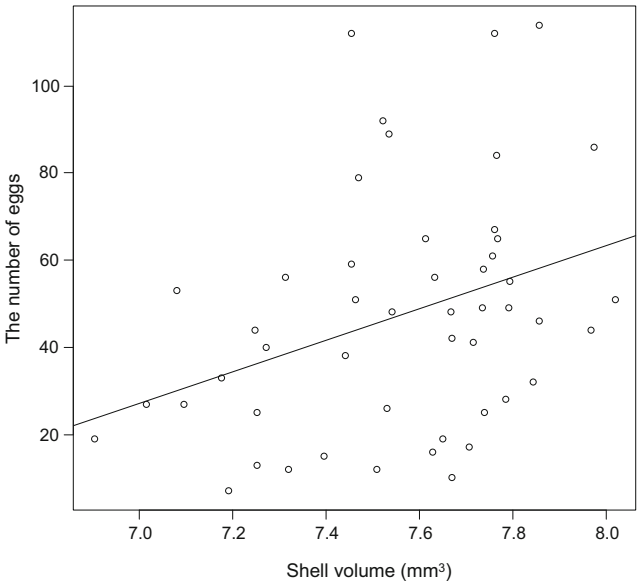

Fig. 1 The relationship between body size and life-span fecundity in *B. pellucida* (n=50). Linear regression of the number of eggs on log-natural transformed shell volume

Discussion

As seen in many studies on simultaneous hermaphrodites (e.g., Peters and Michiels 1996; Koene et al. 2007), the number of eggs increased with body size in *B. pellucida* (Fig. 1). Because we examined the number of the eggs that the snails laid throughout their life, our findings were not compromised by an increase in egg laying rates and short experimental time. Although further experiments are needed to investigate life-span fecundity when snails undergo several mating events, our result suggests that larger snails achieve higher reproductive success as a female. Our study also suggests that body size can be a useful indicator of the quality of potential mating partners in *B. pellucida*. In the experiment in which individuals were allowed to mate freely, we found a tendency of assortative mating in terms of body size (Fig. 2). A possible mechanism driving size-assortative mating other than sexual selection is the physical difficulty for large and small snails to mate (e.g., Brown 1993). However, the largest and smallest individuals in our study mated and donated successfully. In both the free-pairing and large-small pairing experiments, mating started during the first 10 min of the experiments and lasted 150–200 min. This result suggests that the mating process is not limited by such mechanical constraints. Therefore, our study suggests that the size-assortative mating in *B. pellucida* is driven by a mate preference for large individuals with high fecundity.

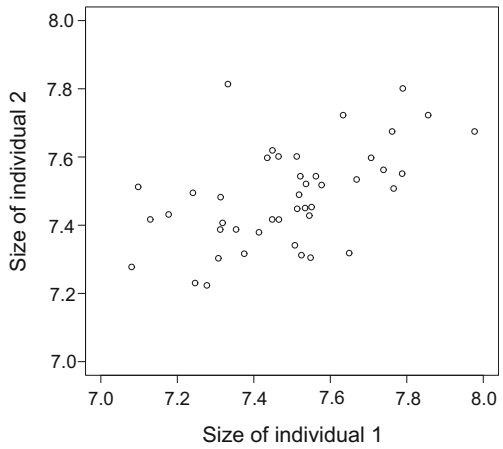

Fig. 2 The relationship between body sizes of the mating snails (n=44 pairs). Snail sizes were randomly assigned as individual 1 or 2

As Ridley (1983) showed for simultaneous hermaphrodites with reciprocal intromission, *B. pellucida* shows a size-assortative mating pattern. However, such size assortment pattern seems to be less frequent than expected (Chaine and Angeloni 2005). In order to consider the cause of this inconsistency, here, we discuss the previous work which did not show size assortment and the proposed underlying mechanisms of the results, though there are limited number of literatures on the relationship between size and mating pattern in hermaphrodites. Baur (1992) found no evidence for size-assortative mating in the simultaneously hermaphroditic land snail *Arianta arbustorum* and discussed the cost of searching for a mate as a possible explanation for the pattern. When mate searching is costly (e.g., because of low population density or the presence of predators), individuals are thought to be less selective in mate choice and thus choose any individual they encounter. Indeed, the population density of our study species is quite high compared to *A. arbustorum*, supporting the idea that the cost of mate searching affects the reported species specificity of mating. However, the turbellarian flatworm *Dugesia polychroa*, which has relatively low mate searching cost, showed a random mating pattern with respect to size (Peters and Michiels 1996). Peters and Michiels (1996) presumed that the low cost of mating affected the lack of size-based choice in *D. polychroa*. Further experiments examining the mating cost in cases of previous and present studies are needed to test its effect. To better understand size assortment in simultaneous hermaphrodites, it would be useful to further examine the relationship between mating patterns and the determining factors specifically, the mate-searching process, and mating cost in various species.

In conclusion, body size is positively correlated with fecundity in the land snail *B. pellucida*, which is a simultaneous hermaphrodite with reciprocal intromission. As expected for such hermaphrodites, body size affects the assortative mating pattern.

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