Mating behaviour of the marine snail *Littoraria flava* (Mollusca: Caenogastropoda) on a boulder shore of south-east Brazil

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The mating pattern of *Littoraria flava*, a typical grazer snail of the supralittoral zone and sometimes the midlittoral zone of boulder shores in tropical and sub-tropical regions, was examined to determine the occurrence of size-assortative mating and sexual selection on size. We also evaluated its reproductive behavioural mechanisms, as well as their implications for the evolution of the species. The population was investigated from May 2001 through April 2002, on an artificial rocky shore composed of a boulder wall at Flexeira Beach, Itacuruçá Island, Rio de Janeiro, Brazil (22°56'S 43°53'W). The current study showed that: (1) copulating pairs were observed only from November through March, indicating seasonal reproduction of the population; (2) linear correlation between sizes of copulating mates were weak but significant, characterizing assortative mating by size; (3) there was sexual selection for female size, i.e. large females were favoured as mating partners over small ones; however, sexual selection on size was not observed among males; (4) there were significant positive correlations between male and female shell sizes and the copulation time; (5) there were significant differences in copulation time among different types of copulating pairs; and (6) mating females were significantly larger than non-mating females, while there were no differences between the sizes of mating and non-mating males, indicating differential sexual selection between sexes. These findings may contribute to the evolution of sexual dimorphism in this species. Male choice behaviour plausibly explains the assortative mating and sexual selection on female size of *Littoraria flava*. As males chose larger mates because they benefit reproductively therefore large females have increased chances of mating and fertilization (sexual selection for size). Further evidence suggests that large females are more successful than small females in carrying out mating, because large females remain in copulation for a longer time than do small females.

INTRODUCTION

Mating patterns in natural populations have been studied in several groups of invertebrates (Arak, 1983; Ridley, 1983; Thornhill & Alcock, 1983; Howard & Kluge, 1985). Two patterns of non-random mating have emerged: sexual selection, increasing the mating success of relatively large individuals (Crespi, 1989); and size-assortative mating, which results from size-based mate choice in combination with competition among members of the actively choosing sex (Ridley, 1983; Crespi, 1989). Although studies of mating patterns commonly associate assortative mating with sexual selection (Arnqvist et al., 1996), these patterns of non-random mating may act independently. Size-based mate choice in both sexes or in either of the two sexes indicates assortative mating, or homogamy for size, giving rise to sexual selection (Erlandsson & Johannesson, 1994).

In most species, males, even selecting mating partners (Parker, 1979; Lande, 1981; Manning, 1985), can mate indiscriminately because each copulation will increase their fitness. However, in most of these situations, females choose their partners with care, in search of mates with high fitness for their offspring (Manning, 1985). Female mate choice may vary with respect to which character is preferred and how choosy the female is (Andersson, 1994; Jennions & Petrie,

1997; Widemo & Sæther, 1999). For example, females are predicted to become less choosy when search costs are high or mate densities are low, but choosiness should increase with an increase in mate quality variation (Borg et al., 2006). In summary, both sexes may commonly be expected to choose mates even in species in which only one sex contributes parental effort.

Sexual selection on size and size-assortative mating are common in the genus *Littorina* (Erlandsson & Johannesson, 1994; Rolán-Alvarez et al., 1995; Rolán-Alvarez & Ekendahl, 1996; Erlandsson & Rolán-Alvarez, 1998; Hull, 1998; Johnson, 1999; Takada & Rolán-Alvarez, 2000; Erlandsson, 2002). Males of this genus prefer to mate with large females (Erlandsson & Johannesson, 1994; Erlandsson & Rolán-Alvarez, 1998; Johnson, 1999). This behaviour can be explained by the typical positive correlation between fecundity and size of females (Hughes & Answer, 1982; Janson, 1985; Ross & Berry, 1991). However, assortative mating in littorinids snails may be affected by other factors other than size. Pickles & Grahame (1999) and Hollander et al. (2005) observed assortative mating within ecotypes of *Littorina saxatilis* (Olivi, 1792), independent of females size.

The species *Littoraria flava* (King & Broderip, 1832), classified until recently in the genus *Littorina* (Reid, 1986, 2001; Rios, 1994), is a common grazer snail of certain rocky

shore communities on the Brazilian coast. This species has been poorly studied, and only recently have its anatomy, aggregation pattern and genetic variability been elucidated (Simone, 1998; Moutinho & Alves-Costa, 2000; Andrade et al., 2003). In the present study, mate-choice behaviour was assessed by examining the size at mating; copulation time, and the influence of size on copulation time. We also examined whether shell size could be considered as an indicator of mating success and evaluated its importance for the mate-choice behaviour of this species.

MATERIALS AND METHODS

Monthly samples were taken from May 2001 through April 2002, on an artificial rocky shore composed of a constructed boulder wall, located at Flexeira Beach, Itacuruçá Island, Rio de Janeiro, Brazil (22°56'S 43°53'W). The wall is 150 m long and 1–1.5 m high. Fleixeira, a microtidal beach, was characterized as sheltered according to the ranking system of McLachlan (1980).

Twenty sectors (1 m long) were randomly positioned along the whole boulder wall (150 m). In each sampling sector, non-copulating individuals and mating pairs of *Littoraria flava* were collected monthly during spring low tides, counted, and taken to the laboratory.

The number of mating pairs was recorded monthly in each sector along the entire rocky shore. Mating pairs consisted of a male (active snail) moving towards a female (passive snail). Mating started with a male climbing onto a female assessing female shell size with its tentacles. After that, the penis is inserted into the mantle cavity in the right shell margin of the female (Erlandsson & Johannesson, 1994). Pairs were monitored until mating was completed. The height above waterline (rocky shore position) was recorded for each copulating pair. The pairs were then gently picked up and separated, and the partners were placed in separate containers and taken to the laboratory. All adult females found within a 10-cm radius of a copulating pair were also collected, to represent currently non-mating but potential mates. In February and March 2002, the copulation time was recorded for each copulating pair.

In the laboratory, the maximum shell lengths of all individuals, mating and non-mating, were measured with a vernier caliper (0.01 mm). They were then dissected to determine their sex, according to Simone (1998). The snails were divided into groups based in median shell length: small males (<10.5 mm), large males (≥10.5 mm), small females (<11.5 mm), and large females (≥11.5 mm).

The distribution of size groups (small–large) between mating and non-mating individuals was compared by chi-square test (χ^2), with Yates correction for continuity (Zar, 1996), to determine a possible over-representation of any one size group among the mating individuals.

To compare the sizes of mating versus non-mating individuals in both sexes, Student's t-test (Zar, 1996) was used. A size ratio was estimated by dividing the mean shell size of mating individuals by the mean shell size of non-mating individuals. This size ratio can indicate the occurrence of assortative mating (Crespi, 1989).

Cochran's test showed homogeneous variances in copulation time between types of pairs (small male–small
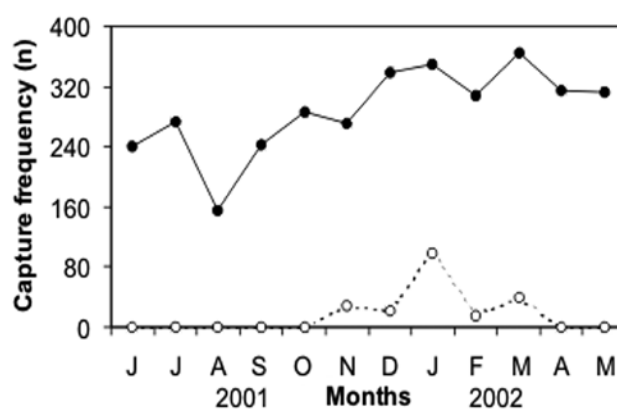

Figure 1. Monthly fluctuation of capture frequency of (•) non-mating individuals and (o) copulating pairs for the period June 2001 to May 2002.

female, small male–large female, large male–large female, and large male–small female). Thus, one way analysis of variance (ANOVA) and Tukey's Honest Significant Difference (HSD) test for unequal sample sizes were used a posteriori to detect differences in copulation time between the possible types of mating pairs. We considered copulation time as the time during which the mating pair remained in the mating position, (the male had its penis inserted into the mantle cavity of its partner, see Saur, 1990).

Correlation analysis was used to assess the relationship between the shell size of copulating pairs (both sexes) and (1) the copulation time and (2) the shore height of copulating pairs. This last analysis can suggest an existence of stratification by size as a function of the microhabitat characteristics.

We used the copulating pairs collected to test the correlation between sizes of males and females, in order to examine whether they mated randomly or size-assortatively. Assortative mating by size of population was measured by Pearson's correlation coefficient (r_p) between the sizes of copulating pairs. To assess the type of assortative mating ('true' or 'apparent'), we used a heteroscedasticity index, according to Arnqvist et al. (1996), when the absolute values of male residuals, generated by regression analysis between male and female shell length, are correlated (Spearman's non-parametric correlation coefficient, r_s) with the female shell length, by Spearman's non-parametric correlation coefficient (r_s). 'True' assortative mating is described by a linear relationship between mating male and female sizes, where points are symmetrically distributed around the regression line; while the 'apparent' type are recognized by linear relationship between male and female sizes where points are delimited by a triangle around the regression line (Crespi, 1989; Arnqvist et al., 1996).

Sexual selection on size was examined by comparing the sizes of mating and non-mating individuals in each sex, and thus determining whether any size of mate was favoured over any other. Sexual selection on size can be measured by the sexual selection intensity index (SSI) (see Falconer, 1981; Erlandsson & Rolán-Alvarez, 1998).

The SSI was estimated by: $SSI = (MSMI - MSP)/SDP$, where MSMI is the mean size of mating individuals, MSP

Table 1. *Sexual selection on male and female size of* Littoraria flava. *Mean shell length, standard deviation of both sexes. Sexual Selection Intensity (SSI) is represented by (mean size of mating snails–mean size of all snails/standard deviation of all snails). F, estimate for a one-factor ANOVA and its significance (P) were presented.*

Sex	Mean non-mating individuals (SD)	Mean mating individuals (SD)	SSI	F	*P*
Males	10.90 mm (2.28)	10.76 mm (1.72)	−0.0636	0.94	0.3310
Females	10.95 mm (2.31)	11.80 mm (1.80)	0.3684	33.72	0.0000

is the mean size of population (mating plus non-mating), and SDP is the standard deviation of the population (all individuals). The statistical significance of sexual selection was evaluated by comparing mating and non-mating sizes in each sex separately by ANOVA (one-way). When mating individuals are significantly larger than non-mating individuals, there is positive sexual selection intensity. Conversely, when mating individuals are significantly smaller than non-mating individuals, there is negative sexual selection intensity.

RESULTS

The population of *Littoraria flava* was most abundant in the summer, between November 2001 and March 2002. The lowest abundance was recorded in winter 2001 (Figure 1). Reproductive activity occurred between late spring and summer, over a 5-month season from November through March, peaking in January (Figure 1). This indicate that *L. flava* reproduces seasonally.

Homosexual copulations were not observed. Copulating pairs seldom moved during copulation. Males were the active partners, while females were passive during the course of mating. Copulating males did not hinder other males from coming near or mounting their females. Thus males showed no apparent competitiveness against other males in searching for an ideal partner (large females). In the copulating pairs, shell length varied between 6.0 and 16.0 mm in males, and from 7.0 to 17.0 mm in females. The mean length of mating males (10.76 mm) was significantly smaller than that of females (11.80 mm) (*t*-test=47.17; *P*<0.0001; df =544). Mating females were also larger than potential females (10.48 mm) (*t*-test=3.92; *P*<0.0002; df=177).

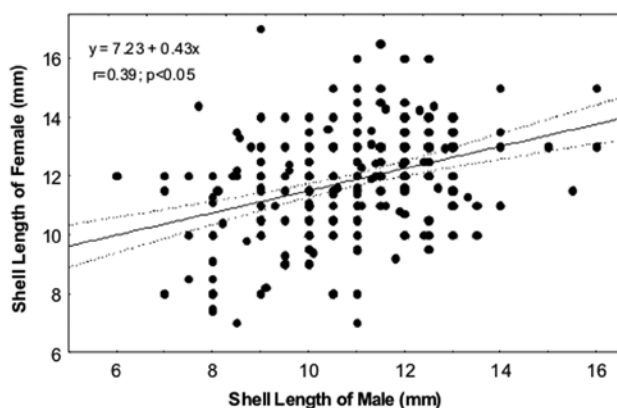**Figure 2.** Bivariate correlation (±95% confidence intervals) between shell length of females and males for the period June 2001 to May 2002.

Littoraria flava showed weak 'true' assortative mating by size, measured by linear correlation between sizes of copulating pairs. The size of mating females was positively and significantly correlated with that of mating males (Figure 2). Males tended to mate with females larger than themselves. This pattern was observed in 75.82% of the copulating pairs found. Mating females were, on average, 11.55% larger than their pairs. The greatest difference in size of the copulating pairs was 8 mm (male 9 mm and female 17 mm). In copulating pairs in which the females were smaller than the males, the greatest size difference (4 mm) was observed in two pairs (male 11 mm and female 7 mm; and male 15.5 mm and female 11.5 mm).

The heteroscedasticity index (r_s) was 0.005, and did not differ significantly from zero (*P*>0.05), indicating a 'true' assortative mating (sizes of mating males and females to be distributed symmetrically around the regression line, see Figure 2).

Sexual selection on size was observed only for females. Large females mated more frequently than did small females (χ^2=19.94; *P*<0.0001). However, there was no significant effect of sexual selection on size (large-small) in the males (χ^2=2.19; *P*>0.05).

Sexual selection was also studied by comparing the mean lengths of mating and non-mating males and females. The mean size ratio of mating to non-mating individuals was 0.9867 in males and 1.0778 in females. The mean shell length of mating males was not significantly smaller than that of non-mating individuals (*t*-test 1.16; *P*>0.05; df=1863). Mating females were, however, significantly larger than were non-mating females (*t*-test=6.93; *P*<0.0001; df=1902). Thus, positive sexual selection intensity (SSI) was found for females (Table 1).

There was a linear relationship between copulation time (Y) and shell length (X) for both sexes. Copulation time increased significantly with shell length, for both males and females (Figure 3,B).

One-way analysis of variance revealed significant differences in copulating time among the different types of mating pairs (Table 2A). The large male–large female pairs showed significantly longer copulation time on average (96 min) than did the small male–small female pairs (69 min). Copulation times of the large male–small female pairs (93 min) and small male–large female pairs (82 min) did not show significant differences between each other, nor among the remaining pairs (Table 2B).

There was no stratification by size in either sex on the rocky shore studied. The linear correlation between size of mating pairs and their shore position was not significant (males: *r*=0.05, *P*>0.05; df=240 and females: *r*=0.001, *P*>0.05; df=240).
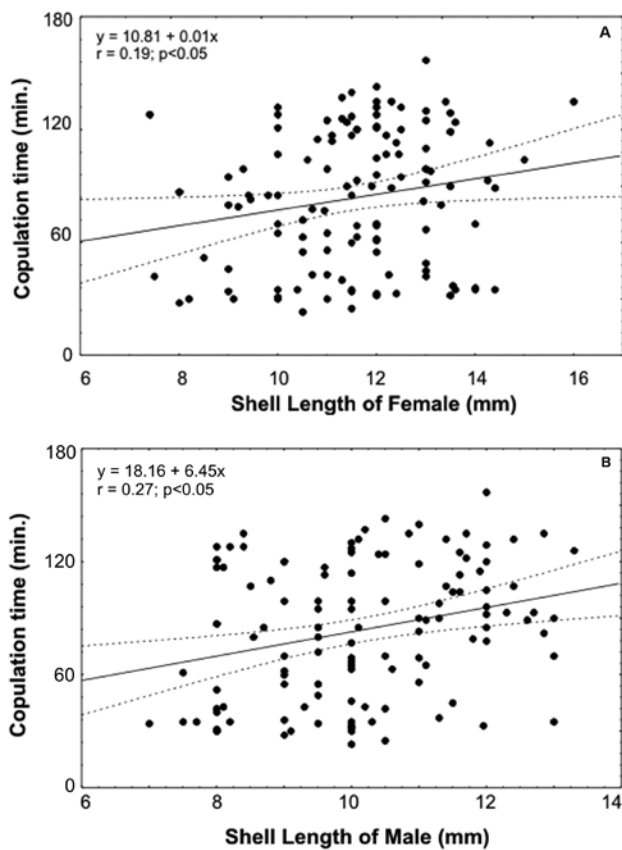
Figure 3. Bivariate correlation (±95% confidence intervals) between copulation time and shell length of (A) females and (B) males for copulating pairs from March and February.

Table 2. (A) ANOVA unifatorial. Relation among pairs types (male large–female large, Ml–Fl; male small–female small, Ms–Fs; male large–female small, Ml–Fs; and male small–female large, Ms–Fl) and copulation time of Littoraria flava. (B) Results of Tukey (HSD) post-hoc test to indicate statistical significance.

(A)	df	Sum of squares	Mean squares	F	P
Inter-pairs	3	14308.4	4769.4	3.94	0.01
Intra-pairs	117	141708.0	1211.18		
Total	120	156017.0			

(B)				
Pairs types	Ms–Fs	Ms–Fl	Ml–Fs	Ml–Fl
Mean time (min)	69.38	81.74	93.35	96.05

df, degrees of freedom; P, probability level.

sizes; and (c) mating females were significantly larger than non-mating females.

True assortative mating by size may be caused by different mechanisms (Crespi, 1989; Arnqvist et al., 1996; Erlandsson & Rolán-Alvarez, 1998; Hull, 1998; Johnson, 1999). Several alternative hypotheses explain size-assortative mating in littorinids: (1) there may be mechanical constraints on copulation between unequally sized mates. However, the sizes of copulating pairs did not support this hypothesis in *Littoraria flava*. Some of the copulating pairs showed maximum differences of 4 mm, when males were larger than females (♂11 mm ♀7 mm and ♂15.5 mm ♀11.5 mm), to 8 mm, when males were smaller than females (♂9 mm ♀17 mm). (2) There may be non-random distribution by size at a local site (microhabitat characteristics) (Crespi, 1989; Ward & Porter, 1993). Cracks and crevices of the barnacle cover, may for instance, provide a suitable microhabitat for small specimens of *Littorina littorea* (Linnaeus, 1758) creating refuges from crab predation (Choat, 1977). Little & Williams (1989) described settlement and recruitment of the same littorinid gastropods, especially in cracks, amongst barnacles and in their empty carapaces. However, this was neither the case as there were no significant correlations between the size of *Littoraria flava* copulating pairs and their shore position. Thus, the microhabitat of barnacle zone (based on the presence of cracks and crevices among the barnacle and in empty carapaces) did not produce a segregation by size in the boulder. (3) The male-choice hypothesis is a third possible explanation of assortative mating in *Littoraria flava*. In other words, true assortative mating can be verified if males choose larger mates because they benefit reproductively (Darwin, 1871; Ridley, 1983). This hypothesis suggests the existence of an interaction between large-male mating advantage and male choice of large mates. In our case, intrasexual competition among males was not observed, since mating and non-mating males did not show significant differences in shell length (Table 1). Hence, mating within males was size-independent, but

DISCUSSION

Reproductive activity in *Littoraria flava* occurred in late spring and summer, with a peak in January, indicating seasonal reproduction. Several studies on species of *Littorina* have also demonstrated seasonality in their reproductive activity (Roberts & Hughes, 1980; Hart & Begon, 1982; Hannaford-Ellis, 1983; Son & Hong, 1998; Johnson et al., 2000). Johnson et al. (2000) observed reproductive activity in the summer months for *Littorina saxatilis* and *Littorina neglecta* (Bean, 1844). Conversely, Son & Hong (1998) found copulating pairs of *Littorina brevicula* (Philippi, 1844) only in winter. Thus, there is considerable variation in duration and seasonality of breeding activity among littorinids. Erlandsson (2002) revealed a clear relationship between reproductive strategy and the presence or absence of a distinctive breeding season in *Littorina*. Species with pelagic development always have a distinct reproductive season, while species with nonpelagic development often reproduce throughout the year. This variation may reflect locally adjusted phenotypes (Stearns & Koella, 1986), or a combination of plastic and genetic reproductive responses in order to optimize fitness of a species in different environmental conditions.

There was a clear evidence of non-random mating by size, as defined by Arnqvist et al. (1996). Our results revealed three patterns indicating the existence of true assortative mating: (a) a weak but significant correlation between the sizes of males and females; (b) the absence of any tendency towards heteroscedasticity in plots of female versus male

mating females were larger than non-mating females because males chose large females. However, Crespi (1989) noted that these processes (large-male mating advantage and male choice) are antagonistic, and their effects may not coincide. The female-biased sex ratio observed (1 male:1.52 female; Cardoso, in preparation) may also strengthen the male choice hypothesis. Male behaviour may be dependent on the local sex ratio, with males becoming increasingly choosy when the sex ratio is female-biased, and more competitive when the sex ratio is male-biased (Lawrence, 1986). The combination in a single sex, of competition for mates and mate choice is not predicted by classical sexual selection theory (Lawrence, 1986). In our case, female-biased sex ratio lead to males mating with larger females regardless of their own sizes, explaining weak correlation coefficient between males–females sizes ($r =0.39$, Figure 2). This sex ratio biased to females increases the intensity of sexual selection for large female shell size and could explain male choice hypothesis. However we cannot conclude which hypothesis explains the assortative mating observed in *Littoraria flava*. Thus, our analysis of mating behaviour should be complemented with laboratory experiments in order to reveal the mechanisms behind assortative mating in this species.

Sexual selection intensities (SSI) on size differed between sexes of *Littoraria flava*. Large females were significantly favoured as mates (mating females were larger than non-mating females), with a positive sexual selection intensity. This selection intensity is of evolutionarily importance, as it may contribute to the enhancement of size dimorphism between sexes. Moreover, differences in growth rates between sexes also result in sexual size dimorphism (Reid, 1996).

Sexual selection on size among males was not verified. Large males were not more successful in mating with females than small ones. However, sexual selection on female size was verified. This reproductive behaviour may also be explained by the male-choice hypothesis, because males preferred to mate with large and probably more fecund females; consequently, large females may have an increased chance of mating and fertilization. We also suggest that small females are less successful in mating than large females, as they spend less time in copulation. This was also observed in *Littorina littorea* (Erlandsson & Johannesson, 1994). Longer copulation time with large females may favour the transfer of more sperm. Parker (1970) and Thornhill (1976) observed that in insect species, the amount of sperm transferred to the receptaculum seminis of the females is correlated with copulation time. According to Dewsbury (1982), the number of ejaculations that a male can perform in a given amount of time is limited. Hence, males may limit copulation time with females. This can be corroborated by higher correlation coefficient that was found between male size and copulation time ($r=0.27$), versus between female size and copulation time ($r=0.19$) (Figure 3A,B). However, the differences in size of males and females explained only about 8% and 4%, respectively, of the observed differences in copulation time.

Contrary to the statement of Arnqvist et al. (1996), true assortative mating can be independent of the male size ratio, provided that there is no intrasexual competition within males. Males of *Littoraria flava*, might likely grow faster than females, meaning that they may reach maturity before females. Littorinid populations tend to have mating males significantly smaller than mating females; thus, strengthening a possible and incipient sexual dimorphism in *Littoraria flava* (Johnson et al., 2000).

In summary, our results showed that *Littoraria flava* displays true assortative mating by size. However, assortative mating in this species seems to be less important than sexual selection on female size. According to Darwin (1871), sexual selection is an evolutionary consequence produced by within-sex competition and inter-sex choice. Thus choice and competition are likely to have a stronger influence in sexual selection than other biological mechanisms when compared with size-assortative mating. Besides, sexual selection can contribute to sexual dimorphism on size. Therefore, future investigations on mating behaviour of littorinid species should examine the influences of biological factors such as the sex ratio, population density, the presence of predators and/or competitors, food availability, fecundity, maturity period, and circadian and circatidal mating rhythms on sexual selection and size-assortative mating.

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