MECHANICAL USE OF CRAYFISH CHELAE

TROY A. KELLER* and BRIAN A. HAZLETT

University of Michigan, Department of Biology, Ann Arbor, MI 48109-1048 and
University of Michigan Biological Station, Pellston, MI 49769

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Chela mechanical function was investigated by comparing individuals of the crayfish Orconectes propinquus (Girard) with and without the mechanical use of their chelae (dactyls held closed with rubberbands or glue) to determine if crayfish need the mechanical function of chelae to feed, to deter predators, to survive in the field, and to copulate with mates. Laboratory studies showed that crayfish did not require the use of their chelae to consume algae or snails, but fewer crayfish consumed juvenile insects when their pincers were non-functional. Male and female crayfish with functional pincers were just as susceptible to snapping turtle predators in the laboratory and just as likely to be recaptured in the field as those with non-functional pincers. Laboratory mating experiments with two males and a single female showed that only males with the mechanical use of their chelae copulated. These results indicate that O. propinquus require their chelae for mating but do not require functioning chelae to feed or to survive in the field.

INTRODUCTION

The observation that male and female crayfish show a marked sexual dimorphism in chelae size has prompted a number of studies concerning the function of these conspicuous chelate appendages. Chelae play a role in predator avoidance (Stein and Magnuson, 1976; Stein, 1977; Stein, 1976), mate acquisition (Mason, 1970; Stein, 1976; Snedden, 1990), and aggressive interactions (Garvey and Stein, 1993; Bovbjerg, 1956). While chelae may serve some purpose in these activities and possibly others (i.e., feeding), it is unknown whether chelae are serving primarily display functions (Rabenstein and Hazlett, 1974; Stein and Magnuson, 1976) or primarily mechanical functions (i.e., grasping and crushing).

Male Orconectes propinquus have larger chelae than females (Berrill and Arsenault, 1982; Garvey and Stein, 1993); these chelae can constitute up to 40% of an adult male's dry weight (Stein, 1976). The size of the male chelae increases

* To whom all correspondence should be addressed.
allometrically with age, and males undergo annual changes in the length of their chelae relative to their body size (Stein et al., 1977; Hobbs, 1988). Males molt to a larger pinched, reproductive morphology (FI) before the fall breeding season and molt to a smaller relative chela size for the summer (FII). These observations led Stein (1976) to hypothesize that chelae are used primarily for social interactions and reproductive activities i.e., copulation and male-male competition for mates.

Chelae may serve functions in addition to reproduction and fending off predators. Crayfish are omnivorous, feeding on detritus, algae, and other invertebrates (Hobbs, 1993). Crayfish could use their chelae to manipulate food items such as algae and to capture and crush invertebrate prey such as snails. Crayfish could also use their chelae to defend or acquire shelter. The use of shelter appears to be an important factor affecting crayfish susceptibility to predators (Mather and Stein, 1993) and access to shelter could be affected by chelae use (Levenbach & Hazlett, in prep.).

This study examined whether individuals of the crayfish _O. propinquus_ require the mechanical use of their chelae to feed, to survive in the field, to avoid turtle predators, and to copulate in the laboratory. If the mechanical use of chelae appears to be of minor importance, this would suggest that the display function is perhaps more important in determining the size and size variations of crayfish chelae.

**METHODS**

The _Orconectes propinquus_ used in this study were collected from the Maple River near the University of Michigan Biological Station, Pellston, Michigan and most of the laboratory experiments were done at the Biological Station. Crayfish were captured at night and were returned to the stream at the conclusion of each experiment. We measured carapace length as an estimate of body size and manus length as a indicator of the chela size using dial calipers.

**Feeding Experiments**

The feeding experiments were done during the summers of 1992 and 1993. Adult crayfish were randomly assigned to either the control or experimental group for each of the different tests conducted. Rubberbands were placed around chelae to eliminate the mechanical function of chelae for crayfish in the experimental group. To control for handling effects, rubberbands were placed on all crayfish, but were removed from the control crayfish just before each trial.
Crayfish were starved for the 48h prior to each trial. Crayfish were then placed singly in aerated, visually isolated, 20cm diameter arenas containing 1.25L of Douglas Lake water and a half clay pot shelter. Feeding trials on algae, snails, and aquatic insects were conducted separately and all trials lasted 24h.

For the tests involving algae, Cladophora sp., a green, filamentous alga, was collected from the Maple River. Cladophora is an important food for this species at least in Michigan (Creed, 1994). The Cladophora was rinsed to remove aquatic insects and other invertebrates and hand-dried. Each arena received 3g (+/-0.001g) of live, hand-dried algae. After each feeding trial, a 1mm wide wire mesh colander was used to separate the Cladophora and fecal matter. We weighed the remaining algae after oven drying at 60C for 24h. Fifty-two O. propinquus were tested over the course of three replicate trials, but only 45 crayfish were included in the analysis (19 FI; 11 FII; and 15 female). Seven crayfish were omitted from the analysis, because they molted or lost their rubberbands during the experimental period. Analysis of covariance (ANCOVA) was used to compare the amount of algae remaining for FIs, FIIIs, and females (the covariate was carapace length) because the amount consumed was positively related to carapace size. Since no difference in consumption was found between males and females, data on the sexes were combined before the analysis.

Gastropods are thought to be an important protein source for crayfish (Covich, 1977; Hanson, et al., 1990) and would present a very different mechanical challenge than the other foods tested. Four species of snails were collected from Douglas Lake and used in feeding experiments. Three individual Elimia livescens, two Planorbella smithi, two Stegnicola marginatus, and one Campeoloma decius were placed in each arena containing one crayfish. After each feeding trial, we counted the number of snails that were alive, dead, or damaged. We measured the minimum diameter of the shell aperture for all snails. A total of 49 crayfish were tested in three separate replicates. Only 44 were included in the analysis (19 FI, 5 FII, 20 Females) because there were five arenas for which all eight snails could not be accounted. The g-test (GT) was used to compare number of crayfish that consumed snails between the sexes and the chela treatments as well as all comparisons of the numbers of snails eaten and damaged during the experiment. Due to a lack of data for replicate 1, damage (defined here as visible destruction of some portion of the shell aperture) was analyzed for replicates 2 and 3. A Wilcoxon-Mann-Whitney test (WMW) was used to compare the size of the shell openings of the damaged and undamaged E. livescens (n = 33).

While gastropods are relatively slow moving and thus not hard to capture, aquatic insects present a range of mobility as potential prey items. Three orders of aquatic insects commonly occurring with O. propinquus were col-
lected from the Maple River. In one set of experiments, two stonefly nymphs (one Paragnetina media and one Acronyuria lycorias) and one Dobsonfly larva (Nigronia sp.) were placed in arenas containing one crayfish. Dobsonfly larvae are large (4–5 cm), slow crawling aquatic insects with strong mandibles. Stonefly nymphs are smaller (1–2 cm) but can move rapidly when startled (personal observation). Sixty-eight crayfish were fed Dobsonflies and stoneflies in five different replicate trials (totaling 27 control and 41 pincer disabled crayfish). Seven crayfish were omitted from the analysis, because these crayfish molted or lost their rubberbands during the feeding trials. A g-test (GT) was also used to compare the number of crayfish that consumed insects. Male and female data were combined for all of the analyses because the proportion of males and females that ate insects in the trials did not differ statistically (GT P = 0.486).

To determine if crayfish use their chelae to feed on the mayfly Baeiis sp., a common insect in the Maple River, 40 crayfish matched by sex and size (1mm cl) were tested in two, 24h replicate feeding trials (20 females and 20 males). Chelae function was removed by adhering the distal tips of the chelae using SuperGlue (Intac™). To control for possible glue effects, we also placed adhesive on the lateral edge of the dorsal side of the control crayfish chelae. The number of pairs of crayfish that consumed mayflies was analyzed using the sign test (ST). This test compares the number of cases where only the treated crayfish in the pair ate mayflies to number of cases where only the control ate mayflies. The Kruskal-Wallis (KW) test was used to compare how many of the original 5 mayflies were remaining in the control and glued crayfish tanks.

**Predator Avoidance**

Snapping turtles are known to feed on crayfish (Hazlett, et al., 1974; Hobbs, 1993) and have been found in the areas of the Maple River studied (pers. obs.). To test whether chela function affects susceptibility to this type of predator, two size-matched adult male (one control, one glued) and two adult female (one control, one glued) O. propinquus (size data in Table I) were placed in tanks with snapping turtles (Chelydra serpentina). Three snapping turtles with shell diameters of 5.5, 17.5, and 24.5 cm and gape widths of 1.5, 4, and 5.5 cm, were used in the experiment. Replicate trials were conducted in the laboratory in chambers (4 m long, 55 cm wide and 17 cm deep) containing a mixture of aquatic plants (including Elodea canadensis, Myriophyllum spp., Potamogeton spp., Najas spp., Ceratophyllum sp. - all collected from Douglas Lake), a sand substrate, and four, broken clay pots for crayfish shelters. Turtles received no animal food for 24h prior to each trial. Crayfish were acclimated for 5min before the beginning of each replicate. After 24h the number, size, and treatment of
crayfish remaining was recorded. These experiments were conducted in July and August of 1993 using a total of 68 crayfish (34 males and 34 females).

The fate of crayfish was analyzed using a sign test (ST). Data on males and females were pooled for a comparison of treatment effects as no difference in their susceptibility to turtles was detected (GT P = 0.332). Cases where either both or neither crayfish was eaten were scored as ties and could not be included in the statistic.

### TABLE I

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Cephalothorax</th>
<th>Chelae</th>
</tr>
</thead>
<tbody>
<tr>
<td>male unglued</td>
<td>23.1 (0.746)</td>
<td>19.1 (1.115)</td>
</tr>
<tr>
<td>male glued</td>
<td>23.1 (0.681)</td>
<td>18.6 (1.058)</td>
</tr>
<tr>
<td>female unglued</td>
<td>23.0 (0.634)</td>
<td>13.2 (0.576)</td>
</tr>
<tr>
<td>female glued</td>
<td>23.1 (0.654)</td>
<td>13.7 (0.558)</td>
</tr>
</tbody>
</table>

**Survivorship in the Field**

A 1000m² area directly downstream from a culvert on the East Branch of the Maple River (Pellston Quadrangle, T36, R4W, S2, N.E. Quadrant) was utilized from 27 June to 14 August 1993 as the site for the mark and recapture study. During this study, 338 crayfish were captured and marked using a pleural clip code (Hazlett, *et al.*, 1974). Carapace and chela length was measured to the nearest 0.1mm using dial calipers. There were 157 MIs (25.2 ± 0.22), 57 FIs (22.2 ± 0.39) and 124 females (24.0 ± 0.21, X±s.e.). Each crayfish was dried with a cloth, weighed to the nearest 0.01 gram (wet weight), and placed in aerated tanks until their release after the following day's collecting period. Size- and sex-matched crayfish (within approximately 1 mm carapace length) were randomly assigned one of two treatments: chelae glued closed (treated) or glue placed on the manus but the chelae were fully functional (control). Sampling usually occurred every other day, but on occasion sampling was done on successive days.

We compared survivorship among control and experimental crayfish in the field by determining the number of crayfish that were recaptured once, twice, three or more times. If survival is related to mechanical chela function, then crayfish with functional chelae should survive longer than those without the use of their chelae and should have a greater chance of being recaptured. The probability of recapture was determined based on the number of sampling days an individual could have been recaptured, not on the absolute number of days a crayfish was in the field. We tested whether the number of crayfish captured differed between the sexes or treatments using a g-test (GT).
Mating

In September of 1993, crayfish were collected from the Maple River and brought to the laboratory in Ann Arbor, Michigan. They were kept in wading pools, and were acclimated to a 12 hour photoperiod. Each individual was marked using a unique pleural clip code and measured (carapace length, chela length, chela width; and wet weight). The crayfish were kept in same-sex groups when not being tested. Twelve pairs of size-matched, male crayfish were randomly assigned one of the two treatments. Glue was used both on the control and on the treated crayfish as described elsewhere. For each trial, we took a pair of male crayfish (one control and one experimental) and placed them in an aerated tank (30 cm × 35 cm) containing a female, two broken clay pots for shelters and fresh 8L of water. Females were acclimated to the experimental tanks for more than an hour before we introduced the two males. Between 1800 and 2400 hours, we checked the tanks every half hour and recorded which males were copulating with which females. Three additional observations were made starting at 1030 the next day. Each pair of males was tested twice, but we switched the treatments and the individual female present in the second trial. Female crayfish were used more than once as well, but they always had several days rest before each bout.

McNemar test (MT) was used to compare the reproductive success of the treated and control male crayfish (Conover, 1980). The McNemar test was appropriate for comparing reproductive success of males, since all males were observed with and without the treatment. The alpha for this test was adjusted to 0.0624 as this is the exact probability closest to the original alpha of 0.05 (given that there were seven observations of matings used in the McNemar test).

Statistical Analyses

Deviations from normality were tested using Lilliefors’s test, skewness, kurtosis, quantile plots, and probability plots. Homogeneity of variances was tested using Bartlett’s Test and Box’s modification of Bartlett’s Test (for small sample sizes). Non-parametric tests were performed when there existed significant departures from the above mentioned assumptions or where no appropriate parametric model was available. The SYSTAT statistical package (Wilkinson, et al., 1992) was used for all of the analyses unless referenced otherwise.
RESULTS

Feeding

Crayfish consumed similar amounts of Cladophora regardless of whether they had functional chelae or not. The dry mass of the algae remaining in tanks with crayfish did not differ between the treatments (control or chelae disabled) or between the sexes (ANCOVA, $P = 0.289$, $P = 0.174$ respectively).

Among the gastropods offered, crayfish ate only Elimia livescens and Stegnicola emarginatus in the experimental trials (Table II). Snail susceptibility apparently was not determined by the size of the snail’s shell opening, since only two Campeloma decium, the species with the largest minimum aperture diameter, were eaten during the experiment (Table II). Similar proportions of crayfish consumed snails, regardless of their chelae treatment (GT $P = 0.850$) or sex (GT $P = 0.540$). In addition, the number of snails eaten by crayfish was independent of the sex (GT $P = 0.820$) or treatment (GT $P = 0.524$) of the crayfish tested. Crayfish, regardless of their sex or treatment, damaged many of the E. livescens (GT $P = 0.720$, $P = 0.234$ respectively). Damaged E. livescens were more likely to be eaten by both control and chelae disabled crayfish (GT $P = 0.007$). E. livescens that were eaten were smaller in minimum shell opening diameter than uneaten individuals (Table II, WMW $P = 0.012$).

| Table II | The mean size of snails that were eaten or not eaten by crayfish. Snail shell aperture size was measured as the distance across the narrowest diameter of the shell |

<table>
<thead>
<tr>
<th>Snail Species</th>
<th>Eaten</th>
<th>Not Eaten</th>
<th>Dead</th>
</tr>
</thead>
<tbody>
<tr>
<td>Campeloma decium</td>
<td>22.9 ± 1.5 [2]</td>
<td>11.9 ± 1.1 [41]</td>
<td>7.0 [1]</td>
</tr>
<tr>
<td>Elimia livescens</td>
<td>3.1 ± 0.1 [22]</td>
<td>6.9 ± 0.5 [111]</td>
<td></td>
</tr>
<tr>
<td>Planorbelia smithi</td>
<td>8.7 [1]</td>
<td>8.0 ± 0.4 [85]</td>
<td>5.9 ± 0.1 [2]</td>
</tr>
<tr>
<td>Stegnicola emarginatus</td>
<td>11.6 ± 1.2 [31]</td>
<td>10.7 ± 0.08 [56]</td>
<td>6.5 [1]</td>
</tr>
</tbody>
</table>

Unlike the feeding trials with snails and algae, crayfish without the use of their chelae showed reduced feeding on insects (Figure 1; GT $P < 0.001$). Although the treatment significantly decreased the number of crayfish that ate insects, it did not eliminate predation altogether; five crayfish preyed upon stoneflies and Dobsonfly larvae even without the use of their chelae (Figure 1). The same result was found when the stoneflies and Dobsonfly larvae were analyzed separately: fewer treated crayfish consumed Dobsonflies and stoneflies (GT $P < 0.001$, $P < 0.001$ respectively).
Crayfish did not use their chelae in capturing all aquatic insects. The number of *O. propinquus* that ate mayflies was similar regardless of whether they had functioning or disabled chelae (ST P = 0.210). In contrast to the Dobsonfly and stonefly larvac trials, the number of mayflies remaining was similar between the control and treated crayfish (KW P = 0.180). On average 2.7 ± 0.34 (mean ± s.e.) of the mayflies remained in the control tanks while 3.3 ± 0.24 remained in the tanks with treated crayfish.

![Graph showing percent of control and treated crayfish that consumed insects.](image)

**FIGURE 1** The 'percent' of control and treated crayfish that ate stonefly nymphs and antlion larvae. Control crayfish, those with the use of their pinchers, are represented by the open bars. The cross-hatched bars represent the crayfish whose pinchers were disabled using rubberbands (GT P < 0.001).

**Predator Avoidance**

Snapping turtles consumed half of the 68 crayfish they encountered in the experimental chambers. We found that turtles ate both or neither of the crayfish in 56% of the 34 pairs, and they consumed only the treated crayfish in 24% of the pairs tested (Figure 2; ST P = 0.788). Thus for the sizes of predators and prey tested, there was no effect of chelae mechanical function on susceptibility to predation.
Survivorship

The data from the mark and recapture study indicated no differences in survivorship in the field among the different crayfish groups (males and females nor control and glued) (Table III). There were also no detectable differences between males and females (GT P = 0.945) nor between the control and treatment groups (GT P = 0.137) in the number of crayfish recaptured various number of times (zero, one, two, three, and more than four times).

FIGURE 2  The percent of crayfish in laboratory tanks eaten by snapping turtles (Chelydra serpentina) over a 24hr period. The treated crayfish had their pincers glued closed while control animals had their pincers glued but still functional. Turtles were placed in tanks with two males and two females (one treated and one control) and four shelters (ST P = 0.788).

TABLE III  The number of crayfish recaptured in a study of crayfish populations in the Maple River, Michigan. Neither male and female nor control and glued crayfish differed in their frequency of recapture (GT P = 0.137 and P = 0.945)
TABLE III (Continued)

<table>
<thead>
<tr>
<th># of Times Recaptured</th>
<th>Control</th>
<th>Glued</th>
<th>Control</th>
<th>Glued</th>
<th>Control</th>
<th>Glued</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>1</td>
<td>7</td>
<td>0</td>
<td>2</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>≥4</td>
<td>6</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Total*</td>
<td>75</td>
<td>75</td>
<td>21</td>
<td>29</td>
<td>57</td>
<td>57</td>
</tr>
</tbody>
</table>

* Twenty-four crayfish could not be reliably identified upon recapture and were omitted from the analysis.

Mating

Males used their chelae in copulation. We observed matings in approximately one-third of the 24 replicates. All seven copulation events that occurred during this experiment involved males that had mechanical use of their chelae (MT P = 0.008). We closely followed each trial till 2400 hours; we made no late-night observations. No acts that could be construed as male-male aggression (Rubenstein & Hazlett, 1974) were observed during the scan sampling periods. In addition, copulation was always initiated by the male crayfish. All approaches by males with glued pincers resulted in retreats by the females and never resulted in successful pairing.

DISCUSSION

Crayfish chelae can have both display and mechanical functions. Because evolutionary change in one type of function (i.e., display) could lead to reduced effectiveness of another (i.e., mechanical function) (Levinton, et al., 1995), attention to the specific functions of chelae will be pivotal if inference is to be made about the evolutionary maintenance of crayfish chelae morphology. This paper investigates the mechanical use of chelae in several areas of the life-history of the crayfish *O. propinquus*. While the display functions of chelae were not experimentally altered in these analyses, it is possible to conclude that the mechanical function of chelae plays a role in only two aspects of crayfish life-history: a minor one in feeding and a more important one in mate acquisition.

Mechanical Use of Chelae in Feeding

The diet of crayfish includes detritus, insects, mollusks, and algae (Mason, 1974; Hobbs, 1993). *O. rusticus* can feed on macrophytes, but it does not significantly reduce the biomass of the invertebrates in a lake littoral community.
(Lodge, et al., 1994). While Hanson, et al. (1990) did find a significant impact of O. virilis on molluscan species, Hazlett (1994) observed that O. virilis consumed zebra mussels (Dreissena polymorpha) without using their pincers. Most food items can be handled efficiently using the second and third pairs of chelate walking-legs and may not require the use of the chelae at all.

In this study, O. propinquus used its chelae only occasionally if at all in feeding. Unlike many marine crustaceans where chelae are used to crush prey such as mollusks (Lee and Seed, 1992), O. propinquus consumed snails without utilizing functional chelae. Damage to shells was recorded for the snail Elimia livescens, but appeared to be caused by the action of the hardened areas of the mandibles not the chelae. Chelae did serve a function when crayfish fed on large aquatic insects. Observations of O. propinquus in the feeding arenas would suggest that these crayfish occasionally trap insects using their chelae and once trapped, manipulated the insects using their second pair of walking legs. Functional chelae are not required for successful predation of all aquatic insect taxa; crayfish consumed the small-sized mayflies equally well irrespective of the condition of their chelae.

Chelae must play a role in other aspects of crayfish life-history other than foraging. Because of the paucity of evidence to indicate that crayfish use their chelae to capture food items (in laboratory experiments) and because it is not possible for chelae to serve a display function in feeding, the evolutionary maintenance of chelae cannot be explained by feeding requirements alone. Chelae are not needed to meet the nutritional and energetic requirements of these crayfish. Furthermore, the sexual dimorphism in chela size appears not to act as a mechanism to allow differential resource use or niche partitioning (Shine, 1984; Dayan, et al., 1989).

Chelae Function and Predator Avoidance

Crayfish use rapid abdominal contractions for the swimming escape-response and chela threat displays to avoid fish predators (Stein and Magnuson, 1976). Freshwater fishes such as smallmouth bass (Micropterus dolomieu), rockbass (Ambloplites rupestris), and yellow perch (Perca flavescens) consume large numbers of crayfish (Stein, 1977). Crayfish have been shown to constitute 60–100% of the dry mass of bass stomach contents (Stein, 1975 cited in Stein, 1977). Stein (1976) found that males with smaller chelae experienced higher mortality from smallmouth bass in the laboratory. Smaller chelae, while not as formidable for deterring predators, are lighter and have reduced drag and thus may increase the speed of the swimming escape-response. In contrast to Stein’s findings with a fish predator, elimination of chela function did not reduce
O. propinquus' susceptibility to (snapping turtle) predators. Snapping turtles are sit and wait predators, so the backward escape-response by crayfish would seemingly be an effective method to avoid predation by this type of predator. Snapping turtles, with their powerful, bony jaws, would have little difficulty crushing even large-pinchered crayfish. Turtles, unlike fish predators, do not seem to be inhibited by chelae threat displays (personal observations). Crayfish do not require the mechanical use of their chelae to deter all types of predators, since not all types of predators are affected by similar avoidance behaviors. Furthermore, it may be hypothesized that crayfish can adjust their behavioral response to the type of predator present and so effectively avoid enemies regardless of their predatory tactics. In the case of turtles, crayfish may seek shelter or use their swimming escape-response to avoid these predators.

Survival and the Mechanical Use of Chelae

Survival in a natural stream requires that crayfish avoid predators, obtain shelters, and find and capture prey. Because survival integrates all of these factors, the removal of the mechanical function of chela, should manifest itself in obvious changes in the mortality schedule of crayfish if crayfish require functioning chelae in nature for any of these functions.

The experimental manipulations performed here had no measurable effect on the recapture rates of crayfish. Although recapture frequencies are not a direct measure of crayfish survival, they should reflect differences in survival if mortality from any source has been altered by the experimental treatment. The population studied here was rather large and relatively stable. Several crayfish were captured multiples times (greater than four times), and frequencies of capture were too similar among treatment groups to suggest that the removal of the mechanical function of chelae has an effect on crayfish survival. This mark/recapture technique may have failed to find a reduction in survivorship among crayfish because the treatment effect was not acute enough to affect mortality rates over the time-period studied. In addition to failing to alter survivorship, the removal of chelae mechanical function had no measurable effect on crayfish growth rates and the molt frequencies in this system (Keller, unpublished). Thus, chelae appear not to play an important role in the summer survival of the crayfish O. propinquus in northern Michigan.

Mate Acquisition and Chelae Function

There are reproductive advantages to having mechanically functional chelae. Male crayfish use their chelae to maneuver and hold females during copulation
(Ameyaw-Akumfi, 1976; Andrews, 1904; Mason, 1970). *O. propinquus* males succeeded in copulating with females only when they had use of their chelae. *O. propinquus* use their chelae to position themselves dorsally over the female (Ameyaw-Akumfi, 1976) after which other appendages may then play a significant role. Males will also use their chelae to fend off intruding males (Berill and Arsenault, 1982) and chelae appear important in dominance hierarchies (Bovbjerg, 1956). While there is evidence to suggest the importance of chelae in male-male agonistic interactions (Snedden, 1990; Stein, 1976), none of the males in this mating experiment were seen attacking other males; crayfish were kept at low densities in the mating arenas. Males without functioning pincers were observed approaching females, but these males never successfully copulated with the females. While chelae displays may play a role in reproduction especially in species such as *O. virilis* (Ameyaw-Akumfi, 1976), mechanically functioning pincers appear to greatly enhance copulatory success. Mechanically functional pincers enable males to initiate the process of copulation that can ultimately lead to the transfer of sperm.

Stein’s (1976) hypothesis that chelae serve a function primarily in reproduction appears to be supported by the results presented here for *O. propinquus*. This evolutionary explanation assumes that male *O. propinquus* reduce the relative size of their chelae during the summer because larger chelae have added costs (energetic and otherwise) at a time when their benefits are not significant enough to outweigh the costs. While this hypothesis was not tested here, the results are consistent with this idea. Chelae did serve a mechanical function in reproduction and as other studies have shown larger chelae are better than smaller for obtaining mates (Snedden, 1990). While chelae do function in predator avoidance for some types of predators, it is yet unknown whether the cost of growing larger chelae are matched by significant survival advantages in nature. Further data on the costs of large chelae to crayfish are needed for a more complete examination of this hypothesis.

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