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Fight Strategies Differ with Size and Allometric Growth of Claws in Crayfish, Orconectes Rusticus

Lisa Schroeder, *Bowling Green State University - Main Campus*
Robert Huber, *Bowling Green State University*

FIGHT STRATEGIES DIFFER WITH SIZE AND ALLOMETRIC GROWTH OF CLAWS IN CRAYFISH, ORCONECTES RUSTICUS

by

LISA SCHROEDER and ROBERT HUBER[1,2)]

(J.P. Scott Center for Neuroscience, Mind & Behavior and Department of Biological Sciences, Bowling Green State University, Life Sciences Building, Bowling Green, OH 43403-0212, USA)

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Summary

This study examines differences in fighting strategies between small and large male crayfish, *Orconectes rusticus*. Due to allometric growth of claws, fighting weapons are of disproportionate size in large crayfish compared to those in smaller individuals. Presumably, such differences in the prominence of claws are reflected in differences in the likelihood of injuries, and we thus explored fighting in size-matched pairs of small or large crayfish and assessed associated strategies in situations of conflict. Although fighting reached the highest intensities in a similar proportion of instances in small and large pairs, differences in fighting strategies were evident. Small crayfish escalated more rapidly, fights were settled more quickly, and were resolved overall at lower intensities. This may be explained by lower risks of injury compared to encounters among larger males due to proportionally smaller claws. Larger males thus appear to spend considerably more time in assessing their opponent's fighting ability before each escalation event.

Introduction

In situations of conflict, combatants in many animal taxa are thought to assess an opponent's relative fighting ability, compare it with their own (Parker, 1974; Hack, 1997; Whitehouse, 1997), and thereby identify the existence and

1) Corresponding author; e-mail address: lobsterman@caspar.bgsu.edu

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extent of asymmetries in the potential for eventual victory (Enquist *et al.*, 1990; Leimar *et al.*, 1991; Neat *et al.*, 1998). Based on such information, decisions are made on whether to initiate, escalate, retaliate, or retreat (Maynard Smith, 1982). In most instances agonistic encounters are settled based on initial displays with little or no further escalation (Parker, 1974). Asymmetries in size influence the outcome of fights in many animals, including squid (Dimarco & Hanlon, 1997), ants (Nowbahari *et al.*, 1999), prawns (Evans & Shehadi-Moacdieh, 1988), crayfish (Pavey & Fielder, 1996), hermit crabs (Hazlett, 1968), spiders (Riechert, 1978), fish (Beaugrand *et al.*, 1991), lizards (Stamps & Krishnan, 1994a, b; Zucker & Murray, 1996), and snakes (Schuett, 1997). Experience (Beacham, 1988; Schuett, 1997; Hsu & Wolf, 1999), prior residency (Grossman, 1980; Bronstein, 1984; Peeke *et al.*, 1995; Hack *et al.*, 1997; Chellappa *et al.*, 1999; Bridge *et al.*, 2000), and asymmetries in weapons (Jennions & Backwell, 1996; Edsman & Jonsson, 1996; Sneddon *et al.*, 2000) also aid in determining the outcome of a fight in many taxa. Encounters between animals closely matched in these factors are more likely to lead to escalation (Evans & Shehadi-Moacdieh, 1988; McDonough, 1994). As escalated encounters are accompanied by an increased chance of injury, animals should fight with strategies that limit the associated risks (Maynard Smith, 1982), particularly when destructive weapons are involved.

Thus, possession of weapons may play a large role in the fighting strategies of crayfish, especially when these weapons differ in size between individuals. Many species exhibit sexual dimorphism in weapon size, with males generally possessing weapons that are proportionally larger than those in females (Lee, 1995). Specific examples include crabs (Sneddon *et al.*, 1997), thrips (Crespi, 1986), lobsters (Cadrin, 1995), crayfish (Snedden, 1990), and different morphotypes of male prawns (Barki *et al.*, 1992, 1997).

Dimorphism is not limited to differences between males and females, but also exists between sexually immature and adult males. Claws of juvenile animals are usually proportionally smaller compared to those in adults and thus presumably pose a lesser risk of injury. Due to such differences in danger, fighting behavior among juveniles may show different characteristics compared to those in adult crayfish with regard to escalation, intensity, or duration of encounters. In male fallow deer, immature males included antler contact in the majority of agonistic interactions, while mature males used

antlers in less than half of the time (McElligott *et al.*, 1998). In thrips, which possess forceps-like appendages, fighting between small males escalated more rapidly than that between pairs of large males (Crespi, 1986). Sexually immature male prawns possess proportionally smaller forceps than larger mature males. During agonistic contests, the frequency of acts with physical contact was higher when immature, small clawed males fought each other, but shifted towards more ritualized acts when larger clawed individuals fought (Barki *et al.*, 1991).

In decapods, sexual dimorphism is minor in juveniles but becomes increasingly pronounced as sexual maturity is reached (Lee, 1995). Thus, small (sexually immature) male and female decapods possess chelae of similar size. During subsequent development, growth rates of chelae greatly outpace that of the rest of the body in males and to a lesser degree in females (Hartnoll, 1982). Therefore, the chelae of adult males become increasingly prominent compared to those of much smaller males (Fig. 1). Little is known

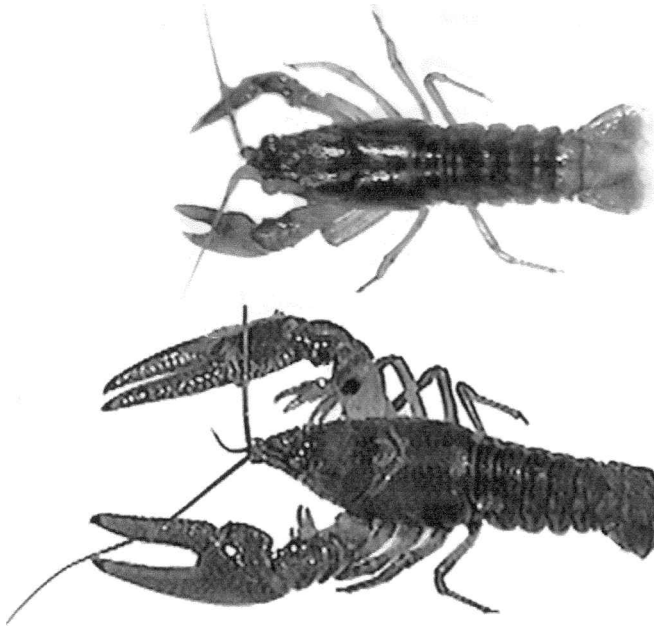

Fig. 1. Allometric growth of claws in *Orconectes rusticus*. Visual comparison illustrates the disproportionate increase in claw size between small and large crayfish which have been scaled to the same carapace length.

whether this difference in relative chelae size is also reflected in different fighting strategies of small and large individuals.

Crayfish are ideal subjects for this study because of the presence of potentially lethal fighting weapons and stereotypical agonistic behaviors (Huber *et al.*, 2001). Crayfish and lobster fighting consists of stereotypical threat displays, such as a meral spread, in which the animal raises its body high on its walking legs and extends its claws upward for a visual display with maximized size (Bruski & Dunham, 1987; Huber & Kravitz, 1995; Huber *et al.*, 2001). If neither opponent backs down, escalation of fighting advances through various intensity levels, and may even include instances of unrestrained use of the chelae. During these highly structured escalated encounters, crayfish may be continually assessing the fighting ability of the opponent so as to reduce the risks of injury (Huber & Kravitz, 1995).

The goal of this study is to examine the fighting strategies of small and large symmetrically paired male crayfish, *Orconectes rusticus*, to determine whether a difference exists in the duration, intensity, and the rate of escalation of fights due to differences in relative chelae size. As large crayfish presumably carry more dangerous weapons, we hypothesize that the latter will fight more conservatively and escalate their encounters more slowly.

Materials and methods

Experimental set-up

Male crayfish were obtained from the Portage River near Bowling Green, Ohio, and all experiments were performed between July and November of 1999. Experimental animals with all appendages intact were isolated for a minimum of 5 days in plastic containers (large animals in flowerpots with diameter = 12.6 cm, height = 9.5 cm and small crayfish in plastic fish tackle boxes 5.5 × 4.5 × 4.0 cm). Pairs of crayfish within groups were matched to within 10% body weight, with a mean weight of 17.9 ± 2.5 grams in the large group and 1.8 ± 0.35 grams in the small group. Descriptive statistics for body weight, chelae size (entire appendage), and claw lengths are listed in Table 1. Water temperature was kept constant at 21°C and a light/dark cycle of 16:8 h was used. Small crayfish were fed half a rabbit pellet and large crayfish a whole rabbit pellet once a week.

A total of 30 trials were conducted and analyzed: 15 trials from the small group and 15 from the large group. Aquaria were constructed of opaque plexiglass for the sides with a clear plexiglass face. Water was continuously pumped through the tanks via symmetrically arranged pairs of inlet and outlet holes in the back. Two separate fighting arenas were built in scale to the size of the test animals (56.5 × 26.3 × 18.5 cm for large and 17.9 × 8.3 × 10.0 cm for small crayfish). Animals were marked individually on the carapace with white typing correction fluid. A plexiglass divider was placed midway in the tank to separate the opponents

TABLE 1. *Summary statistics of the number of crayfish used, their mean weights, relative weight difference, mean carapace length, mean claw size, and mean chelae length for the two size groups*

	N	Weight [g]	Weight diff. [%]	Length [cm]	Chelae size [cm]	Claw size [cm]
Small	30	1.8 ± 0.35	2.3	7.3 ± 0.51	6.5 ± 0.45	3.7 ± 0.29
Large	30	17.9 ± 2.5	2.8	3.6 ± 0.33	2.2 ± 0.43	1.2 ± 0.28

visually for a 10-15 minute acclimation period. Following acclimation, the divider was removed and individuals were allowed to interact for 30 minutes. All interactions were recorded using a Canon XL1 digital camcorder.

Analysis of agonistic behavior

The video recordings were used for a quantitative analysis of behavior according to criteria indicated below with additional detail described elsewhere (Huber *et al.*, 2001). In summary, a variety of behavioral measures were obtained for each dyadic encounter, including their duration and maximum intensities as well as their total number. An encounter began when two individuals approached within one body length of each other and responded in some way (a tail flip, threat display, *etc.*) to the presence of the opponent. A retreat, when an animal tail-flips or walks away, marked the end of an encounter.

The duration of each encounter in seconds was recorded. Fight intensity was characterized on an ordinal scale where one animal retreated from an approaching animal or both animals ignored each another (intensity 0); presented their claws towards an opponent in threat displays without touching each other (intensity 1); physical contact involving claws, wrestling, and restrained fighting (intensity 2); and unrestrained fighting where a crayfish attempted to rip or tear off appendages from the opponent (intensity 3). The rate of escalation of an agonistic encounter was obtained as the slope of a best-fit line derived from a regression analysis with fight intensity (y) as a function of fight duration (x).

Statistical analysis

Fight duration was compared between the two size groups (small vs. large) using a nested Analysis of Variance (ANOVA). Moreover, the proportion of time spent at each intensity level (ordinal values) as a function of size was analyzed using negative log-likelihood-ratio tests. From these, G-statistics were obtained and compared to a χ^2 distribution. A complete model regression analysis was performed to determine the rate of escalation within and between groups, and an ANOVA was performed on the regression lines to test for 'goodness of fit' of these lines. Significance criterion was set at $p < 0.05$.

Results

An initial view suggested that aggressive state was higher in larger animals compared to smaller individuals (see descriptive statistics in Table 2). Spe-

TABLE 2. *Behavioral analysis of fighting in different size groups*

	N	Mean duration	Intensity: 0	1	2	3
Small	151	16.7	114	17	15	5
Large	133	30.6	75	18	34	6

The table lists total number of encounters (N), mean duration per interaction and the number of occurrences at each intensity level.

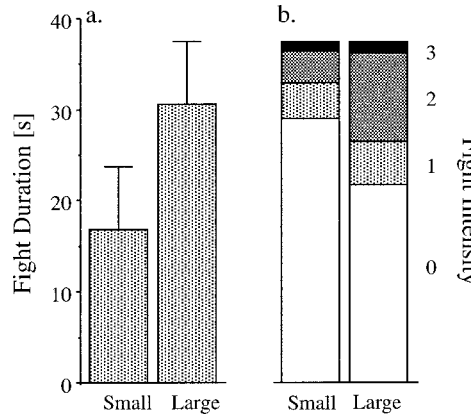

Fig. 2. Behavioral characteristics of agonistic encounters in small and large crayfish. (a) Bar graph of mean fight duration ± standard error for dyadic encounters in small and large pairs illustrates that fighting lasts longer in large pairs. (b) The proportion of interactions reaching different maximum levels of intensity is graphed as a function of size. A greater number of encounters are resolved at low intensities in small individuals compared to those in larger dyads ($\chi^2_{3,278} = 14.648$, $p < 0.05$).

cifically, encounters between large crayfish lasted longer (ANOVA $F_{1,282} = 7.01$; $p < 0.01$; Fig. 2a) and included more instances of fighting at high intensities ($\chi^2_{3,278} = 14.6$, $p < 0.01$; Fig. 2b). A somewhat different picture emerged, however, when our analysis included the timing of different decisions and individual fighting strategies. Although small crayfish fight less long and less intense, they escalate much more rapidly (Regression analysis: $y = 0.2 + 0.0149x$; $F_{1,149} = 87.4$, $p < 0.01$; Fig. 3a) than large pairs (Regression analysis: $y = 0.5 + 0.0095x$; $F_{1,131} = 49.5$, $p < 0.01$; Fig. 3b). ANOVA demonstrated that the slopes differed significantly between size groups (Table 3).

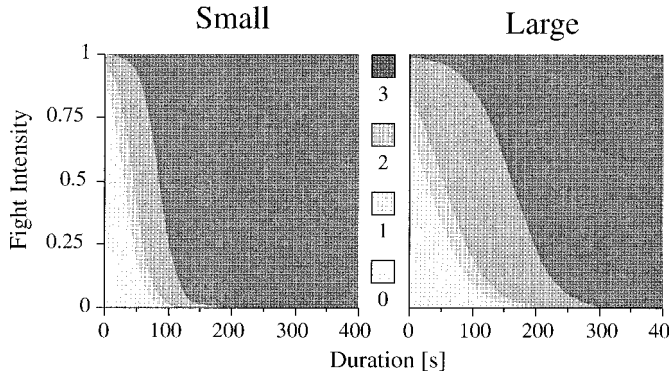

Fig. 3. Small individuals escalate more rapidly. Cumulative logistic probability curves depict the likelihood that a fight will feature a particular maximum intensity for any given duration in small (a) and large pairs (b).

TABLE 3. *ANOVA table lists levels of significance for different treatment effects*

Source	df	SS	MS	*F* ratio	*p*
Model	5	84.16	16.83	31.45	<0.01
Size	1	7.3	7.3	13.63	<0.01
Pairs (Size)	2	3.99	1.98	3.72	0.03
Duration	1	67.1	67.1	125.36	<0.01
Dur * Pairs	1	3.05	3.05	5.7	0.02
Error	278	148.81	0.54		
Test	283	232.97			

Discussion

This work has illustrated that small crayfish escalated fights more rapidly, while fighting among larger-sized and larger-clawed crayfish proceeded in more measured fashion. Larger individuals thus took considerably more time to fight at any given intensity level before escalating to the next higher one. This pattern is compatible with an increased likelihood of incurring injury in relatively large-clawed individuals, necessitating increased assessment of opponent strength. In crabs, greater claw heights and lengths allowed the animals to exert a greater force when engaged in fights (Levington & Judge, 1993; Sneddon *et al.*, 2000). Disproportionately small chelae of small crayfish may thus carry a reduced potential for causing physical

damage (Elner & Campbell, 1981; Gabbanini *et al.*, 1995). With reduced chances for injury, small crayfish are thus more likely to proceed rapidly into higher intensities resulting in fights that are resolved more rapidly overall. Conversely, fights among larger crayfish escalate more slowly as contestants may gather more information about their opponent's fighting strength (Parker, 1974). These results are consistent with evidence from other systems. Thrips (*Elaphrothrips tuberculatus*) feature weapons used in agonistic interactions that are poorly developed in small individuals. When paired symmetrically, smaller male thrips escalated fights more rapidly than did larger males (Crespi, 1986).

In addition to the hazards of injury, highly escalated agonistic encounters carry the danger of losing a claw which represents an essential tool in defense (Stein, 1976), agonistic encounters (Bovbjerg, 1956; Berrill & Arsenault, 1984; Bruski & Dunham, 1987), and reproduction (Stein, 1976; Snedden, 1990). Although crayfish of all sizes are able to regenerate appendages, claws represent a considerably greater investment for large individuals due to their larger relative size. Moreover, with reduced frequency of molting it takes considerably longer to regain functional use of claws in large individuals (Juanes & Smith, 1995), which only molt about once or twice a year (Skinner, 1985). Differences in fighting strategies between small and large individuals may thus be a reflection of the disproportionately greater consequence of claw loss in large crayfish.

Additionally, more rapid rates of escalation by small crayfish may be of adaptive value in animals more susceptible to predation. Smaller body and chelae sizes make individuals more vulnerable to predation (Garvey *et al.*, 1994; Jordan *et al.*, 1996), while larger crayfish are at a lesser risk (Stein, 1976; Garvey & Stein, 1993). Fighting increases risks of predation by decreasing vigilance (Jakobsson *et al.*, 1995; Brick, 1997) and rapid escalation among small crayfish may thus serve to minimize time spent fighting.

Although small crayfish escalated fights more rapidly, fighting reached the highest intensities in both groups in a similar number of instances. This may be due to the fact that large crayfish may have more to gain and to defend than smaller crayfish. In prawns, dominant individuals gain preferential access to food and mates in the vicinity (Barki *et al.*, 1992). Crayfish with smaller chelae compared to body size may not yet have reached sexual maturity, or may not be able to properly secure females during mating (Stein, 1976;

Snedden, 1990). Therefore, access to mates among smaller crayfish may play a less important role than among larger individuals.

Moreover, size is inextricably entwined with age; an individual may modify its behavior as a result of experience (Dunham, 1983). Although stereotyped fighting among lobsters and crayfish occurs without any prior experience (Huber & Kravitz, 1995), fighting strategies may be ontogenetically modified. Crayfish may consequently be able to adopt different strategies as they learn to manage the complex tradeoffs between obtaining and defending resources, avoiding injury, and reducing the dangers due to predation.

It is likely that some behavioral plasticity results from an exchange of information during behavioral assessment of each other's fighting abilities. The question remains in what way and via what sensory channels such assessment is achieved. Visual cues are likely to play a role (Bruski & Dunham, 1987), as is chemical signalling (Zulandt-Schneider *et al.*, 1999, 2001).

This study successfully characterized differences in fighting strategies and individual decisions that parallel allometric growth of claws in crayfish. Such results illustrate the way in which an analysis of aggressive state may support conflicting interpretations depending on which particular variables are included. Although large crayfish fought longer than did small crayfish, they took considerably more time between successive escalation events — the rate of increase in fight intensities was thus slower. Crayfish fighting proceeds in a step-wise manner where longer fights will automatically lead to higher intensities (Bruski & Dunham, 1987; Huber & Kravitz, 1995; Huber *et al.*, 2001). This work serves as a reminder that aggression is a multidimensional concept and great care must thus be taken to base conclusions about aggressive state on a comprehensive view of the behavior in question instead of relying on any single measure alone.

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