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Symmetric Fights as a Measure of Escalation Potential in a Symbiotic, Territorial Snapping Shrimp

Nancy Knowlton and Brian D. Keller
Department of Biology, Yale University, P.O. Box 6666, New Haven, Connecticut 06511, USA

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Summary. The shrimp *Alpheus armatus* territorially defends the sea anemone it occupies, using as a weapon its large, specially modified 'snapping' claw. This behavior was studied in experimental contests which were symmetric (matched individuals) with respect to sex, size, and residency. Characteristics of these contests were compared for two size-classes of male and female shrimp.

There were no significant differences between these groups of shrimp in the number of bouts required to establish dominance or in the number of snaps exchanged. Large females had shorter contests than either small or large males, and losers of contests between large females were injured more frequently and more severely.

This distinctiveness of large female contests could be interpreted as evidence that (i) controlling anemones is more important for large females, (ii) injuries are less important for large females, or (iii) large females lose the ability to assess one another because their contests are less frequent.

If injuries are an accurate measure of the most important costs associated with fighting, then these results indicate that short contests are not necessarily the least costly, and that females can be more aggressive than males, as measured by escalation potential, in sexually selected species.

Introduction

Why are some groups of organisms more aggressive than others? Models predict that animals should be more likely to 'escalate' fights when the value of contested resources is high relative to the risks associated with fighting (Maynard Smith and Price 1973; and many others). Thus when comparing populations or species which differ little in the development of weaponry, differences in resource value have been stressed (Hyatt and Salmon 1978; Caldwell and Dingle 1975; Riechert 1979). In comparing groups which differ widely in weapon development (either different species or males and females in strongly sexually dimorphic species), on the other hand, reduction of escalation in groups with larger weapons is typically attributed to the risk of injury associated with their use (e.g. Maynard Smith and Price 1973).

The best way to assess the potential for escalation is to observe contests symmetric with respect to size, sex, and resource ownership (e.g. size- and sex-matched contestants which have comparable histories with respect to the resource in question). Although symmetric fights would not frequently occur in natural populations, they provide the most sensitive index of escalation by eliminating the cues of asymmetry which otherwise might be used to settle fights without employment of weapons (Parker 1974; Parker and Rubenstein 1981).

The snapping shrimp *Alpheus armatus* (Decapoda; Caridea; Alpheidae), an obligate symbiont of the Caribbean sea anemone *Bartholomea annulata*, is an excellent subject for studies of symmetric contests. The shrimp territorially defend individuals or clusters of this anemone against conspecifics of the same sex (adults) or both sexes (juveniles) (Knowlton 1980), using asymmetrically developed claws on the first pair of legs. When the larger claw is rapidly closed, a jet of water and a clearly audible 'snap' are produced (Ritzmann 1974). This specialized claw is not used to capture or manipulate food. Males and females have morphologically similar snapping claws, but with sexual maturity males develop larger snapping claws than females (Knowlton 1980).

Materials and Methods

Shrimp showing no signs of recent molting or serious injury (e.g. missing appendage) were collected from backreef areas in Discov-

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Table 1. Median snapping claw length and relative claw size as a function of total length for male and female *A. armatus* used in experimental contests. *CL* claw length; *TL* total length

Total length (mm)	Male			Female		
	Median claw length (mm)	Median CL/TL	*n*	Median claw length (mm)	Median CL/TL	*n*
10–14.5	4.5	0.43	11	6.0	0.45	6
15–19.5	9.0	0.50	15	9.0	0.49	9
20–24.5	11.0	0.52	13	12.0	0.50	15
25–29.5	14.0	0.55	8	14.0	0.52	9
30–34.5	19.0	0.59	9	16.5	0.54	8
35–39.5	23.75	0.63	32	19.0	0.49	19
40–44.5	26.0	0.63	8	20.5	0.49	29
45–49.5				21.0	0.46	4

ery Bay, Jamaica (SAI and vicinity; Knowlton 1980) during May–August 1980 and March–July 1981. Shrimp were designated as size-matched if the sum of the differences in rostrum-telson (total) length and major chela propus (claw) length did not exceed 2 mm (see Table 1 for summary of shrimp sizes used). Matched individuals were placed immediately after collection in aquaria on opposite sides of a central, removable partition. The opaque partition was fitted to prevent visual and tactile communication, and the quiescent behavior of the shrimp indicated that it was an effective barrier. With each shrimp and near the central partition were one or more anemones, the number selected to generate an anemone-shrimp size ratio similar to that observed in the field. Coral rubble was placed at the far ends of the aquarium as an alternative shelter for animals subsequently evicted from the anemones during a contest.

The shrimp were allowed to acclimate for 90 to 180 min. Afterwards, the partition was gently removed while the shrimp were facing away from and not touching it. Initial contact between the shrimp generally occurred within the canopy of long tentacles of *B. annulata*, which intermingled between the two adjacent clusters of anemones once the partition was removed. This arrangement eliminated the distinction between 'resident' and 'intruder'.

Contact between the shrimp was immediately followed by agonistic behavior (similar to that described by Hazlett and Winn 1962; Nolan and Salmon 1970; Schein 1975, 1977). The shrimp were observed until the identity of the subordinate was clearly established by its remaining with the rubble refuge continuously for two minutes (something a dominant or solitary individual never did) or by its being chased up the sides of the aquarium. At this point the partition was re-inserted to separate the shrimp, thus preventing the dominant from inflicting additional injuries. Most interactions were staged between 14.00 and 18.00 h.

Establishment of dominance typically occurred during a single bout of agonistic behavior, defined as a period of continuous contact in a head-to-head orientation. We timed with stopwatches the duration of each bout and the delay between the beginning of the bout and the first snap, and we counted the snaps during each bout.

After the contest each shrimp was allowed to back into a test tube (thus restraining its movements) and was carefully examined under a dissecting microscope for injuries inflicted during the contest. Physical damage was the result of direct contact (not water jets from snapping), and included punctures of the cuticle, broken antennae, loss of walking and feeding appendages, and loss of the minor chela (loss of snapping chela was never observed). Statistical tests of differences among groups of shrimp were based on the following simplified code: 0 – no injury, 1 – injury without loss of minor first chela, and 2 – loss of minor first chela.

The shrimp were kept in the laboratory for an additional two days. Few shrimp (8%) molted during this period, and no effect of molting on pre-molt fights was detected. Shrimp had one antenna removed before their return to the field, making them recognizable for several months (while the antenna regenerated) and insuring that they were not used again during this period.

For analyses of the influence of size on fight characteristics we assigned shrimp to two size categories, small (<27 mm total length) and large (≥27 mm). These size categories have biological significance, because reproductive activity and sexual dimorphism in movement increase sharply across this size interval (Knowlton 1980). Nonparametric statistics were used in all cases.

Results

Haphazard movements of the shrimp near the anemones usually resulted in an encounter within five minutes of the removal of the partition. Upon contact, the shrimp generally began to antennulate each other in a head-to-head position (Nolan and Salmon 1970), sometimes while laterally spreading and opening the claws. This interval of mutual antennulation was almost always followed by one or more snaps, often accompanied by lunging and sometimes by grappling. Eventually the subordinate shrimp ('loser') turned away or broke free, often leaving the anemones.

Usually one bout occurred (81 of 97 contests), and subsequent encounters between the shrimp resulted in the immediate withdrawal of the previously established loser. A 'main bout' was defined for multiple-bout contests as either the longest bout, or in cases where bout durations differed by less than five seconds, the bout having the most snaps. Determining the dominant shrimp was ambiguous in only three cases.

Our criterion for size symmetry, that the sum of the differences in total length and claw length not exceed 2 mm, was supported by the outcomes of the contests. Within this range there was not a significant tendency for the larger individual to dominate (females: 24 of 41, $P=0.13$; males: 25 of 44, $P=0.21$; Fisher exact probability test). Nor were there any significant correlations between fight characteristics and size differential within the 2 mm range of size differences (Table 2).

Comparisons among the four size-sex classes of shrimp revealed no significant differences in the number of bouts (Fig. 1A) or in the number of snaps exchanged (Fig. 1B) ($P>0.05$, nonparametric multiple comparison tests). Large females, however, differed from both small and large males in the length of their contests (Fig. 1C, D); the time intervals between first contact and first snap (Fig. 1C), and between first snap and retreat by the loser (Fig. 1D), were both significantly shorter for large females (see

Table 2. Correlation of fight characteristics and the absolute value of the sum of the differences in total length and claw length (≤ 2 mm) for *Alpheus armatus* used in contests. r_s Spearman's rank correlation coefficient

Fight characteristic	Male			Female		
	r_s	P	n	r_s	P	n
Number of bouts	−0.03	>0.8	48	0.06	>0.6	49
Number of snaps (main bout)	0.10	>0.5	47	0.01	>0.9	48
Seconds from first contact to first snap (main bout)	−0.02	>0.9	30	0.14	>0.4	30
Seconds from first snap to retreat (main bout)	0.18	>0.3	30	0.08	>0.6	30
Injury	−0.05	>0.7	47	−0.02	>0.9	48

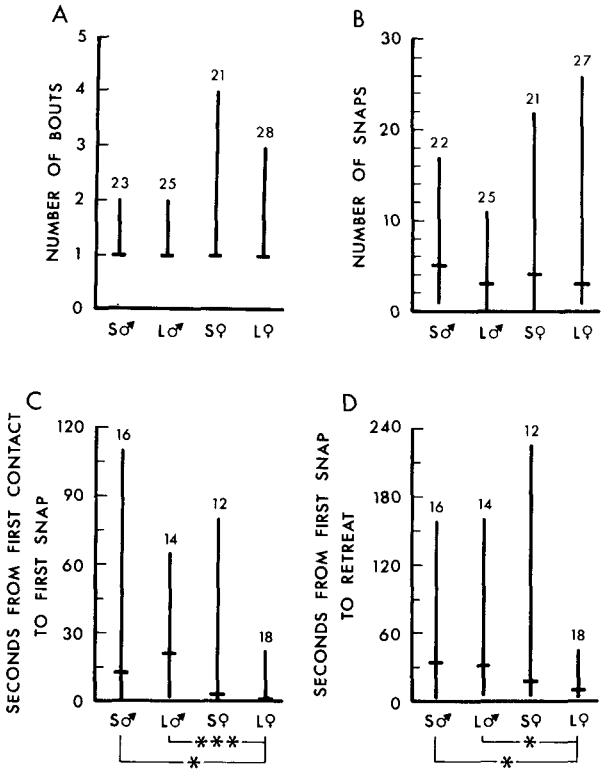

Fig. 1 A–D. Characteristics of symmetric fights between *A. armatus* as a function of size and sex. The cut-off between small (*S*) and large (*L*) individuals was 27 mm total length. The *crosses* are medians, the *bars* are ranges, and the *sample sizes* are shown above each category. Discrepancies in sample sizes are due to incomplete records for some fights, particularly for **C** and **D**, which were not initially recorded. Significant differences (nonparametric multiple comparison tests) are denoted by *lines* and *asterisks* between the categories compared (* $P<0.05$, *** $P<0.001$). See text for full description of the characteristics shown (**A–D**). For multiple-bout contests, counts of snaps (**B**) and bout durations (**C** and **D**) are for the 'main bout' (see text)

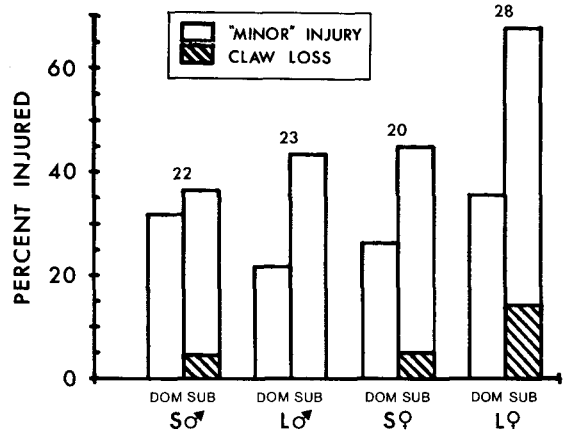

Fig. 2. Injuries received during symmetric contests between *A. armatus*, shown as percentages of contests with claw loss and 'minor' injuries (injury without claw loss) as a function of size, sex, and status as dominant (*DOM*) or subordinate (*SUB*). The distribution of injured ('minor' injury+claw loss) and uninjured individuals is significantly heterogeneous among the eight groups ($P<0.05$, χ^2-test; see text for further details). Size, sex, and sample size are noted as in Fig. 1

Fig. 1 legend for statistical details). For 50% of the fights between large females there was no measurable delay between first contact and first snap.

This distinctiveness in large female contests was also seen when injury levels were compared. The losers of contests between large females were more likely to suffer injuries (Fig. 2); when each of the eight size-sex-winner/loser classes was compared against the remaining aggregated seven, only for large female subordinates was there a statistically significant difference ($P=0.001$, Fisher exact probability test), a difference which remains highly significant even when multiplied by the total number of comparisons made ($P=0.011$, the probability that any of the eight comparisons would by chance differ to that extent). Of the six instances of minor claw loss that we observed, four occurred among large female subordinates (Fig. 2).

Discussion

Why do large females consistently shorten or eliminate the period of contact (and probably assessment) prior to the delivery of the first snap, and why do more of their fights continue until one individual is injured? Geist's (1974) interpretation of 'conventional' fighting as the result of the interaction of offensive and defensive strategies does not explain why large females should behave less defensively. It would also be difficult to argue that escalated fights between large females are risk-free; their snapping claws are absolutely much larger and proportionately similar

in size when compared with the snapping claws of more conventionally fighting juveniles (Table 1), and large females can severely injure each other during fights (Fig. 2 and unpublished data).

There remain at least three, not necessarily mutually exclusive hypotheses for the distinctiveness of large female contests. First, anemones may be more valuable for large females than for other individuals; eviction could have a detrimental effect on egg production, or large females could be more susceptible to predation when moving between anemones. Factors which could increase predation probabilities for large females include their bulky clutches of brooded eggs and their more sedentary habits (Knowlton 1980), which might decrease their familiarity with the local environment. Second, injuries may have less serious consequences for large females than for other individuals. Because adult females are less likely to encounter one another and molt more frequently (Knowlton 1980), they are more likely to be able to repair any injuries, including claw loss, before another contest occurs. Finally, there is the possibility that large females become less proficient at assessment because they interact less often.

More generally, our results illustrate the difficulties associated with defining and comparing aggressiveness. We have chosen to compare the maximum potential for escalation among these groups of shrimp, a behavioral measure central to all theoretical treatments of fighting behavior and related to Parker and Rubenstein's (1981) concept of 'reserve strategy'. Yet having settled upon some aspect of escalation as the critical feature of aggressiveness, the problem of interpreting various types of behavioral data remains. For example, it is often assumed in both theoretical and empirical studies (e.g. Davies 1978; Parker and Rubenstein 1981) that longer contests are more highly escalated (more costly). Although this seems likely when comparing short asymmetric with long symmetric contests, it seems less valid for comparisons of the various types of symmetric contests described here.

Finally, if injuries are the best measure of cost, then our results may provide an exception to the general pattern of greater male aggressiveness in sexually selected species. This potentially contrary pattern in *A. armatus* is not a simple consequence of the absence of a mate in the experimental situation, for encounters involving a male-female pair and a single male resulted in male-male fights indistinguishable from those reported here (unpublished data). The fact that males are morphologically more specialized for agonistic behavior in sexually selected species implies that conflicts are more frequent between males, or that the value of winning any contest is greater for males, but only the latter condition would result in greater escalation in male-male contests. The occasional reports of more 'severe' fights between females in other species (fiddler crabs: Schöne 1968; the marine iguana: Lorenz 1964) indicate that the pattern observed in *A. armatus* is not unique.

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