Body size and shelter possession in mature signal crayfish, *Pacifastacus leniusculus*

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Adult signal crayfish were used to examine the significance of body size in affecting possession of shelters. When there was a shortage of shelters, the likelihood that an intruder would take over increased as a function of body weight ratio between the contestants. In females a smaller difference was needed to achieve a given likelihood to win than in males. For example, a probability of 80% for the heavier individual to win requires a weight ratio of about 1.5 in females, while the ratio should be close to 2 in males. Shelter occupants were able to resist eviction by intruders rather well, yet take-overs were frequent. Removal of the shelter from a previous smaller owner proved that they were able to evict the larger one in 20% of cases tested. When larger owners were left without a shelter, the smaller shelter-holders could resist the larger intruders in 43% of the cases tested. These results support the conclusion that not only correlated asymmetries (i.e. body size) affect the outcome of shelter ownership conflicts, but also uncorrelated asymmetries (i.e. prior ownership) are in effect.

1. Introduction

Conflicts arise when many individuals are interested in a resource in short supply but required by all (Huntingford & Turner 1987). For example, the signal crayfish (*Pacifastacus leniusculus* Dana) resides during the daylight hours in crevices and burrows. At dusk it leaves, e.g. for food, and at dawn it returns to the shelter or finds another one (Hogger 1988). A burrow provides protection from predators, it might provide cover against cannibalism, and individuals may monopolise food items by dragging them into their hides (Goddard 1988). Some burrows may be more favourable than others, they may be in short supply, or their values differ for some reason. Under these circumstances conflicts over shelter possession can be expected every dawn.

Prior ownership of a resource, such as a sheltering burrow, confers asymmetry on the contest (Maynard Smith & Parker 1976). Size differences between individuals are another

source of asymmetry. Here our focus is on mature individuals of the signal crayfish and the effect of correlated (body size) and uncorrelated (prior ownership) asymmetries (Parker 1974, Maynard Smith 1982) on conflict outcomes. Hammerstein (1981) has proposed that when fighting costs are high relative to the payoff from winning, prior ownership should determine the outcome. Additionally, the owner is expected to win if the resource has only short-term value (Grafen 1987). The signal crayfish, like its relatives, has well developed chelipeds which are frequently used in aggressive interactions and defence against predators (Bruski & Dunham 1987, Hogger 1988). The existence of such weapons suggest that fighting costs can be quite high, as severe injuries are possible. Also, there is large body size variation in the population, and one therefore expects body size to be an important determinant of an individual's fighting ability.

Surprisingly little information is available on shelter size choice and conflicts over shelter occupancy in freshwater crayfish (Salmon & Hyatt 1983, Hogger 1988). In this study we examine in what way the body size of an individual affects its choice of shelter size, its ability to obtain a shelter and its ability to maintain a shelter (see also Ranta & Lindström 1992). We also investigate the effects of past experience, i.e. either successful or non-successful shelter occupant on an individual's performance in conflict situations. These data will serve as a baseline reference for our subsequent examination of fighting behaviour among individuals competing over shelter possession.

2. Material and methods

The experiments were made in July – August (prior to the crayfish breeding season in Finland) at the Porla Fish Hatchery (Finnish Games and Fisheries Research Institute, Fisheries Division) at Lohja, Southern Finland. Crayfish (adults; carapace length range 30–65 mm) for the experiments were trapped from two different adult-holding ponds, both having a population over 500 individuals. As an index of body size we shall use the length of the carapace. Some individuals were taken for measurements (to the nearest full mm) of right cheliped length (Fig. 1),
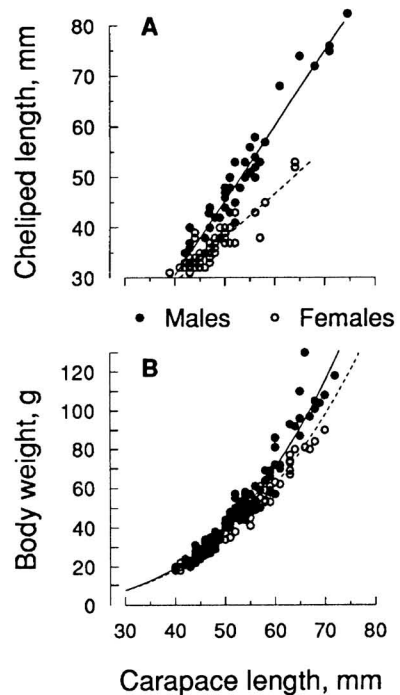

Fig. 1. Cheliped length (A) and body weight (B) plotted against carapace length in male and female signal crayfish. Regression models, as fitted to the data (p. 127), are shown in both cases.

and for a number of crayfish we also measured their body weights to within an accuracy of 1 g. All individuals used in the experiments had non-injured chelae. While the animals were in the experiments they were not fed, but they had been supplied with ample food in the holding ponds. Depending on the question addressed, individual crayfish spent no longer than about 12 h or 36 h in our experiments.

We used grey polyethylene containers (80 × 60 × 40 cm, L,W,D) as aquaria. They were filled up to 30 cm with water. The aquarium bottom was covered with about a 2 cm layer of coarse sand, serving as an adequate substratum for crawling but not providing enough room for digging a sand-shelter. The aquaria were kept outdoors but protected from direct sunlight and rain. During the experiments water temperatures ranged from 8 to 15°C.

First, we selected small (range 35–45 mm) and large (55–65 mm) crayfish. A single indi-

vidual of known size was introduced into an aquarium having a small (diameter 5 cm) and a large (8 cm) flower pot shelter lying on its side. Shelter occupancy was checked after one night of crayfish residence in the aquarium.

Second, pairs of animals differing in size were left overnight in an aquarium with one shelter (8 cm). The carapace length of the shelter owner and that of the one left without a shelter were then checked the next morning. In this experiment we used pairs of animals among which the size differences ranged from 1 mm to 15 mm. Sexes were tested separately. Using carapace length vs. body weight regression equations, we converted body sizes to body weights (g). The likelihood of the larger individual to win the shelter was assessed with a logistic regression model, weight ratio (larger/smaller) being the independent variable.

Third, the experimental set-up for the owner-intruder conflicts was as follows. For the first night an aquarium was split into two equal-sized parts with a removable divider. A red-earth flower pot (8 cm, depth 10 cm) was placed as a shelter on each side. Two individuals were introduced into each of the two compartments. The carapace lengths of the individuals on the side with smaller individuals were X–5 mm and X mm, while on the other side of the aquarium the corresponding sizes were X mm and X+5 mm (here X is a trial-specific constant, e.g., 40 mm vs. *45* mm, and *45* mm vs. 50 mm, or 52 mm vs. *57* mm, and *57* mm vs. 62 mm).

For the first night there were always two individuals (of the given size difference) per a single shelter. The size-status of the shelter owner was checked the following morning. When this was done, the extra individuals — those without shelters — were removed. Also, the aquarium divider was removed. Because large individuals tended to be shelter holders after the first night (details below) we usually had a small resident and a large resident left in each aquarium. In half of the cases we removed the shelter from the smaller one, and in 50% of the cases it was removed from the larger occupant. The crayfish were left for one more night in the aquarium, and the size-status of the shelter holder was checked again the next morning.

In a number of cases the shelter was over-turned the first morning in one or both of the compartments, causing the termination of the experiment. This, together with the few cases when no crayfish was found in the shelter the second morning, or due to an overturned shelter during the second night, explains why our data for the shelter owner status for the first morning are larger than those for the second morning.

3. Results

Sex-related differences in size are rather obvious in the signal crayfish (Fig. 1). The statistics for the regression models (CL = carapace length, mm) in Fig. 1 are as follows:

Body weight, g
females $10^{-3.54} \times CL^{3.00}$, $r = 0.986$, $n = 88$
males $10^{-3.82} \times CL^{3.19}$, $r = 0.974$, $n = 111$

Cheliped length, mm
females $-4.4 + 0.85 \times CL$, $r = 0.909$, $n = 58$
males $-29.0 + 1.48 \times CL$, $r = 0.967$, $n = 47$.

The data show that males of a given carapace length are, on average, heavier than females (Fig. 1B). For example a female measuring 40 mm in carapace length weighs 19 g, and a 70 mm female 100 g. The corresponding figures for males are 20 g and 116 g, respectively. This is largely due to the fact that males have larger chelipeds than females (Fig. 1A). Chelipeds for 40 and 70 mm females measure 30 and 55 mm, while for males they are 30 and 75 mm. These differences are likely to affect the outcome of fights.

When we checked the outcome of shelter size selection with small (40–45 mm) and large (50–55 mm) animals we could see that small females were residing more frequently in the smaller of the two shelters. In large females no such differences were found (Fig. 2). Contrary to females, males of both size categories were consistently found more often in large shelters. Test statistics for the four 2×2 comparisons are: small vs. large females $\chi^2 = 3.52$, $P = 0.06$; small vs. large males $\chi^2 = 0.73$, $P = 0.39$; small females vs. small males $\chi^2 = 10.61$, $P = 0.001$; large females vs. large males $\chi^2 = 9.28$, $P = 0.002$.

Body weight ratio (larger/smaller) was used as a measure of size difference between individuals competing for a single shelter. The prob-
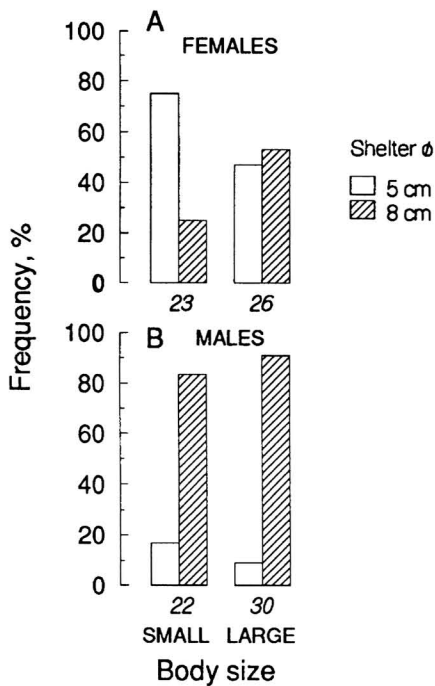
Fig. 2. Frequency of small (carapace length 35–45 mm) and large (55–65 mm) female (A) and male (B) signal crayfish in shelters of diameter 5 and 8 cm. A single individual per aquarium was allowed to chose between shelters of the two sizes. Sample sizes are indicated below the columns.
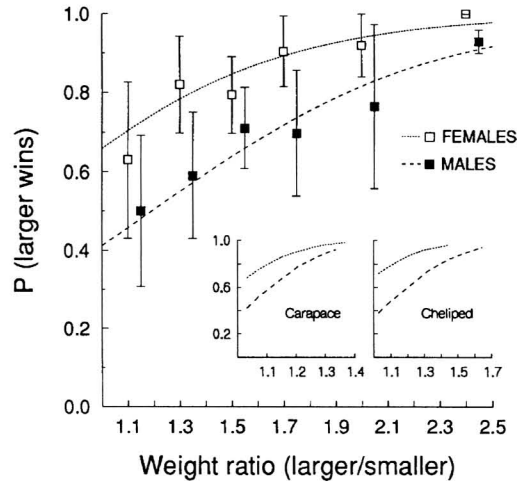

Fig. 3. Two individuals, differing in body size, were introduced into an aquarium with a single shelter. The body size of the shelter holder was checked after 12 h. The graph shows the proportion of cases (±95% confidence limits) in which the larger individual was in the shelter against size difference between the two individuals (weight ratio). Males and females are plotted separately (for clarity male values are shifted along the *x*-axis). The expectation based on random outcome is 0.5, the broken lines describe the fitted logistic regression models. In the insets the size difference is estimated by the carapace length and cheliped length ratios.

ability for the larger individual to win (P) as a function of body weight ratio (X) is readily characterised by a logistic regression model. The model parameters for females are

$$\ln[P(X)/(1-P(X))] = -1.45(\pm1.40) + 2.10(\pm1.00)X.$$

The fit is good: $\chi^2 = 162{,}7$, $df = 176$, $P = 0.756$. The corresponding model for males is

$$\ln[P(X)/(1-P(X))] = -2.20(\pm1.13) + 1.84(\pm0.77)X,$$

also with a reasonable fit: $\chi^2 = 163{,}5$, $df = 156$, $P = 0.324$. Notice, however, that there are pronounced differences between the sexes (Fig. 3; the error bars are also rather wide). Checking the results against carapace length and cheliped length ratio yielded qualitatively similar results. It should be noted that theoretically when the size ratio

between two individuals is 1:1 the probability of the "larger" to win should be $P = 0.5$. Because the above two models are empirical, the winning probability functions, due to error variation, do not intercept the *y*-axis at $P = 0.5$ at size ratio 1:1. We have decided not to attempt to force them through these coordinates as these functions only serve for illustrative purposes.

When individuals of different size fight over shelter ownership it is likely that the larger one wins. But a much larger size difference is needed in males to achieve the same winning frequency as in females. The discrepancy is largest at the smaller size ratios (Fig. 3). Furthermore, it seems to be independent of the size-difference measure used.

The conclusion that larger individuals win conflicts over shelter ownership is further substantiated by the first-day observations from the "divided aquarium" experiment. The crayfish pairs were selected so that the larger individual
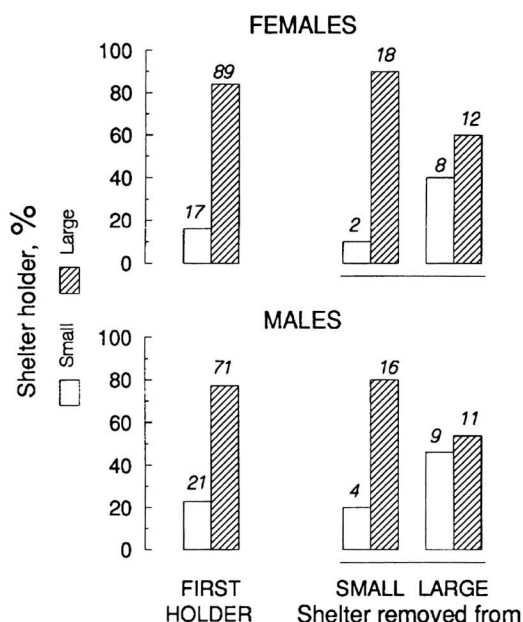
Fig. 4. An aquarium was divided into two with a removable wall. Two individuals differing in carapace length (5 mm difference) and a single shelter were introduced into each compartment. The crayfish pairs were always selected so that the larger individual on one side of the wall matched the size of the smaller one on the other side of the divider. The body size of the shelter holder (sexes shown separately) was checked after 12 h (first holder; numbers in italics indicate sample sizes). Individuals without shelter were then removed, as was the dividing wall. For the next part of the experiment we accepted the trials in which the larger individual was in the shelter. In half of the cases we removed the shelter from the smaller individual and in half of the cases the shelter was removed from the larger individual. The size of the shelter occupant was assessed again after one night.

on one side of the wall matched the size of the smaller on the other side of the divider. Larger individuals were found more often (about 80% of all cases) inside the shelter than smaller ones (Fig. 4; no differences were observed between sexes, $\chi^2 = 1.46$, $P = 0.23$). But the outcome was different once an individual had been successful in a conflict.

The successful shelter owners were used in the second part of this experiment. In half of the cases the shelter was removed from the larger of the two first-night winners and in half of the

cases it was taken away from the smaller one. When the size of the shelter owner was checked the next morning we observed that when the shelter had been removed from the smaller one, this individual could still take over the shelter from the larger one in about 20% of the cases (Fig. 4). This closely matches the proportion of smaller individuals found inside the shelters the first morning (sexes pooled $\chi^2 = 0.56$, $P = 0.45$). The smaller individual was able to resist the take-over attempts by the larger one rather well when the shelter was removed from the larger one of the two (Fig. 4). The proportion of smaller individuals found still inside their shelters the second morning was 43%. A comparison of the two treatments (shelter removed from small vs. shelter removed from large) yielded a test result of $\chi^2 = 4.38$, $P = 0.04$. This suggests that the outcome of the owner-intruder conflict is dependent on both the size of the owner and the size of the intruder (testing the "first owner" against "removal from large" gives $\chi^2 = 7.15$, $P = 0.008$; $df = 1$ in all the tests above). In the owner-intruder conflict experiments no obvious differences were found between females and males.

4. Discussion

Our experiments show that shelter diameter choice of females and males is different. Females were found in small shelters, while males of matching body length markedly more often took up residence in the larger of the two available. Sexual dimorphism is pronounced in signal crayfish (Holdich & Reeve 1988). Measurements taken by us indicate that the most obvious difference is that males of a given size are somewhat heavier and have longer chelipeds than females. According to our observations the signal crayfish, when residing in a shelter, keeps its chelae folded in the mouth of the pot. Larger chelipeds block the entrance more effectively than smaller chelipeds. If females lose more conflicts between females and males of similar size, they may be inclined to prefer shelters suiting their physical dimensions.

If size differences are linearly related to dominance hierarchies among individuals, such differences are likely to affect conflict outcomes

in favour of the bigger individuals (Bovbjerg 1953, Stein 1976). Therefore, one would expect that in agonistic encounters males should win over females of matching body length, provided that chelipeds play a role in settling the conflict. This seems to be the case, as Bovbjerg (1956) was able to show that in matching female-male pairs, males were the ones that dominated (73% of 'tension contacts' were won by males).

The likelihood of winning a shelter increases with increasing size difference between the contestants in the signal crayfish. This is, in fact, a very common determinant of conflict outcome (Huntingford & Turner 1987, Archer 1988). Dominance hierarchies in many crayfish species are correlated with body size (Bovbjerg 1953, 1956; *Orconectes virilis* and *Procambus alleni*, respectively) or chela length (Stein 1976; *O. propinquus*), Berril & Arsenault 1982, 1984, Bruski & Dunham 1987, Snedden 1990; *O. rusticus*) and Copp (1986; *Procambarus clarkii*).

In a competitive situation with no role assymmetries size was a much more clear determinant of shelter occupancy probability in females than in males. To further substantiate the statement the information given in Fig. 3 is rearranged into the following tabulation indicating the proportion of larger individuals winning:

weight ratio:	<1.5	>1.5
females	0.78	0.90
males	0.58	0.69.

This indicates that females for some reason might find a shelter much more valuable than males and therefore determination of ownership is much more finely tuned to fighting ability. Why females should find shelters to be very much more valuable than males thus becomes a pertinent question. There are at least three alternative explanations that could apply to the situation.

The availability of unoccupied burrows should be equal for both sexes. However, if females are worse off against males than males are against females then the relative availability of occupied burrows is smaller for females. Females might, therefore, put more effort into trying to evict another female from a burrow and consequently observed takeover rates should be higher in females than in males. Alternatively, males have

proportionately larger chelipeds than females, therefore fights among males may be more costly. Hence, males might avoid escalating conflicts resulting in a situation where takeovers occur only when the intruder is very much larger than the defender. There could also be a difference in the long-term value of a burrow between males and females. For example, in the autumn, females might anticipate the forthcoming breeding season and the need for a shelter where they can incubate their eggs. This would increase the motivation to fight for a longer time, resulting in small differences in resource holding power determining contest outcome (Leimar & Enquist 1984).

Our data show that small individuals are rather badly off against large individuals in situations where shelters are limiting. When a small and a large individual are simultaneously interested in an empty shelter, the larger one usually wins. However, once the small individual happens to reside in a shelter things become different. Its size disadvantage is rather well compensated for by actual possession of the shelter, as shown by the high percentage of shelters small individuals could keep.

Whether the ownership of a shelter increases a male's fighting ability, either due to positional advantages or because of knowledge about resource value (Austad 1983), remained unclear in this experiment. The expectation would have been that when the shelter was taken away from the larger individual, the smaller would have performed better, i.e. retained his shelter in more cases. This also occurred in practice. The larger crayfish was able to take over the shelter from the smaller owner in only half of the trials. However, when the shelter was removed from the smaller male the expectation was that he would not be able to take over a shelter at all. Instead it turned out that takeover rates now were equal to the takeover rates with no role asymmetries. Thus it seems that ownership does affect the performance of small individuals but not large individuals. One explanation for this could be that for some reason the payoff from possessing a shelter differs for large and small individuals, perhaps because small individuals are more vulnerable to predation (Stein 1977, Hirvonen 1992). Alternatively, a small crayfish may have smaller expectations of obtaining a

shelter and therefore, once it has succeeded in doing this, it will put more effort into defending it. For example, small sand goby males initiate more fight displays when defending large nests, whereas large males show no difference in behaviour with nest size (Lindström 1992). However, answering this question requires further experiments.

Though we did not carry out any systematic survey on the interactions between owners and intruders, we were able to observe many agonistic encounters, even to the extent that the flower pot used as a shelter had frequently been turned upside down. On one occasion a 65 mm male had killed his 60 mm non-moulting opponent in an overnight experiment. According to Ameyaw-Akumfi (1979) and Snedden (1990), antagonistic encounters escalate to physical encounters in interactions between individuals in many crayfish species. In fact, knowing that crayfish are mainly active when the light is low, physical contacts between individuals may be a necessity. The resource holding power model by Parker (1984) suggests that in conflicts with correlated asymmetries animals should assess the fighting abilities of their opponents before beginning the fight. As the light diminished *Orconectes rusticus* used more time and performed more fighting acts than in well-lit conditions (Bruski & Dunham 1987). However, it is unclear at present which of the acts involved are for display and which belong to the actual fight.

Interactions between crayfish individuals are elaborate and aggressive (Bovbjerg 1953, Rubenstein & Hazlett 1974, Bruski & Dunham 1987, Snedden 1990) and it is likely that visual cues play a significant role, even more so in the signal crayfish because it has a prominent white spot at the junction of the propodus and dactylus, while the ventral side of the chelipeds is bright red (Holdich & Reeve 1988). If the spot size correlates with body size it could serve to advertise an individual's fighting ability. Therefore, physical contacts between the contestants may not be necessary for size assessment. Nevertheless, threatening with exposed chelae frequently leads to physical contacts with chela strikes and pinching and intensive wrestling with interlocked chelae (Ameyaw-Akumfi 1979, Bruski & Dunham 1987). In the signal crayfish such fights

may last up to several minutes, and they may even lead to violent overturning of the weaker opponent (own unpubl. observations). All these facts call for more detailed research on the role of fighting in shelter ownership.

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