

Movement of male *Heterozius rotundifrons* (Crustacea: Decapoda: Brachyura) depends upon local sex ratio

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Abstract *Heterozius rotundifrons* is a New Zealand endemic crab that lives in the intertidal zone and is found under rocks during low tides. We investigated the role of the local sex ratio (= under rock) in affecting movement patterns of this crab. In the laboratory, male crabs moved more when the sex ratio was male biased. Field surveys suggested that there is an upper limit to the number of males found under rocks, even as the number of females increases. Field manipulations demonstrated that when the sex ratio under a rock is female biased there is no effect on female movement but when the ratio is male biased, males move away more frequently and move further. This increased movement by males is probably related to avoidance of male-male competition for females.

Keywords *Heterozius*; intertidal; male-male competition; movement patterns; sex ratio

INTRODUCTION

Movement by animals often increases the probability the animal will come in contact with needed resources. Although movement incurs costs in terms of both energy expenditure and increased predation risk, the advantages of movement in terms of resource acquisition outweigh those costs in many situations (Werner & Anholt 1993). The resources gained can be food, shelter, or access to receptive mates.

Given that the rate or probability of movement should reflect a compromise between the costs of movement and advantages in terms of resources gained, we would expect that animals should remain longer in areas where there are more resources. Although territoriality is an extreme example of behaviours linked to resource defense, animals in general should attempt to move towards areas of higher resource density or, if in such an area, defend such areas, even if only temporarily.

One factor we would predict could alter movement patterns is the local sex ratio, given that it influences the availability of members of the opposite sex. Lawrence (1987, 1988) reported that male milkweed beetles (*Tetraopes tetraophthalmus*) left host-plant patches at a higher rate if the sex ratio in the patch was male biased. Similar results were found in the laboratory for the soapberry bug, *Jadera haematoloma* (Carroll & Salmon 1995). Lawrence (1986) also found that male milkweed beetles fly further when leaving male-biased patches. Mathews (2002) manipulated the local sex ratio of snapping shrimp, *Alpheus angulatus*, but found no effect upon the frequency of males switching burrows.

Heterozius rotundifrons is an intertidal New Zealand endemic crab in the Family Belliidae (McLay 1988). During low tide it is found under rocks that are exposed by the receding tide and individuals may stay under the same rock for a number of days (Snell 1991). The number of individuals found under a given rock is variable although a tendency towards similar numbers of males and females has been noted (McLay 1988).

The sex ratio in the mature size classes is female biased (2:1) and ovigerous females can be found during all months except February (Jones 1978). The apparent continuous breeding is mainly because of the comparatively large egg size, and long embryonic phase, rather than continuous mating. In *H. rotundifrons*, mating can only take place for a short time after a female moult, and males guard pre-moult females for some hours to days (Thompson 1999).

In this study we examined the following four questions: (1) Do individuals of *H. rotundifrons* vary their rate of movement in the laboratory when the sex ratio in a tank is manipulated?; (2) In the field, does the sex ratio of *H. rotundifrons* found under a rock in the intertidal vary depending upon the number of animals found under that rock?; (3) If the sex ratio under a rock is manipulated does that affect whether animals stay under that rock?; and (4) Is the distance moved by animals influenced by the sex ratio under rocks from which they move?

METHODS

Laboratory experiment

We first looked at the question of how the sex ratio of a local area affected movement patterns in the laboratory. Work was conducted at the Edward Percival Marine Laboratory at Kaikoura, New Zealand. After several trials using different materials and substrate depths, it was found that red transparent Perspex (180 mm × 180 mm) provided adequate shelter for the crabs and also made viewing non-invasive. A substrate 2–3 mm deep prevented *H. rotundifrons* from burying and provided a natural substrate. The tanks (1.2 m × 0.75 m × 0.25 m) had a constant supply of fresh sea water.

The experimental treatments involved constant numbers of the sex being tested and adding crabs of the opposite sex to create male:female sex ratios of 1:0.5, 1:1, and 1:2. The sex ratio was adjusted within two set densities of 6 and 18 crabs (equivalent to 9 and 21 crabs per m² respectively). The control was a tank with crabs of only one sex (the sex that was tested). Individually marked male and female crabs 16 and 18 mm carapace width (CW) were used. The crabs were allowed to acclimatise for 24 h before each experiment began. Individual crab movement was monitored daily by recording the total number of males and females that moved. Movement rates were then calculated as a percentage of the total number of males or females present. Recordings were taken daily between 0900 and 1000 h. Crabs

were fed fresh mussels daily after recordings were taken. The percentage of animals of each sex that moved for each sex ratio was analysed using a 2-way ANOVA on square root arc-sin transformed data, testing for effects of sex, sex ratio, and an interaction between sex and sex ratio. The data were pooled by density as there were no significant differences in the percentage of moves of each sex for the two densities ($F_{1,94} = 0.33$, $P = 0.86$). Tukey's HSD test was used for pair-wise comparisons of means.

Field experiments

The field portions of this study were carried out in Kaikoura, New Zealand near the Edward Percival Field Station of the University of Canterbury. The initial field surveys and the first field experiment were done at Keane Pt at the north end of the Kaikoura Peninsula and the second field experiment was conducted on the shore opposite the Edward Percival Field Station.

Initial field survey

At Keane Pt, in the range of the mid-intertidal zone where *H. rotundifrons* occurs (McLay 1988), we turned over rocks exposed by the low tide. The study area was bounded by a series of rock outcrops and was c. 14 m wide and 25 m from the highest location for *H. rotundifrons* to the lowest location for individuals of that species. For each rock that had more than 4 individuals of adult *H. rotundifrons* under it, we collected the adult crabs and recorded their sex. A total of 34 rocks were sampled on 2 days—3 March and 19 April 2002. For the 24 rocks sampled on 3 March, the size of each rock was measured as the area of substrate covered.

Field experiment 1

Given the pattern seen in our initial survey, we hypothesised that the number of males, but not females, under a rock was limited by male movement patterns. In particular, we hypothesised that males would move away from all-male rocks, i.e., an extreme male sex bias. We used the 24 rocks sampled on 3 March and on that same day marked the rocks with a waterproof marker. We marked each crab with an individual number and measured the CW in mm. We created three experimental conditions in a randomised block design: (1) control rocks; (2) all male rocks; and (3) all female rocks. For eight of the rocks (selected as part of sets of three rocks near each other that had crabs in the survey), we replaced the original crabs back under the rock where they were found, thus the original sex ratio was not altered.

These were later treated as the crabs under control rocks. For another 8 rocks we left the original males found under that rock and replaced the original females with males collected in a separate area of the Kaikoura Peninsula (creating all male rocks). For the final set of 8 rocks we left the original females found under those rocks and replaced the original males with females collected in a separate area (all female rocks). Thus, the experimental manipulations resulted only in changes in sex ratio, not changes in crab density.

The next day we surveyed the area (and rocks c. 4 m higher and lower in the rock-bounded area originally surveyed), turning over all rocks that could potentially have individuals of *H. rotundifrons* under them. We recorded the location of all marked animals, whether from the original rock they were found under or elsewhere in the study area. We repeated the survey and gathered the same information on the following day, 5 March.

Field experiment 2

To separate the factors confounded in field experiment 1 (sex ratio change and the introduction of non-resident males), we conducted a second field manipulation. This manipulation focused upon males since there was no effect on female movement by the treatments done in field experiment 1 (see Results). This experiment was conducted in an intertidal area directly in front of the Edward Percival Field Station, c. 2 km from Keane Pt. This area was bounded by rocky outcrops and was c. 8 m wide and c. 6 m from the highest location in the intertidal where individuals of *H. rotundifrons* were found to the lowest. On 18 April, crabs were collected from Keane Pt, measured, sexed, and individually marked. They were held overnight at the Field Station in running sea water. On 19 April, 20 rocks in the intertidal zone occupied by *H. rotundifrons* were selected, marked, any *H. rotundifrons* removed, and one of two treatments was set up. To control for possible confounding effects of rock size on movement, we chose rocks of similar sizes, ranging from 225 to 400 cm². For 10 of the rocks, four males were placed under the rock. For the other 10 rocks, two males and two females were placed under the rock. Rocks were randomly assigned to treatments. Surveys of all the rocks in the area were conducted c. 24 and 48 h later (exact time period determined by the tides). The locations of all marked crabs were recorded either as under original rock or distance moved from the original rock.

Data from the field experiments were analysed using χ^2 tests for numbers of crabs moving and *t* tests for distances moved. Where means are presented in the text, standard errors of the mean are also presented.

RESULTS

Laboratory experiment

There was a significant difference between the percentage of moves made by males and females ($F_{1,88} = 161.1, P < 0.01$), with males moving more than females (Fig. 1). Sex ratio also had a significant influence on the rate of movement ($F_{3,88} = 21.8, P < 0.01$), and this effect differed significantly for the two sexes ($F_{3,88} = 17.6, P < 0.01$). Tukey's HSD tests showed that males moved significantly more in the 2:1 ratio and control (all males) than the 1:1 and 0.5:1 ratios ($P < 0.01$; Fig. 1), whereas the percentage of females moving did not differ between sex ratios ($P > 0.05$; Fig. 1). Summarising the results, females had similar residence times under shelters for each sex ratio whereas male residence time decreased with increasingly male-biased sex ratios.

Field experiments

Initial field survey

A total of 257 crabs were found under the 34 rocks and of these, 105 were male and 152 female (an overall sex ratio of 1:1.4). The number of crabs per rock ranged from 4 (the self-imposed lower limit) to 20 individuals, with the number of females ranging up to 15 and the number of males up to 7. Fig. 2 clearly shows that there seems to be an upper limit to the number of males under rocks, but not for numbers of females. For females, 9 out of 34 rocks (26.5%) had more than 5 females present, whereas only 1 out of 34 rocks (3%) had more than 5 males present. Furthermore, four all-female rocks were found, whereas no all-male rocks were found. Thus, the number of males appears to be approximately constant rather than increasing proportionally with the number of females.

Further clarification of this pattern comes from the data on the subset of rocks for which rock size was measured (rocks ranged in size from 234 to 2860 cm², with a mean size of 728 cm²). The number of females was positively correlated with rock size ($r^2 = 0.59, P < 0.001$), whereas there was no significant correlation between rock size and number of males ($r^2 = 0.11, P = 0.12$).

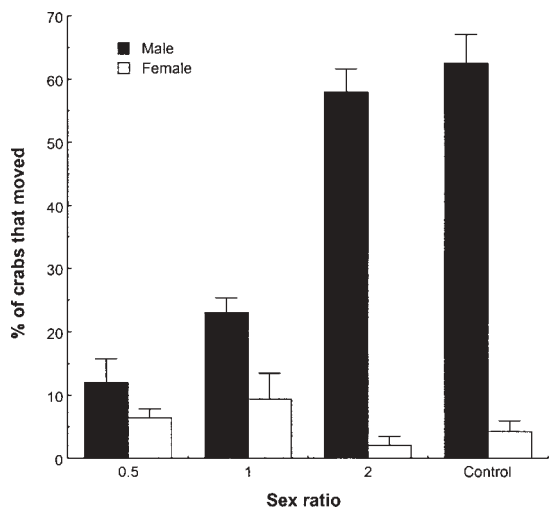


Fig. 1 Percentage of *Heterozius rotundifrons* males (16–18 mm carapace width (CW)) and females (16–18 mm CW) that moved at different sex ratios (male:female) during the laboratory experiment. Control was all females or all males. Error bars represent +1 SEM.

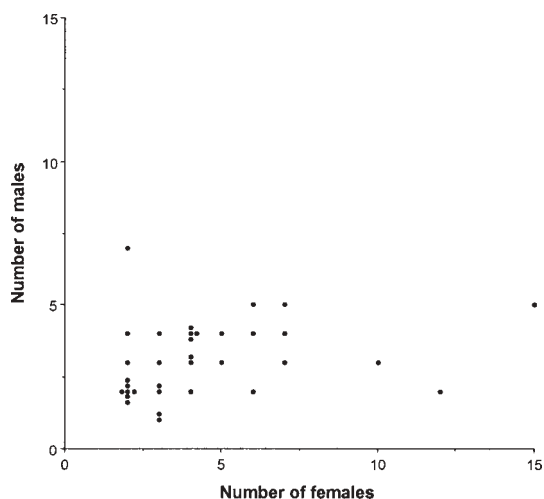


Fig. 2 Relationship between the numbers of *Heterozius rotundifrons* males and females under rocks ($N = 34$ rocks). Where multiple data points occurred at the same location, values were adjusted slightly for purposes of clarity.

These patterns of distribution of the two sexes under rocks could result from a variety of aspects of the behavioural ecology of this crab and thus we set up an experiment to test a particular hypothesis that could explain the pattern: that males move away from rocks with a male-biased sex ratio.

Field experiment 1

Of the 191 animals marked on the first day, 64 were found at least once over the course of the next two days. Overall, a greater proportion of males were found compared to females (36 out of 88 males, 28 out of 103 females; $\chi^2 = 4.01$, d.f. = 1, $P = 0.045$). Significantly more males were found on both days than females (8 males out of 88, zero females out of 103) ($\chi^2 = 12.8$, d.f. = 1, $P < 0.001$). In addition, males that were found anywhere in the study area were larger ($\bar{x} = 17.3 \pm 0.36$) than males never found ($\bar{x} = 16.0 \pm 0.23$; $t = 3.11$, d.f. = 86, $P = 0.003$). For females, there was no difference in the number of animals found anywhere in the study area depending upon treatment (control rock residents, original females under rocks that had been changed to all female rocks, or females introduced to form all female rocks) (Fig. 3). There was also no difference in the size of females found in the study area ($\bar{x} = 16.0 \pm 0.42$) versus those females not found ($\bar{x} = 15.5 \pm 0.28$; $t = -0.88$, d.f. = 101, $P = 0.38$).

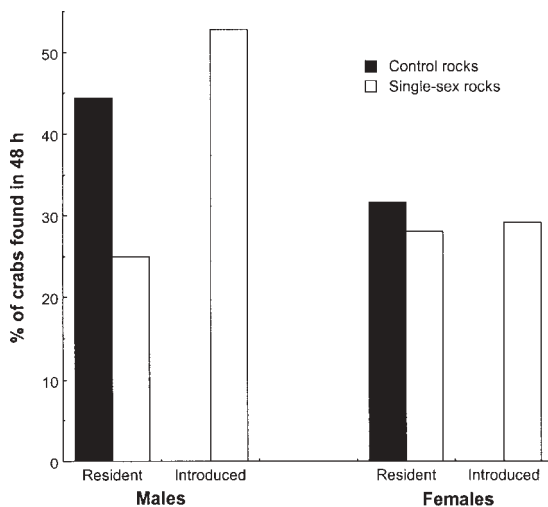


Fig. 3 Percentage of male and female *Heterozius rotundifrons* recaptured after 48 h in Experiment 1 depending upon whether the sex ratio was unaltered (control rocks) or altered to one sex only (single-sex rocks). Results are presented separately for resident and introduced crabs.

Among the male crabs, resident males under control rocks were more frequently found than were resident males under all-male rocks, although this difference was not quite significant ($\chi^2 = 3.52$, d.f. = 1, $P = 0.057$). Introduced males (which were

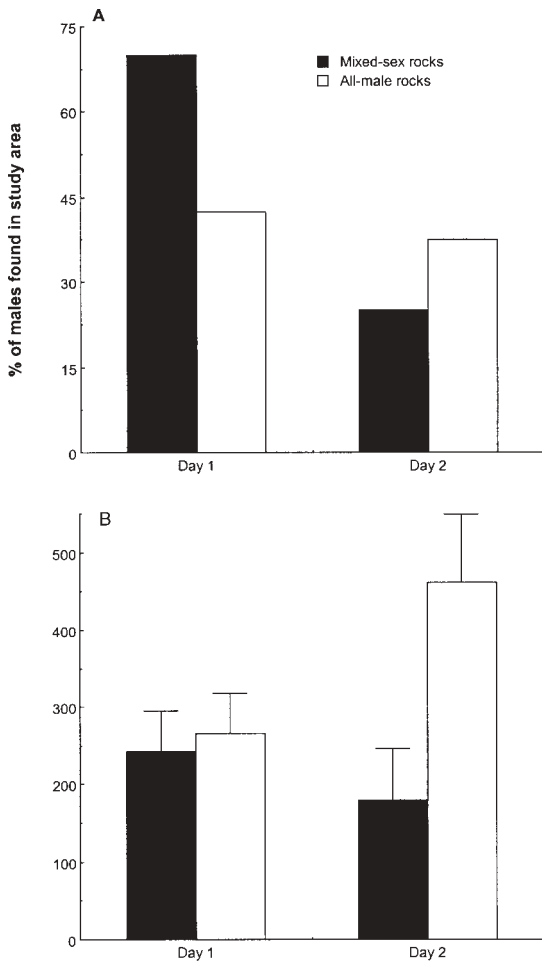


Fig. 4 A, Percentage of *Heterozius rotundifrons* males recaptured and B, distance moved (cm) on day 1 and 2 in Experiment 2 depending upon the manipulated sex ratio under rocks (mixed-sex or all-male).

necessarily under all-male rocks) were found more frequently than were resident males under all-male rocks ($\chi^2 = 7.00$, d.f. = 1, $P = 0.007$) (Fig. 3).

The results from the first field experiment clearly indicated that resident males moved differently when all-male rocks were created by the addition of males from another area. Although this is consistent with the idea that male movement is affected by the sex-ratio under a rock, there is a confounding factor in this experiment. That is, the resident males experienced both a change in the sex ratio and the introduction of “alien” males. The second field experiment was set up to control for this confounding factor.

Field experiment 2

Of the 80 marked crabs placed under rocks, 48 were found at least once over the next 48 h. Of these, 36 were found on Day 1, 26 on Day 2, and 14 were found on both days. More marked males than females were found in the study area on Day 1 ($\chi^2 = 4.31$, d.f. = 1, $P = 0.038$) but there were no differences by sex by Day 2 ($\chi^2 = 0.76$, d.f. = 1, $P = 0.78$).

The proportion of males found in the study area on Day 1 was significantly higher for the mixed-sex rocks compared with the all-male rocks ($\chi^2 = 4.04$, d.f. = 1, $P = 0.044$) (Fig. 4A). This difference did not occur on Day 2 ($\chi^2 = 0.94$, d.f. = 1, $P = 0.33$), although by Day 2 the mean distance moved for males under all-male rocks was significantly greater than the distance moved by males under mixed-sex rocks ($t = 2.58$, d.f. = 16, $P = 0.02$) (Fig. 4B). It would appear that males originally under all-male rocks moved greater distances as time passed. For the males found twice, the maximum distance moved was significantly greater for the crabs from all-male rocks (5.9 m) compared with mixed-sex rocks (1.3 m) ($t = 2.68$, d.f. = 10, $P = 0.023$).

Only one male was found twice under the rock it was originally placed under on the subsequent surveys and this was a mixed-sex rock. Interestingly, two males that were placed initially under the same rock were found together on both days under different rocks, 495 cm and 160 cm from the original rock.

DISCUSSION

If access to females is compromised by the number of males per female in the local area, it makes sense for males to seek areas where such a compromise is not present. This would be particularly important if females are receptive for a short period of time. In *H. rotundifrons*, mating can only take place for a short time after a female moult and males guard females for some hours to days before a female moult (Thompson 1999). Both our laboratory and field observations indicate that male *H. rotundifrons* move more frequently when the sex ratio is male biased. This is similar to the pattern reported for male milkweed beetles (*T. tetraophthalmus*) (Lawrence 1988) and male soapberry bugs (*J. haematoloma*) (Carroll & Salmon 1995).

In the laboratory, males did not alter the rate of movement depending upon the density of crabs present, but did move more when the sex ratio in the

tank was male biased. Given the constraints of a laboratory situation this could result from either males moving to increase their chances of finding an unguarded female or from males moving to avoid aggressive interactions with other males. Male-male aggression is intense in this species, particularly when a pre-moult female is present (Thompson 1999). None of our observations can clearly differentiate between the alternative motivations for increased movement by males. But the fact that larger males did not leave male-biased rocks as frequently as smaller males suggests that avoiding male-male competition may be the basis for increased movement.

In our field surveys, no rocks with all males were found and as the number of females under a rock increased, there was no increase in the number of males. This distribution pattern could result from a variety of aspects of the behavioural ecology of the species, and the female-biased sex ratio in the local areas we surveyed would partially (but not fully) explain the pattern of more females under rocks. The behavioral mechanism consistent with the results of our laboratory study is increased movement of males with increased male-biased sex ratios under rocks.

The results of both field manipulations also point towards the local sex ratio having an effect of male movement patterns. Male-biased sex ratios in the local area (under one rock) result in increased probability of movement by males. The first field manipulation showed that males, but not females, were affected by our experimental alterations of sex ratio. But the design of the experiment meant that we could not differentiate between whether males were responding to males or just introduced animals. Although rock size could have affected movement in the first field experiment, both rock size and space/crab were controlled in the second experiment. The results of the second manipulation clearly showed that males moved more when the sex ratio was male biased, even when all the animals under rocks were introduced. The finding that males under male-biased rocks moved further is similar to the results of Lawrence (1986) on milkweed beetles.

Although the peak time of mating in *H. rotundifrons* occurs in early November (late spring) (Thompson 1999), we found a number of pairs of crabs in which the male was holding a female in a pre-copulatory guarding position during our experiments in May. In one example, a male was guarding a recently moulted female and a female moult (of a slightly smaller size) was right next to the pair. Mating can only occur shortly after a female

moult (Thompson 1999). Thus males would clearly be motivated to seek out mate-guarding opportunities at the time of at least our second field experiment.

The fact that female behaviour was not affected by the local sex ratio in this study, whereas male behaviour was affected, is in some ways similar to the difference in male and female behaviour in the hermit crab *Clibanarius vittatus* (Hazlett & Rittschof 2000). In this species, the detection of a predation-risk cue shut down pre-copulatory behaviour in females, but had no effect on male reproductive behaviour. In both of these examples, the fact that females can probably be assured of being mated (by some male) whereas some males may not obtain any matings dictates the differences in behaviour between the two sexes. Female *C. vittatus* can afford to cease being reproductively active if in doing so she increases her chances of survival and resumption of mating activities after the danger of predation has passed. Similarly, female *H. rotundifrons* will probably be found and guarded by a male at the appropriate time even if the sex ratio is female biased whereas a male may not find a female to guard at the appropriate time if the local environment is male biased.

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