SIZE-ASSORTATIVE PAIRING IN THE BIG-CLAWED SNAPPING SHRIMP, ALPHEUS HETEROCHELIS

by

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Summary

The big-clawed snapping shrimp, *Alpheus heterochelis*, is found in size-matched male-female pairs. A common assumption is that a large size advantage in males, an extended pair bond, and a positive correlation between female size and fecundity promotes size-assortative pairing. Since all of these conditions apply to *A. heterochelis*, we investigated size-assortative pairing in the laboratory by designing experiments in which the pairs were size matched or mismatched using three size categories; large, medium and small. We found that snapping shrimps prefer to pair according to size and that such pairing is stable. We also found that, contrary to the initial assumptions, female-female competition and female choice for large males plays the main role in the pair formation process. Smaller, and hence less competitively successful, females will pair with smaller males, but in a male-biased environment, will preferentially pair with larger males. Large males provide the best protection from shelter eviction, which is crucial for female *A. heterochelis*, as their reproduction is closely associated with moult, and therefore requires shelter and a male present for successful reproduction.

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Introduction

Assortative mating by size is defined as a positive correlation between the size of mates within a population or sample (Arnquist *et al.*, 1996), and is a very common mating pattern in natural invertebrate populations (Crespi, 1989). It is usually accompanied by sexual selection, and thus has potential evolutionary effects on the demography or genetics of a population (*e.g.* Wade & Arnold, 1980; Partridge, 1983), and in some extreme circumstances it may even promote speciation (Udovic, 1980).

Different mechanisms may produce size-assortative mating, some of which can be grouped into mate choice hypotheses (Crespi, 1989). These hypotheses are based on the theory that one or both sexes will choose a larger mate, because they benefit reproductively, and that some individuals are better able to exert choice than others. Attention has been focussed on the evolution of assortative mating based on male-male competition in combination with male mate choice, which has been shown in a variety of taxa, such as isopods (Ridley & Thompson, 1979), amphipods (Elwood *et al.*, 1987), dipterans (Hieber & Cohen, 1983), anurans (Arak, 1993), and coleopterans (McLain & Boromisa, 1987). Male-male competition results in a high correlation between male size and success in access to females, and when combined with male choice for larger, more fecund females, should result in size-assortative mating. Ridley (1983) stated that three factors seem to coincide in size-assortatively mating species: male-male competition, long pair bonds, and high fecundity of large females.

Size-assortative pairing as a result of female choice also occurs (Crespi, 1989), although it has not been demonstrated unequivocally, because the opportunity for female choice would coincide with male-male competition, and hence its expression would be masked by male activity. Studies on a variety of species, such as marine isopods (Jormalainen *et al.*, 1994; Jormalainen & Merilaita, 1995), water striders (Rowe & Arnquist, 1996), Coleoptera (*e.g.* Johnson, 1982, 1983; Harari *et al.*, 1999), Japanese medaka (Howard *et al.*, 1998), and a crab (Greenspan, 1980), have implicated a role for females in size-assortative mating. These studies suggest that female and male choice for large partners, often in conjunction with male-male competition, influence size-assortative mating. None of these studies, however, demonstrated unequivocally that female choice is operating separately from the result of male choice or male-male competition.

Preference for large mates has evolved because both larger females and larger males tend to have greater reproductive success than smaller animals (Brown, 1990). In contrast to male-male competition for large mates, however, female-female competition has not been implicated as a mechanism of size-assortative pairing. Competition between females has been shown to occur in many species where there is large variation in male quality (Gwynne, 1991; Rosenqvist & Berglund, 1992; Ahnesjo *et al.*, 1993). Female-female competition is associated with sex role reversal, wherein the dominant females monopolize the preferred males through repeated courtship, leaving the subordinate females to mate with the less desirable males (Jennions & Petrie, 1997). When attractiveness is associated with large size, the result of intraspecific competition combined with mate choice could lead to size-assortative mating.

Most snapping shrimp are small, benthic crustaceans that share burrows as male-female pairs. The majority of field caught pairs are matched in body and major claw size (Nolan & Salmon, 1970; Schein, 1977; Hughes, 1995, 1996), but with a tendency for males to have slightly larger claws and females slightly larger body size (Schein, 1977). In the laboratory, male-female pairs remain together for several weeks (pers. obs.). Data from the field on *Alpheus armatus* suggest that they stay together for months (Knowlton, 1980), however, no comparable field data are available for *Alpheus heterochelis*.

Both sexes have an enlarged claw, which can snap, producing a strong water jet and a sharp sound when closed rapidly (Hazlett & Winn, 1962; Ritzmann, 1974). The snap is mostly used in aggressive interactions and can injure or kill an opponent (Nolan & Salmon, 1970; Knowlton, 1980; Knowlton & Keller, 1982). It has been shown in several studies that aggressive interactions occur in shelter acquisition and shelter defence (*e.g.* Nolan & Salmon, 1970; Knowlton & Keller, 1982), and may play a role in mate acquisition (Schein, 1977; Hughes, 1995). Body size has been shown to be an important factor with regard to resource holding potential, *i.e.* the ability to acquire and hold a shelter (Nolan & Salmon, 1970; Schein, 1975, 1977).

Females can reproduce after each moult, which occurs every 17 to 23 days, at least when they are reproductively active. After successful copulation, the female produces a clutch of eggs, that remains attached to her pleopods until the larvae hatch and are released into the water, about two weeks later. There is a significant positive correlation between female size and fecundity (Knowlton, 1980; pers. obs.).

All three criteria in Ridley's (1983) theory for size-assortative mating are met by snapping shrimp: a large male advantage exists, at least in male-male competition for shelter access, there is an extended pairing duration, and there is a positive correlation between female size and fecundity. Theoretically, males should compete for access to large females because larger females confer a greater reproductive success.

The present study demonstrates size-assortative pairing of the big-clawed snapping shrimp, *Alpheus heterochelis,* in the laboratory with a series of experiments, and suggests that, contrary to expectations, female choice and female-female competition play the main roles in the size-assortative pairing process.

Methods

Animals were obtained from the intertidal zone near the Duke University Marine Laboratory at Beaufort, North Carolina, and shipped to Toronto. Laboratory facilities for housing the animals consisted of 25-liter aquaria, partitioned into twelve compartments using plastic screening. This avoided physical contact between animals to prevent injury, but allowed chemical and visual interaction. Tanks were equipped with an under-gravel filter and gravel covered the bottom to a depth of approximately 2 cm. Artificial seawater (specific gravity 1.023) was prepared using 'Instant Ocean' brand mix. Animals were kept at 27°C on a light-dark cycle of 14 : 10 h. They were fed a blend of shrimp, beef heart, and carrots, as well as a commercial fish hatchery product, Purina brand 'Trout Chow', on a daily basis.

Animals were checked for moult twice a day. Only animals that had moulted 3 to 5 days previously were used in experiments, to ensure that they would not moult during the experiment, and that they had hardened after the previous moult. Each animal was only used once per experiment, and we ensured that two animals that had encountered each other in an experiment were not used together again.

Body length was measured from the end of the tail to the tip of the rostrum, and snapping claw length was measured as the maximum length of the propodus, using a dial caliper accurate to 0.01 mm. Two animals were considered to be of equal size ('size-matched') when they were within 3% of each other's body size (range: 0-1.5 mm, difference in body length, 0-1 mm difference in claw length).

In Experiments 1 through 3, sets of six different animals were used: three males and three females of the three size categories viz. large, medium, and small. The body size differences between adjacent size categories were approximately 15% (range: 3.9-7.1 mm). The male and female of each size category were matched in size. In Experiment 4, two large males were used in addition to the standard six animals. These two males were matched in size to the other large male. Animals were marked for individual recognition with white typewriter correction fluid that was applied to their carapace.

Prior to each experiment, animals were placed in holding tanks (L: 40.5 cm × W: 20 cm × H: 26 cm) containing a gravel substrate and a clear plastic cylinder (10 cm long and 2 cm in diameter) as a shelter, for 24 h. The animals were held individually or as pairs, depending on the experimental design. Pairing was accomplished in these holding tanks by introducing a male and female that were either size matched or mismatched depending on the design of the experiment. If these two animals were observed within the first hour to share the shelter, they were considered to have paired.

Following the 24-h period in the holding tank, the animals were transferred, together with their shelter, to an experimental tank (L: 115 cm × W: 92 cm × H: 15 cm). When first introduced to the experimental tank, the animal (individual or paired) along with its shelter was placed in a mesh cage for 30-45 minutes. In Experiment 1, six mesh cages were placed along the edges of the tank: one in each corner, and two along the long sides of the tank. In Experiments 2 and 3, three mesh cages were provided for the three pairs in their shelters, and in Experiment 4, five mesh cages for the three pairs and the two single males. In addition, three extra empty shelters were placed in the experimental tank so that every individual could occupy a shelter alone, if it chose.

After the mesh cages were removed, the animals' behaviour was observed and recorded for one hour. During this initial 60 min period of interaction, the following behaviours were recorded: approach, claw snaps, and claw touching. Claw touching involves a male and a female stroking their claws over each other for a time period exceeding 5 sec. This activity can occur after initial encounters, and is a necessary but not sufficient component of pre-pairing behaviour. Time spent in a shelter unpaired or with a partner was determined for each animal.

Following the initial interaction period, the position of each animal in the experimental tank was recorded at half hour intervals for the remainder of the day, as well as for the following day. In total, 30 such position records were made for each animal and this constituted the time parameter for the duration of being paired or unpaired. As well, these 30 data points indicated the number of partner changes.

Four experiments were done and each is separately described below.

Experiment 1: Size-assortative pair formation

To determine whether single shrimp will pair size-assortatively in the laboratory, and what behaviour may underlie this phenomenon, three males of different sizes and three females of different sizes were introduced to one another and monitored over two days. Twenty-five replicates were run.

Experiment 2: Pair stability

To test how well size-matched pairs stay together in the vicinity of other pairs, and whether size plays a role in pair stability, three size-matched pairs of different sizes were monitored over two days. Twenty-five replicates were run.

Experiment 3: Stability of mismatched pairs

To test whether size-mismatched pairs would show similar pairing behaviour to size-matched pairs, three mismatched pairs of different sizes were allowed to interact for two days. The design represented every combination of mismatched pairs equally. One combination (abbreviations) was: large female – medium male (LF-MM), medium female – small male (MF-SM), small female – large male (SF-LM), and the others: LF-SM, MF-LM, SF-MM. Fifteen replicates of each combination were run.

Experiment 4: Pair stability in a large male biased environment

Three size-matched pairs of different size and two large single males were allowed to interact for two days. Twenty replicates were run.

Statistical analysis

Parametric tests were used where normality of the data allowed; otherwise non-parametric tests were used. Group comparisons were done using a Kruskal-Wallis One-way ANOVA on Ranks, and the post-hoc pairwise comparisons were analysed using Student-Newman-Keuls Test for all pairwise comparisons, or the non-parametric application Dunnett's Method on ranks to test multiple comparisons with a control. Pairwise comparisons were tested with the Mann-Whitney Rank Sum Test or the t-Test depending on the normality of the data.

Results

The behaviour recorded for Experiments 1-4 was identical and consisted of observing approaches, claw snaps, and claw touches for the first 60 min. Shelter occupancy within the first 60 min was recorded and compared between Experiments 2 and 3. For the remaining 7 hr of the day, at half hour intervals, only the pairing behaviour was recorded, and the same was done for 8 hr the next day. Hence, the results are presented in a consistent manner for Experiments 1-4, as initial interactions for the first 60 min, and pairing behavior over the next two days.

Experiment 1: Size assortative pair formation

Snapping shrimp are found in size-matched pairs in the field. Three males of different sizes and three females of different sizes were placed in an experimental tank.

Initial interactions

Approaches: Four different approach orientations were compared: males to males, females to females, females to males, and males to females. Females approaching males was significantly more frequent than the other orientations ($p < 0.001$) (Fig. 1A). Females approached larger or similar-size males significantly more often than smaller males ($p < 0.001$), whereas males did not show size dependence in approach towards females ($p > 0.1$).

Snaps: Snaps were grouped as follows: females at females, females at males, males at males, males at females. The mean number of snaps was significantly higher in the females at females group than in any other group ($p < 0.01$) (Fig. 1B). Both sexes showed significantly higher snapping frequencies toward same sex conspecifics than toward opposite sex conspecifics (females: $p < 0.001$, males: $p < 0.05$), which is a commonly observed difference in *Alpheus heterochelis* (Nolan & Salmon, 1970; Hughes, 1995).

Claw touches: Females touched claws significantly more often with larger or same-size males than with smaller males ($p < 0.05$) (Fig. 1C). The large male and the large female touched claws more frequently than did any of the other animals ($p < 0.05$). The small male touched claws significantly less often than the other two males ($p < 0.001$), whereas there was no significant difference in claw touching frequency among the three sizes of females ($p > 0.1$).

Pairing behaviour

Over the course of two days, each animal remained paired significantly longer when with a size-matched partner, than when with a non-matched partner ($p < 0.01$) (Table 1). Among the size-matched pairs, the large pair spent significantly more time together over the two days than the medium or the small pair ($p < 0.01$).

Experiment 2: Pair stability

To test how well size-matched pairs stay together in the vicinity of other pairs, and whether size plays a role in pair stability, three size-matched pairs of different sizes were monitored over time.

Initial interactions

Approaches: Comparing the four different approach orientations (males to males, males to females, females to females, females to males), there were no significant differences among the four groups ($p > 0.1$) (Fig. 2A). The males did not show a size-dependent preference among females in their approaches ($p > 0.1$), nor did the females in their approaches towards males ($p > 0.1$).

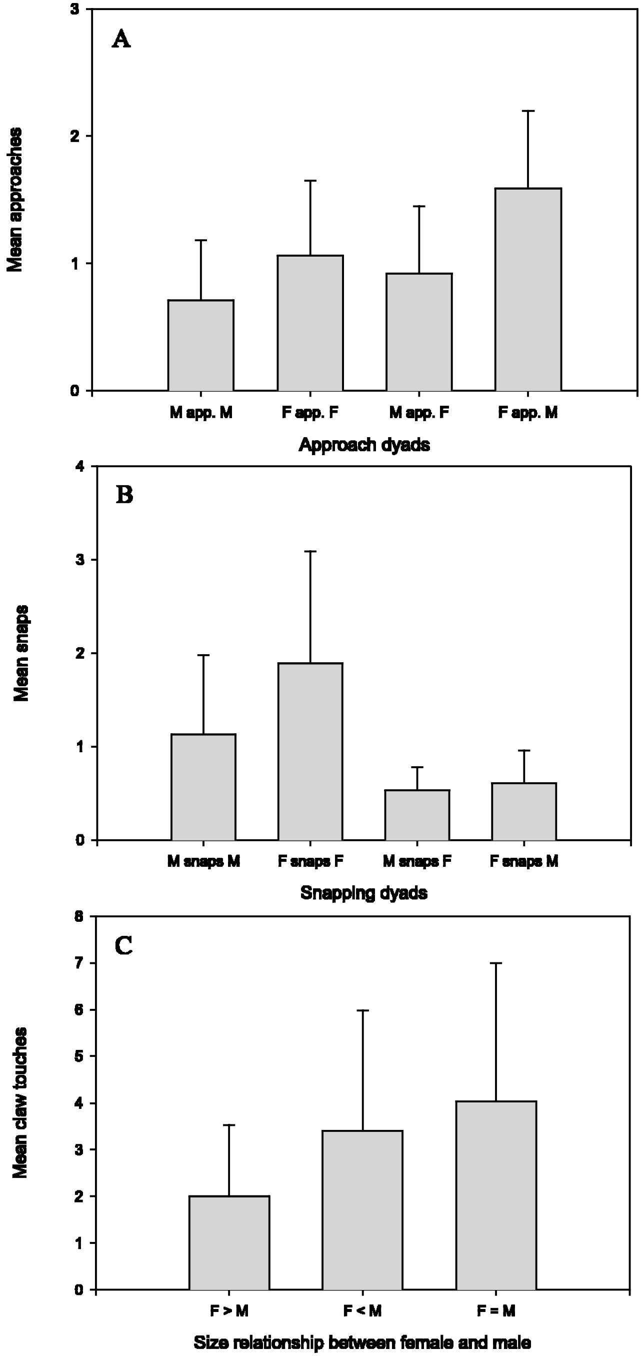

A
Mean approaches
0
1
2
3
M app. M
F app. F
M app. F
F app. M
Approach dyads
B
Mean snaps
0
1
2
3
4
M snaps M
F snaps F
M snaps F
F snaps M
Snapping dyads
C
Mean claw touches
0
1
2
3
4
5
6
7
8
F > M
F < M
F = M
Size relationship between female and male

TABLE 1. *Pair formation of three males and three females of the size categories large, medium, and small*

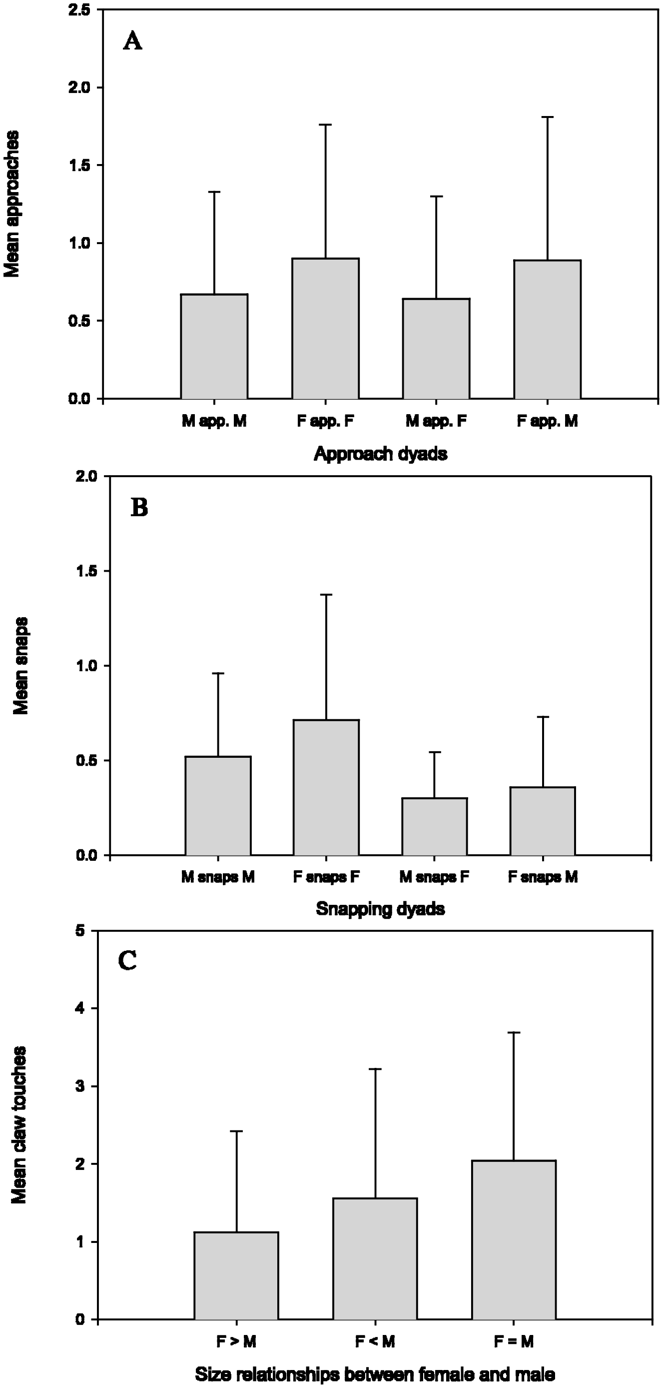
Animal	% Paired			% Unpaired
	Size-matched	Size-mismatched		
Large male (LM)	57.6 (17.3 ± 8.2)	14.5 (MF) (4.36 ± 7.31)	1.73 (SF) (0.52 ± 1.61)	26.1 (7.84 ± 7.58)
Large female (LF)	57.6 (17.3 ± 8.2)	7.7 (MM) (2.32 ± 6.16)	0 (SM)	34.7 (10.4 ± 6.6)
Medium male (MM)	32 (9.6 ± 9.25)	7.7 (LF) (2.32 ± 6.16)	11.8 (SF) (3.56 ± 4.91)	48.5 (14.56 ± 9.25)
Medium female (MF)	32 (9.6 ± 9.25)	14.5 (LM) (4.36 ± 7.31)	8.93 (SM) (2.68 ± 6.12)	44.5 (13.36 ± 9.19)
Small male (SM)	28.27 (8.48 ± 8.42)	0 (LF)	8.93 (MF) (2.68 ± 6.12)	62.8 (18.84 ± 8.69)
Small female (SF)	28.27 (8.48 ± 8.42)	1.73 (LM) (0.52 ± 1.61)	11.87 (MM) (3.56 ± 4.91)	58.13 (17.44 ± 8.34)

$N = 25$. Pair stability of six animals during two days based on 30 observations, one every half-hour for two days during daytime. Numbers in brackets indicate the mean out of 30 and standard deviation.

Snaps: Snaps were grouped as follows: females at females, females at males, males at males, males at females. There were no significant differences in snapping frequency among the four groups ($p > 0.05$) (Fig. 2B).

Claw touches: Females did not touch claws with larger or same-size males more than with smaller males, relative to their own size ($p > 0.05$) (Fig. 2C). The medium male touched claws significantly more often with females than the large male and the small male did ($p < 0.05$).

Fig. 1. Behaviours of three males and three females of the size categories large, medium, and small in the first 60 min (M = males, F = females, LM = large male, LF = large female, MM = medium male, MF = medium female, SM = small male, SF = small female). Error bars indicate standard deviations. **A**. Mean approach frequency of one animal to another within each category. F to M is significantly greater than the other three categories ($p < 0.001$). **B**. Mean snapping frequency of one animal to another within each category. F at F is significantly greater than the other three categories ($p = 0.002$). **C**. Mean number of claw touches by females with different-size males. Females and smaller males touched claws significantly less than females and the other males ($p < 0.036$).


A
Mean approaches
2.5
2.0
1.5
1.0
0.5
0.0
M app. M
F app. F
M app. F
F app. M
Approach dyads
B
Mean snaps
2.0
1.5
1.0
0.5
0.0
M snaps M
F snaps F
M snaps F
F snaps M
Snapping dyads
C
Mean claw touches
5
4
3
2
1
0
F > M
F < M
F = M
Size relationships between female and male

Shelter occupancy: The data for shelter sharing are not independent. When two animals are paired and share a shelter together, these two animals cannot pair with the remaining four animals, and hence the latter have fewer choices left for pairing. Therefore, cumulative shelter times were calculated by summing the time each pair spent in a shelter. The maximum value would be 180 (three pairs in their shelters for the entire 60-min period). One such unit was labeled a 'shrimp minute' (SM). Mean shelter occupancy of newly formed pairs (1.85 ± 2.78 SM) was significantly lower than that of the initially established pairs (64.69 ± 49.25 SM; $p < 0.001$).

Time spent individually in shelters was also measured (to a theoretical maximum of 360, were each of the six animals to spend the entire 60 min alone in a shelter). The cumulative shelter times of pairs were doubled so that a direct comparison could be made (original data were per pair, not per individual). Within the first 60 min, the animals were found significantly more often paired in shelters (132.96 ± 96.62 SM) than individually in shelters (77.56 ± 45.32 SM; $p < 0.05$).

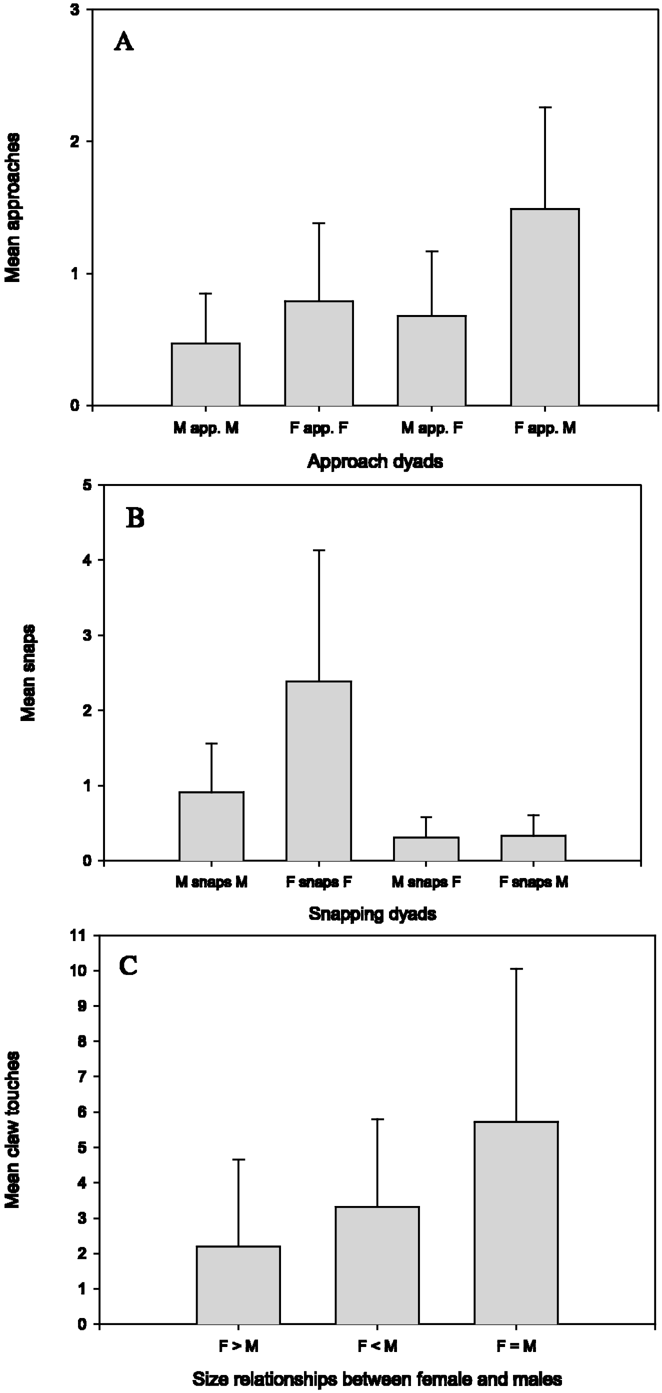
Females and males did not spend a significantly different amount of time alone in a shelter (females: 30.82 ± 30.62, males: 46.32 ± 33.48; $p > 0.05$).

Pairing behaviour

For every animal, the time spent with a new, mismatched partner was significantly less than the time spent with the original, size-matched partner ($p < 0.01$) (Table 2). The large animals spent significantly more time paired with each other than being unpaired ($p < 0.001$). There was no difference between time spent unpaired and time spent in the original pairing for the medium and small animals ($p > 0.05$).

The small male paired significantly less with a new partner than the other animals ($p < 0.05$). In a comparison of the number of partner changes for each animal over the two days, the small male changed partner significantly less often than any other animal ($p < 0.05$).

Fig. 2. Behaviours of three size-matched pairs of the size categories large, medium, and small in the first 60 min (M = males, F = females, LM = large male, LF = large female, MM = medium male, MF = medium female, SM = small male, SF = small female). Error bars indicate standard deviations. **A**. Mean approach frequency by one animal to another within each category ($p = 0.597$). **B**. Mean snapping frequency by one animal to another within each category ($p = 0.066$). **C**. Mean number of claw touches by females with different-size males ($p = 0.094$).


A
Mean approaches
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F app. F
M app. F
F app. M
Approach dyads
B
Mean snaps
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4
5
M snaps M
F snaps F
M snaps F
F snaps M
Snapping dyads
C
Mean claw touches
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10
11
F > M
F < M
F = M
Size relationships between female and males

TABLE 2. *Pair stability of three size-matched pairs of the size categories large, medium, and small*

Animal	% Paired			% Unpaired
	Size-matched	Size-mismatched		
Large male (LM)	69.7 (20.92 ± 8.82)	14.5 (MF) (4.36 ± 7.31)	1.7 (SF) (0.52 ± 1.61)	16.27 (4.88 ± 6.73)
Large female (LF)	69.7 (20.92 ± 8.82)	7.7 (MM) (2.32 ± 6.16)	0 (SM)	24.13 (7.24 ± 7.69)
Medium male (MM)	42 (12.6 ± 9.88)	7.7 (LF) (2.32 ± 6.16)	11.9 (SF) (3.56 ± 4.91)	40.8 (12.24 ± 9.79)
Medium female (MF)	42 (12.6 ± 9.88)	14.5 (LM) (4.36 ± 7.31)	8.9 (SM) (2.68 ± 6.12)	43.3 (13 ± 8.49)
Small male (SM)	51.3 (15.4 ± 9.39)	0 (LF)	8.9 (MF) (2.68 ± 6.12)	48.7 (14.6 ± 9.39)
Small female (SF)	51.3 (15.4 ± 9.39)	1.7 (LM) (0.52 ± 1.61)	11.9 (MM) (3.56 ± 4.91)	37.6 (11.28 ± 7.44)

$N = 25$. Pair stability of animals during two days based on 30 observations, one every half-hour for two days during daytime. Numbers in brackets indicate the mean out of 30 and standard deviation.

Experiment 3. Stability of mismatched pairs

To test whether size-mismatched pairs would show similar pairing behaviour to size-matched pairs, and to examine their pair bond stability, three mismatched pairs of different sizes were allowed to interact in an experimental tank.

Initial interactions

Approaches: There was a gender bias in approaches (male to female; male to male; female to male; female to female), the average approach

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Fig. 3. Behaviours of three mismatched of the size categories large, medium, and small pairs in the first 60 min (M = males, F = females, LM = large male, LF = large female, MM = medium male, MF = medium female, SM = small male, SF = small female). Error bars indicate standard deviations, stars indicate significance. **A**. Mean approach frequency by one animal to another within each category. F to M is significantly greater than the other three categories ($p < 0.001$). **B**. Mean snapping frequency by one animal to another within each category. F at F is significantly greater than the other three categories ($p < 0.001$). **C**. Mean number of claw touches by females with different-size males. All three categories are significantly different (see Text).

frequency of females towards males being significantly higher than any of the other groups ($p < 0.001$) (Fig. 3A). Females approached the large male significantly more often than they did same-size or smaller males ($p < 0.05$). However, there was no difference in the approach frequency of males towards the different size classes of females ($p > 0.1$).

Snaps: Snaps were grouped as follows: females at females, females at males, males at males, males at females. Females snapped at other females significantly more often than any other group ($p < 0.001$) (Fig. 3B). No significant differences were detected among the other groups ($p > 0.05$).

Claw touches: The lowest claw touching frequency was observed between a larger female and a smaller male (Fig. 3C). Females and larger males touched claws significantly less than same-size animals, but still significantly more often than females and smaller males ($p < 0.05$). Claw touching between the two large animals was significantly greater than between any other male and female ($p < 0.01$). There was no significant difference in the claw touching frequency of the three females with males ($p > 0.1$), but the large male touched claws significantly more often than the medium or small male ($p < 0.05$).

Shelter occupancy: During the initial 60-min observation period, shelter sharing by original pairs was significantly greater than between newly formed pairs. The mean shrimp min (± SD) for shelter sharing with an original partner was 22.41 ± 25.23 SM and the mean shrimp min for newly formed pairs was 6.75 ± 12.22 SM ($p < 0.001$).

Animals did not spend significantly more time paired in a shelter (57.68 ± 51.86 SM) than individually (72.23 ± 34.98 SM; $p > 0.1$). Females spent significantly less time alone in a shelter (26.32 ± 22.7 SM) than males (44.04 ± 29.74 SM; $p < 0.05$).

Pairing behaviour

Over the two-day period, the animals paired significantly more often in a size-assortative manner than they remained with their original partners. Each animal had four choices: remain with the original partner, form a new pair with a size-matched partner, form a new pair with a mismatched partner, or remain single.

In the first mismatch design (LF-MM, MF-SM, SF-LM), every animal except for the medium male ($p > 0.05$) spent significantly more time

TABLE 3. *Pair stability of three mismatched pairs during two days, based on 30 observations, one every half-hour for two days during daytime*

A

Animal	% Paired			% Unpaired
	Mismatched (original)	Size-matched	Mismatched (other)	
Large male (LM)	13 (SF) (3.87 ± 5.42)	52.4 (15.73 ± 7.65)	13.8 (MF) (4.13 ± 5.37)	20.7 (6.2 ± 4.52)
Large female (LF)	12 (MM) (3.67 ± 4.03)	52.4 (15.73 ± 7.65)	0.6 (SM) (0.2 ± 0.56)	34.7 (10.4 ± 6.7)
Medium male (MM)	12 (LF) (3.67 ± 4.03)	32.7 (9.8 ± 8.87)	10 (SF) (3 ± 3.57)	45.1 (13.53 ± 8.25)
Medium female (MF)	12 (SM) (3.67 ± 5.33)	32.7 (9.8 ± 8.87)	13.8 (LM) (4.13 ± 5.37)	41.3 (12.4 ± 7.33)
Small male (SM)	12 (MF) (3.67 ± 5.33)	34.4 (10.33 ± 9.12)	0.6 (LF) (0.2 ± 0.56)	52.7 (15.8 ± 8.76)
Small female (SF)	13 (LM) (3.87 ± 5.42)	34.4 (10.33 ± 9.12)	10 (MM) (3 ± 3.57)	42.7 (12.8 ± 7.52)

B

Animal	% Paired			% Unpaired
	Mismatched (original)	Size-matched	Mismatched (other)	
Large male (LM)	21.3 (MF) (6.4 ± 6.94)	54.4 (16.3 ± 9.92)	7.6 (SF) (2.27 ± 4.89)	16.7 (5 ± 4.44)
Large female (LF)	2.4 (SM) (0.73 ± 1.83)	54.4 (16.3 ± 9.92)	20 (MM) (6 ± 7.47)	23.1 (6.93 ± 5.16)
Medium male (MM)	10.7 (SF) (3.2 ± 7.01)	34.9 (10.47 ± 9.72)	20 (LF) (6 ± 7.47)	34.4 (10.33 ± 7.6)
Medium female (MF)	21.3 (LM) (6.4 ± 6.94)	34.9 (10.47 ± 9.72)	8.7 (SM) (2.6 ± 5.95)	35.1 (10.33 ± 7.33)
Small male (SM)	2.4 (LF) (0.73 ± 1.83)	54 (16.2 ± 10.46)	8.7 (MF) (2.6 ± 5.95)	34.9 (10.47 ± 8.35)
Small female (SF)	10.7 (MM) (3.2 ± 7.01)	54 (16.2 ± 10.46)	7.6 (LM) (2.27 ± 4.89)	27.8 (8.33 ± 8.22)

Numbers in brackets indicate the mean out of 30 and standard deviation. **A**. Mismatched design 1 (LM-SF, LF-MM, MF-SM). $N = 15$. **B**. Mismatched design 2 (LM-MF, LF-SM, MM-SF). $N = 15$.

with a new size-matched partner than with the original mismatched partner ($p < 0.05$) (Table 3A). Animals spent significantly more time with a new size-matched partner than with a new mismatched partner ($p < 0.05$), except for the medium female, who did not show a significant difference in her pair stability with the medium male (new size-matched) and the large male (new mismatched) ($p > 0.05$). Only the large male and the large female spent significantly more time paired than unpaired ($p < 0.001$); the other size-matched pairs spent about half the observed time unpaired.

In the second, complementary, mismatch design (LF-SM, MF-LM, SF-MM) all animals except for the medium female ($p > 0.1$) paired significantly longer with a new size-matched partner than with the original partner ($p < 0.05$) (Table 3B). Animals paired significantly longer with new size-matched than new mismatched partners ($p < 0.01$), except for the medium males, who did not show a significant difference in their pair stability with the medium female (new size-matched) and the large female (new mismatched) ($p > 0.1$). All animals spent significantly more time paired than unpaired ($p < 0.01$).

In both mismatch sets, the small male had a significantly lower frequency of partner switches than any other animal ($p < 0.05$).

Comparison of Experiments 1, 2, 3

In the first three experiments snapping shrimp overall remained paired significantly longer with size-assortatively matched partners than with other partners, even if they were initially paired with different-size animals. The large male was paired most in all experiments.

Females showed higher levels of aggression (as measured by number of snaps) in non-size-assortative pairing designs than in size-assortative ones, and also approached and claw-touched larger males significantly more often than same-size or smaller animals. Males, on the other hand, did not show a preference for larger females, nor did their aggression change in the three designs. In the first 60 min, males spent significantly more time unpaired in a shelter than females in the mismatched design, but there was no significant difference between male and female individual shelter occupancy in the size-matched design.

Experiment 4. Pair stability in a large male biased environment

To examine whether females prefer large males, and whether female-female competition plays a role in pairing success with large males, three size-matched pairs of different size and two large single males were allowed to interact in an experimental tank.

Initial interactions

Approaches: The two large single males approached both male and female conspecifics significantly more often than the paired males did ($p < 0.05$). Single large males did not show discrimination among females of different sizes with regard to approaches ($p > 0.1$).

Among the paired males, the large male approached the females significantly less frequently than the small or medium size male ($p < 0.001$) (Fig. 4A). Paired males did not demonstrate a size-contingent approach preference towards females ($p > 0.1$) or males ($p > 0.05$).

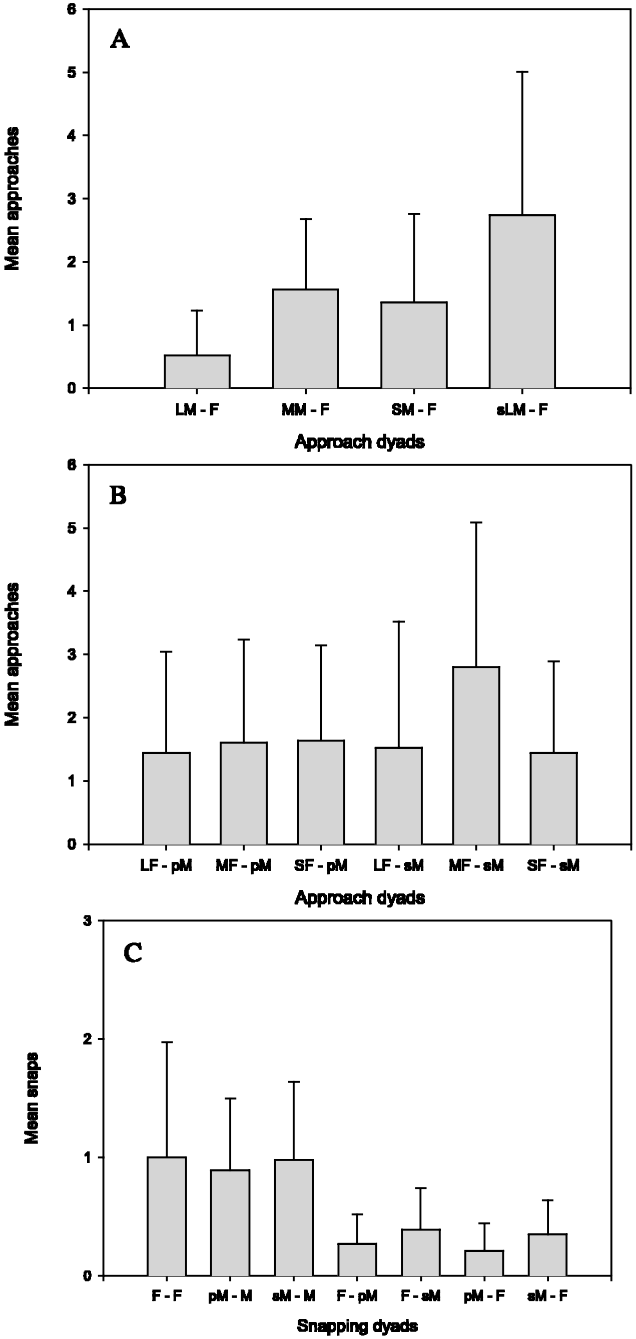
The different-size females did not show a preference for a certain size paired male ($p > 0.1$) (Fig. 4B). The large and the small female did not show different approach frequencies towards paired and single males (large female: $p > 0.1$; small female: $p > 0.1$). The medium female, however, approached the single males significantly more often than the paired males ($p < 0.05$).

Snaps: The mean number of snaps between females did not differ from the mean number of snaps exchanged between males ($p > 0.1$) (Fig. 4C). Intrasexual snapping was significantly higher than intersexual snapping for both genders ($p < 0.001$).

Claw touch: The two single large males touched claws significantly more often with females than the paired males did ($p < 0.01$). The medium female touched claws significantly more often with a large male than with other males ($p < 0.01$) (Fig. 4D). The large and the small female both did not show this discrimination (LF: $p = 0.171$, SF: $p > 0.1$). Overall, there was no significant difference in claw touching frequency of the different-size females with males ($p > 0.1$).

Pairing behaviour

The medium pair was found together for a significantly shorter time than the large and small pair ($p < 0.01$). The medium female paired significantly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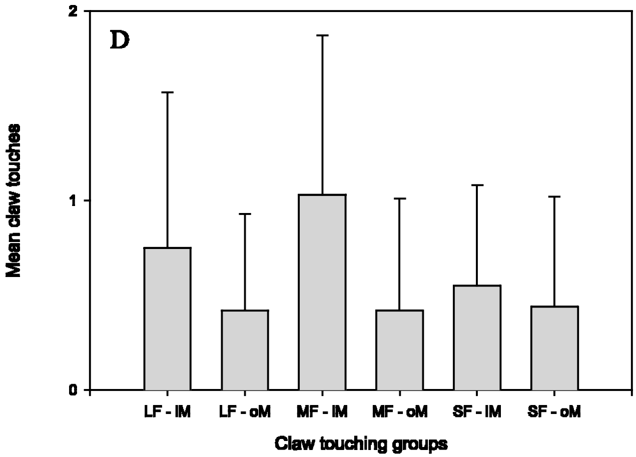

Fig. 4. Behaviours of three size-matched pairs of the size categories large, medium, and small, and two large single males in the first 60 min (LM = large male, LF = large female, MM = medium male, MF = medium female, SM = small male, SF = small female, sLM = single large male, M = males, F = females, pM = originally paired male, sM = originally single male; lM = a large male, oM = other (medium or small) male). Error bars indicate standard deviations. **A**. Approach frequency by the males to females. LM approaches females significantly less often than the other paired males, and single males approach females significantly more often than do paired males ($p < 0.001$). **B**. Size-dependent approach frequencies by females towards paired and single males. The medium female approached single males significantly more often than did the other two females ($p = 0.032$), but female approach frequencies towards paired males are not significantly different ($p = 0.891$). **C**. Mean snapping frequency between males and females. **D**. Mean claw touching frequency of females with large males (lM) or other (medium or small) males (oM). MF touched claws significantly more often with large males than with other males ($p = 0.006$).

more often with a single large male than the small female did, but there was no difference between the large and the medium, or the large and the small female in their pairing with single large males ($p < 0.05$) (Table 4A).

Of the three originally paired males, the large male was paired significantly longer than the medium male, but there was no difference in pairing durations between the small and medium males, and the small and large males ($p < 0.05$) (Table 4B). Females were significantly less often unpaired than males ($p < 0.05$).

Comparison of Experiment 4 with Experiments 1, 2, 3

When two single large males were introduced (Experiment 4), the medium and small female were significantly more paired with larger males than in

TABLE 4. *Pair stability of three size-matched pairs (size categories large, medium, and small) and two single large males during two days, based on 30 observations, one every half-hour for two days during daytime*

A

Animal	% Paired with			% Unpaired
	Original partner	Other paired male	Single large male	
Large female	37.3 (12.1 ± 9.83)	10.2 (3.05 ± 5.6)	24.4 (7.25 ± 8.08)	25.3 (7.6 ± 5.32)
Medium female	14 (4.2 ± 5.21)	13.2 (3.95 ± 7.06)	38.3 (11.5 ± 7.76)	34.5 (10.35 ± 6.31)
Small female	42.2 (12.65 ± 9.2)	13.7 (4.1 ± 5.77)	14.8 (4.45 ± 5.53)	29.3 (8.8 ± 6.46)

B

Animal	Paired	Single
Large male	55.2 (16.55 ± 8.71)	44.8 (13.45 ± 8.71)
Medium male	32 (9.6 ± 7.78)	68 (20.4 ± 7.78)
Small male	46.5 (13.95 ± 9.25)	53.5 (16.5 ± 9.25)
Large single male	38.8 (11.62 ± 8.37)	61.25 (18.38 ± 8.86)

Numbers in brackets indicate the mean out of 20 (or 40 for single males) and standard deviation. $N = 20$. **A**. Females. **B**. Males.

the same-size or male-biased design (MF: $p < 0.001$, SF: $p < 0.01$), whereas the large female's pairing with large males did not differ in the three experiments ($p > 0.05$).

Males snapped significantly more often at each other in the male-biased design than in the size-matched design ($p < 0.05$). There was no difference in the frequency of approaches, or snaps, among any other animals, when comparing the size-matched experiment with the male-biased experiment ($p > 0.1$ in each test).

Discussion

Size-assortative pairing is a common mating pattern in natural populations, but its underlying causes can differ. One conventional model is that male-male competition, long pair bonds and size-dependent fecundity of females are complementary conditions that lead to size-assortative mating (Ridley, 1983). Since all these conditions are met by the snapping shrimp *Alpheus heterochelis,* it was initially assumed that male-male competition played an important role in the evolution of size-assortative pairing in this species (Hughes, 1995). We test this assumption in the present study via a series of experiments designed to determine whether size-assortative pairing occurs in the laboratory, and uncover the proximate factors which are important in bringing it about.

Size assortative pair formation and its stability

Experiments 1-3 clearly show that, in the laboratory, males and females paired significantly more often size-assortatively than with a partner of a different size. This agrees with data from the field, where most pairs were within 10-20% of each other's body size (Nolan & Salmon, 1970; unpubl. obs.).

Size assortative pairing in the laboratory was also very stable. Thus, size-matched pairs had higher rates of shared shelter occupancy, and higher pair stability, than mismatched pairs, which broke up and predominantly re-paired with size-matched mates.

Behaviour in the first 60 min indicated factors that promote size-assortative pairing. No major role of male-male competition in the size-assortative process was found, although such a role was expected from Ridley's (1983) predictions of conditions for the occurrence of size-assortative pairing. Males did not show a size-dependent preference in their approach frequency towards females and did not show high aggression. In contrast, increased female-female aggression was observed when animals were not paired size-assortatively. Females approached large and medium size males significantly more often than small males, which suggests a preference by females for large males, and may imply competition among females for access to larger males.

Female preference for large males

Based on the claw touching and pairing data, the large female was more successful than the other females in initiating courtship with the large male. The large male seemed to be the preferred male by all females, as he was approached most, touched claws most with females, and spent the most time of any in a pair bond during the two days in a mismatched design.

In the mismatched design, the small male had the lowest pair stability, and the large female and the small male were never paired, unless they were original partners. This also indicates that females prefer larger males, and do not actively choose smaller males. Forbes *et al.* (1992) observed lack of male competition in brine shrimp, which also form size-assortative pairs. Female choice was instrumental, for females were less reluctant to pair with larger males than with smaller males (Forbes *et al.*, 1992).

When pairs were already matched in size, aggression between females was lower, and females approached males no more often than other animals approaching each other. Petrie & Hunter (1993) predicted from a theoretical model, that two high quality partners should have a low motivation to seek other partners, as they are not likely to find partners so much better as to outweigh the cost of deserting, and perhaps losing, the existing partner. This could underlie the stability of large pairs. The lower approach frequencies of already size-matched medium and small size females towards large males could lie in a lower success rate in pairing with such a higher quality male, because of competitive exclusion by larger females. The cumulative shelter occupancy for pairs was higher, which implies that approaching a male in his shelter often also involved approaching the paired female, too. Females react aggressively to, and defend their shelter from, other females (Nolan & Salmon, 1970; Schein, 1977; Knowlton, 1980), and the larger female usually wins aggressive encounters (Nolan & Salmon, 1970; Schein, 1977).

Throughout the experiments, female behaviour seemed to influence male pairing success. Active female choice, *i.e.* rejecting certain males and favouring others (Andersson, 1994) on the basis of size, seems to be the major factor in size-assortative mating. In a mismatched setting, females paired with smaller males may leave their partners and search for a higher quality, *i.e.* larger, male to pair with. Petrie & Hunter (1993) proposed pair formation and stability to be based on attraction levels in socially monogamous species. An individual with high reproductive value (*e.g.* fecundity, territory) will be considered an attractive partner. The model predicts that two mutually attractive mates should respond well to each other's courtship and stay together, whereas, in mismatched pairs, the higher quality mate should try to find a better mate and not respond to the courtship of the low quality partner.

This model can be applied to the observed pair bond behaviour of *A. heterochelis*. The large female and the large male have the most stable pair bond, and the large female is the most successful in maintaining a pair bond with the large male. The smaller unpaired females try to gain access to a higher quality male by approaching larger males and by fighting with other females for males, especially by snapping.

Effect of single large males on size-matched pairs

With the availability of single large males (Experiment 4), the medium and small female significantly increased their pairing with larger males. The medium male was significantly more often single than paired, but not the large males, or the small male.

Interestingly, the small female and the small male still maintained pair bonds over the two days, even though it was predicted that the small female should prefer a larger male. This could be explained by the fact that small animals are easily evicted or defeated by larger conspecifics (Nolan & Salmon, 1970). A small female pairing with a large male risks being evicted by a larger female, and therefore seems to avoid frequent contacts with large males. It has been observed that smaller animals, which lose contests with stronger animals, subsequently stay away from these animals and also flee from the approaches of any other conspecific. This pattern of behaviour would lead to prediction of the long pair stability between two small animals that was observed.

Although physical incompatibility for copulation could select against pairing between animals of very different size in some caridean shrimp, snapping shrimp males lack the specialised pleopod copulatory organs that require a good size match to function. In fact, we have observed copulation in the laboratory between a small female and a large male.

Female role in pair formation

In territorial species, such as *A. heterochelis*, mate choice by females more likely evolved due to the immediate effects of the male's phenotype on female fecundity (*e.g.* large territory size, better defence), rather than the genetic contribution to her offspring (Maynard Smith, 1991), because by choosing a male who contributes a low quality territory, the female's reproductive success is immediately negatively affected. The male's size influences his ability to protect the female from shelter takeover attempts by other conspecifics (Ridley & Thompson, 1979; Berrill & Arsenault, 1982). Aggressive interactions may result in injury or can even be fatal in *A. heterochelis* (Nolan & Salmon, 1970; Hughes, 1995), and can result in shelter eviction, which could increase her exposure to predators. In female *Alpheus*, reproduction is dependent on a moult, and therefore losing a shelter has a higher cost to females than to males, whose reproduction and moult are not related. Freshly moulted crustaceans are extremely vulnerable in social interactions, and to predation, and therefore a female bears a high cost in losing a shelter or being involved in aggressive interactions during or immediately after a moult. A male and female continue to share the shelter after copulation, when the female is carrying her attached eggs (as also observed in field collected pairs), and ovigerous females are less mobile than non-ovigerous females (Nolan & Salmon, 1970), so successful shelter defense may be very important for protection of the female and survival of the offspring.

In conclusion, size-assortative pairing in *A. heterochelis* does not seem to be based on male-male competition and male choice for larger females, as initially assumed. Instead, female choice and female-female competition seem to be more important in the pair formation process. Females prefer large males, and compete for access to larger males. Smaller, and hence less competitively successful, females will pair with smaller males, but in a male-biased environment, will preferentially pair with larger males. Large males provide the best protection from shelter eviction, which is crucial for female *A. heterochelis*, as their reproduction is closely associated with moult, and therefore requires shelter and a male present for successful reproduction. Size-assortative mating in *A. heterochelis* seems to be driven by females pairing with the largest males they can successfully compete for, and can defend from other females.

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