Appeasement Displays in Cambarid Crayfish (Decapoda, Astacoidea)

Author(s): Christopher Ameyaw-Akumfi

Source: *Crustaceana. Supplement*, 1979, No. 5, Studies on Decapoda (Biology, Ecology, Morphology, and Systematics) (1979), pp. 135-141

Published by: Brill

Stable URL: https://www.jstor.org/stable/25027495

Crustaceana, Suppl. 5, 1979. E. J. Brill, Leiden

APPEASEMENT DISPLAYS IN CAMBARID CRAYFISH (DECAPODA, ASTACOIDEA)

BY

CHRISTOPHER AMEYAW-AKUMFI

Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan, 48109, U.S.A.

INTRODUCTION

Resolution of fighting among animals very often occurs through the adoption by one and the recognition by the other of a non-aggressive posture. During evolution this pattern of behavior has been selected over a 'fight to the death' approach because this behavior, referred to as appeasement, recognised commonly among mammals and birds, prevents further and more damaging clashes between figthing individuals (Marler, 1956; Tinbergen, 1959; Backhaus, 1960; Schenkel, 1967; Kummer, 1968). Among members of a social group it is suggested that the use of appeasement allows continued interaction in the group by the appeaser, to whom departure would be potentially disadvantageous (Ewer, 1968; Manning, 1972). In solitary animals it is believed to function to maintain interindividual distances through reduction in hostilities (Ewer, 1968).

Among crustaceans little is known about the use of appeasement displays during aggressive encounters. Static factors significant in determining the winner of a fight are well documented in crayfish (Bovbjerg, 1953, 1956; Lowe, 1956) and in hermit crabs (Hazlett, 1966, 1968, 1970). So also are postural indicatives and behavioral patterns characteristic of both winner and loser in aggressive encounters (Hazlett & Bossert, 1965; Heckenlively, 1970; Hazlett & Estabrook, 1974; Rubenstein & Hazlett, 1974). In most observations the loser retreats from the winner and this marks the end, even if temporarily, of further fighting. It remains to be shown whether during a fight specific appeasement displays are shown by the would-be loser prior to the termination of a fight.

Crayfish are a suitable subject for such a study. During fighting, the chelae are very often interlocked. Although fighting individuals push against each other, rubbing the inner parts of the dactyls, in intensive fighting they do hold one another by the chelae. In such situations 'being let go' is not a simple matter of withdrawing. The chelae have to be released by the second individual. This raises the problem about what signals are involved.

In four species of crayfish, *Orconectes virilis* (Hagen), *O. propinquus* (Girard), *Procambarus clarkii* (Girard) and *Cambarus robustus* Girard the possible signals used to terminate a fight were studied. Due to availability of larger numbers of *O. virilis* most experimental data were obtained only for this species.

MATERIALS AND METHODS

Orconectes virilis, O. propinquus and *Cambarus robustus* were collected from a stream at Pinckney, Livingston Co., Michigan. *Procambarus clarkii* was obtained from suppliers at Ponchatoula, Louisiana. The animals were maintained separately in 10 gallon aquarium tanks in well aerated water. They were fed regularly with pieces of meat and fish, lettuce, and aquatic plants collected from the stream at Pinckney. Observations of agonistic encounters of two individuals brought together were recorded in the form of notes, still photographs, movie films and occasionally through the use of video tape.

Between October and December of 1974 and October and November of 1975, over 200 aggressive encounters between individuals of *O. virilis,* about 100 encounters in *P. clarkii* and *O. propinquus* and 30 of *C. robustus* were carefully observed. During each encounter, the behavior shown by each individual was noted until one of the two emerged as a clear winner. Most observations were made during late afternoon hours.

RESULTS

As these studies were made during the breeding season observations were made on intrasexual pairings. Male-female fights were less persistent. And in one species, *O. propinquus*, it was difficult to differentiate a precopulatory encounter and an aggressive encounter. In brief inter-sexual aggressive encounters the signals given by a defeated individual were similar to those given by the defeated individual in intra-sexual male or female encounters. So also were the signals given by a copulating female who, for some reason, attempts to terminate the process. The same signals are used by males prior to copulation. Normal as well as blinded animals showed identical behavior.

Signals

Pl. 1 fig. 1 shows a fighting stance used by members of all four species. As they push against each other the abdomen and the telson (not visible in the picture) are almost horizontal. The antennae of one individual do not touch those of the other. Each antenna is held at an angle of 90° to 120° to the anterio-posterior axis of the animal. During fighting no feeding movements are made by the mouthparts of the combatants. These movements consist of rapid up and down motion of the third maxillipeds, often accompanied by motion of the chelate ambulatories to and away from the mouth area. These movements are employed during feeding. Nor are there any grooming movements which involve rhythmic motion of two or three or all pairs of the ambulatories to and away from the ventral part of the body. Repeated chelae strike (Bovbjerg, 1953; Heckenlively, 1970) and inner dactyl rubbing occur. Then abruptly, or following a strong push or a chela twist by his opponent, the would-be loser waves his antennae repeatedly (a range of 10 to 50 was observed, each wave taking a little over a second or two seconds). The latter's antennae, chelae, mouthparts and the dorsal part of the cephalothorax are touched

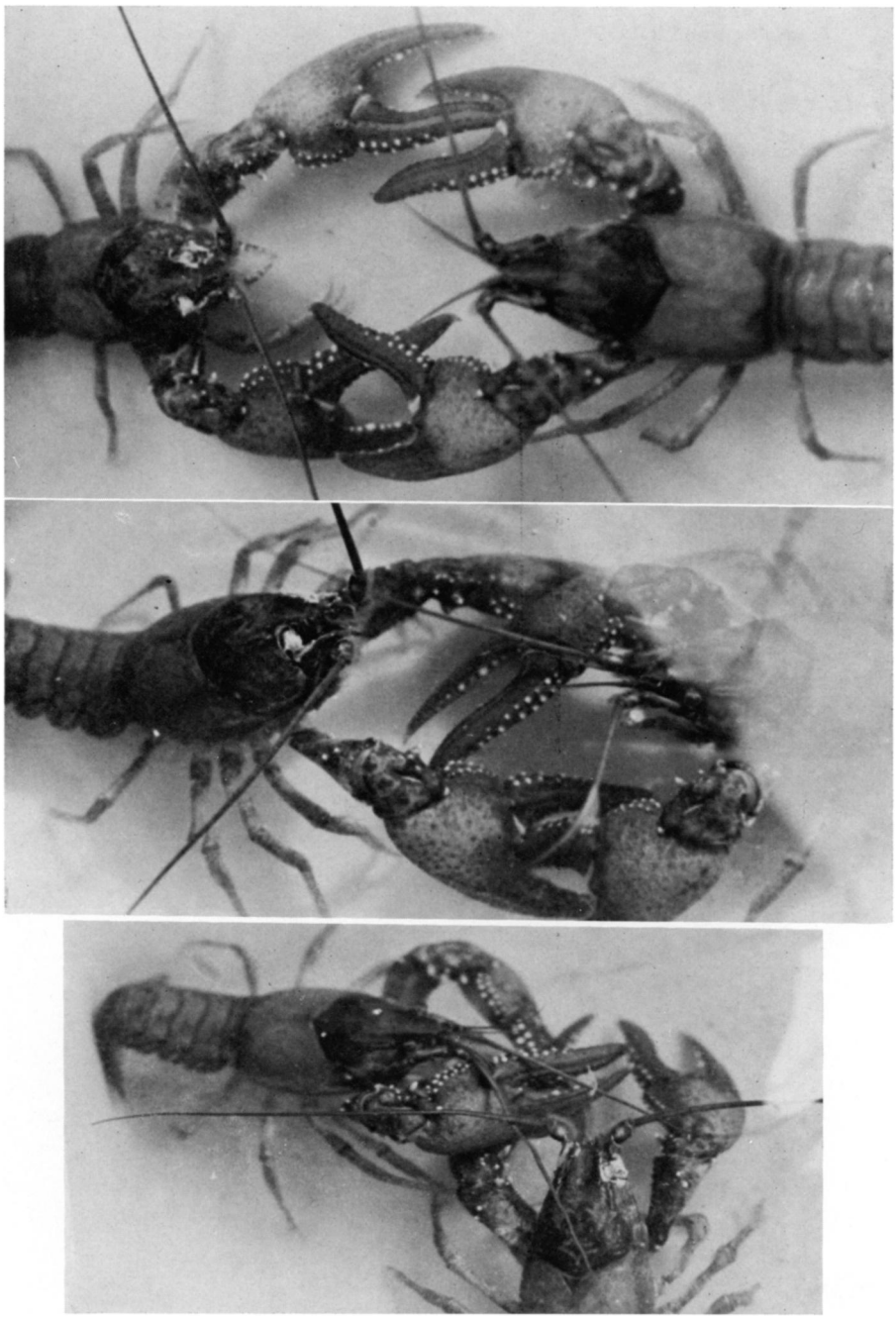


Fig. 1. Two individuals of *Orconectes virilis* (Hagen) in a fighting stance. Note positions of antennae, chelae and ambulatory legs of both. Paint on the eyes of the individual on the left (blinded for other experiments) helps identify the two.

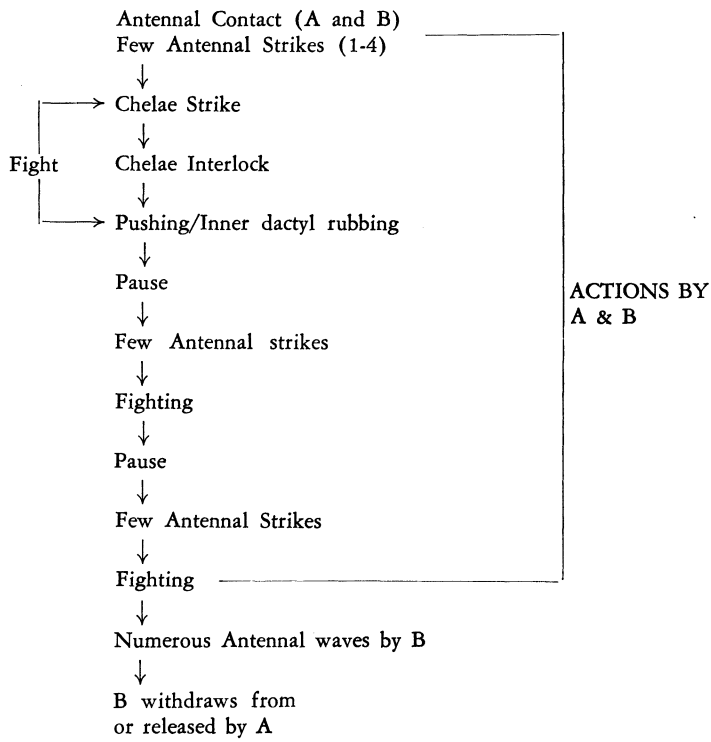
Fig. 2. Note positions of the antennae of the individual on the right.

Fig. 3. The loser (in the foreground) continues to wave his antennae against the anterior part of the winner as he withdraws. Note position changes of the ambulatories of the loser in figs. 1 and 3.

in the process (pl. 1 fig. 2). This is accompanied or soon followed by vigorous feeding and grooming movements (pl. 1 fig. 3). After some seconds, the chelae of the individual showing these movements are released if they are being held. If the chelae are interlocked the would-be retreater backs away (pl. 1 figs. 2, 3). This marks the end of a fighting bout (Table I).

TABLE I

Summary of the sequence of behaviors shown by two interacting crayfish (A and B) during an aggressive encounter



In all the aggressive encounters (over 400) in which a clear winner emerged, the would-be loser showed this behavior. The defeated individual may be attacked again if the two individuals make contact with each other. Although defeated individuals generally show escape tendencies after a fight, they sometimes resist attacks by participating in chelae interlock, which soon ends with appeasement signals by the previous loser. On some occasions, recent appeasers initiated attacks when they made contact with victors of earlier fights.

There is a second type of antennal movement observed in agonistic encounters. During a brief pause in fighting, either or both individuals sweep one or both antennae back and forth 1 to 4 times (but generally once or twice); the antenna is rigid during this wave and a single wave takes 1 to 4 seconds to execute. This

movement is in contrast to the repeated wave of flexed antennae in appeasement display; and after the exchange of those few strikes, fighting is often resumed by both animals. In addition to a slow deliberate motion of the antennae used during searching, the second type of antennal wave observed in aggressive encounters is also used.

In a non-fighting crayfish that is resting, no antennal feeding or grooming movements are observed. An individual in such a resting posture can be subject to an attack by a second individual. Hence although demonstrating general submission, the postures used in resting and in non-aggressive 'mood' do not signify the end of further attacks by the winner of a fight.

For *O. virilis*, quantitative information on the signals used in appeasement was obtained on 25 individuals (Table II). Two individuals of identical size and sex (or differing in size by not more than 1 mm in cephalothorax length) were allowed to fight until one of them began to show antennal wave, feeding and grooming movements. The number of antennal waves was noted. The time taken for the would-be loser to show this behavior (terminating after he has been released by his opponent) was noted. Also noted was the duration of feeding and grooming movements. These two movements tended to occur simultaneously. Members of a fighting pair were about equal size. On the average, animals showed 25.4 antennal waves, with each wave taking 1.14 seconds on the average. The average duration of feeding and grooming movements was 26.28 seconds.

Experiments

Some experiments were conducted to investigate the possible sensory systems mediated by the signals used in appeasement.

Experiment 1. — To investigate the use of the motion of the various structures as a visual cue, the fighting individuals were blinded by using fingernail polish. The behavior of these experimental animals were observed as they went through a fight. All would-be losers (20 of *O. virilis*, 7 of *P. clarkii* and 5 of *O. propinquus*) showed antennal wave, feeding and grooming movements.

Experiment 2. — Aside from the antennae, other structures, notably the first pair of the chelate ambulatories of the appeaser often make contact with some appendages of the opponent. However, this contact is not as regular as antennal contact with the anterior part of the opponent's body. To investigate the possibility of tactile stimulation, the antennae of animals were removed in three series of experiments.

a) Antennae of introduced animals removed. — In this series, the antennae of animals that were introduced into the tanks of other individuals were removed. In some earlier experiments it was observed that in an encounter between a resident animal and an introduced animal of about equal size, the former has a higher probability of winning.

The results of this experiment (Table II) showed that even though the anten-

nule-less would-be losers showed feeding and grooming movements they were held onto for longer periods of time than normal animals ($t = 5.096$, $p<0.001$).

TABLE II

O. virilis: Antennal waves, feeding and grooming movements shown by would-be losers (B) during interaction with winning opponents (A)

Treatment of animals	No. of fighting pairs	Mean No. of attacks initiated by A	SD	Mean No. of attacks initiated by B	SD	Signals by B					
						Mean No. of antennal waves	SD	Mean duration of antennal waves (in mins)	SD	Mean duration of feeding and grooming movts. (in mins)	SD
A and B Normal	25	2.5	1.5	0.96	0.61	25.4	8.59	28.6	8.76	26.3	8.08
A Normal B Antennule-less	20	2.5	1.39	0.65	0.56	43.8	9.3	54.9	10.8		
A Antennule-less	15	2.6	1.49	0.7	0.67	24.6	8.6	29.8	8.7		

b) Antennae of both individuals removed. — In this experiment, both members of a fighting pair had their antennae ablated. During fighting, the stance adopted by these animals was identical to that used by normal animals. Feeding and grooming movements were shown by would-be losers. By observing the bases of the antennae that were left on the operated animal antennal orientation during aggressive exchanges were noted. On the average, would-be losers in this experiment spent more time showing appeasement behavior (about 60 seconds). All this time they were held onto by their opponents.

c) Antennae of resident animals removed. — In this series the antennae of the resident animals (potential winners) were removed. In the aggressive encounters between these animals and normal ones, the mean number of antennal strikes made by the would-be losers was not significantly different from that obtained between normal resident and introduced animals ($t = 0.20$, $p>0.50$).

DISCUSSION

The possible role of repeated antennal wave as an indication of the acceptance of defeat during fighting in *O. virilis* was mentioned by Rubenstein & Hazlett (1974). In addition to this behavior, the current work also shows that movements of the mouthparts and the ambulatories also occur prior to the termination of a fight, all types probably reinforcing one another. Similar observations were made on *Orconectes propinquus*, *Procambarus clarkii* and *Cambarus robustus* suggesting that this behavior pattern is probably widespread among crayfish. In all four species

the individual showing this behavior was momentarily freed by the attacker. It could therefore be suggested that that behavior constitutes an appeasement display.

In nocturnal species, it is not clear whether movements made by the structures are observable. In fact blinded animals show and respond to the same signals as normal ones. The contact made by the antennae with the frontal part of the attacker probably serves a tactile function, causing the attacker to 'recognise' the submissiveness of his opponent. Without the antennae, would-be losers are held onto for a considerably longer period of time, even though they show the other appeasement signals. It is not clear what the sensory mediator is.

In *Homarus americanus* H. Milne Edwards, Scrivener (unpublished) describes 'antenna whipping' during agonistic behavior. 'Antenna whipping' by one is reciprocated by the other. This exchange is followed by pushing and meral spread. The function of this antennal movement is not clear and it may be similar to the second type of antennal movement described above. Antennal movement involved in appeasement leads to the departure of one of the fighting individuals. It is possible that the motion of the antenna during appeasement signifies general locomotory activity informing the attacker, probably mechanically, that the opponent is 'ready to flee'?

The movements by the ambulatories may also be an indication of a general increase in locomotory activity. It is interesting to note that individuals released after showing appeasement behavior show immediate escape tendencies. In diurnal animals it could be suggested that feeding movements are indications of lack of aggression, as in birds. While this may be true for crayfish, such a role for animals that show agonistic interactions in burrows or at night is somewhat doubtful. The possible role of grooming in reducing aggressive tendencies is evidenced by the use of it during mounting and copulation in crayfish (Ameyaw-Akumfi, in preparation). When in motion during agonistic encounters some of the mouthparts and the ambulatories make contact with some parts of the attacker. It is therefore possible that grooming has evolved basically as an appeasement signal.

In crayfish it appears that unisexual groups are not formed, although in the laboratory, observations on the formation of dominance hierarchy have been made (Bovbjerg, 1953). However there is evidence to suggest that male-female pairings are probably common in the breeding season (Ameyaw-Akumfi, in preparation). In a male-male aggressive encounter therefore the advantage of appeasement behavior by the would-be loser is to signify his lack of participation in further fights so that he would escape. To support this hypothesis are two instances of male-male fighting at the entrances of burrows, in both cases with one of the fighting pair only partially out of the burrow. In both instances fighting proceeded for about three minutes after it was observed in progress. The one that turned out as the loser showed antennal, ambulatory and mouthpart movements before slowly withdrawing from the one which was in the burrow. Both defeated individuals began to wander in the stream after their defeat and were not pursued by the winners, one of which returned into his burrow (removed for identification)

and the other emerged from the burrow but stayed around the entrance of the burrow. In a sense therefore crayfish appeasement behavior functions to maintain individual distances as has been observed in mammals and birds that are non-group living. This is true of both male and female crayfish. The use of appeasement signals in mating behavior is, probably, a capitalization by the male as this behavior appears to reduce aggressive tendencies.

ACKNOWLEDGEMENTS

The author wishes to thank Dr. B. A. Hazlett for his valuable criticism of the manuscript.

SUMMARY

Signals given by the would-be loser prior to the termination of a fight between two individuals of crayfish have been reported; these include rapid antennal wave, feeding and grooming movements. It has been suggested that these signals constitute appeasement displays and serve to prevent long and potentially injurious fights.

LITERATURE CITED

BACKHAUS, D., 1960. Uber das Kampfverhalten beim Steppenzebra. Zeitschr. Tierpsychol., **17**: 345-350.

BOVBJERG, R. V., 1953. Dominance order in the crayfish Orconectes virilis (Hagen). Physiol. Zool., **26**: 173-178.

——, 1956. Some factors affecting aggressive behavior in crayfish. Physiol. Zool., **29**: 127-136.

EWER, R. F., 1968. Ethology of mammals: 1-418. (Logos Press Ltd., London).

HAZLETT, B. A., 1966. Factors affecting aggressive behavior of hermit crab Calcinus tibicen. Zeitschr. Tierpsychol., **23**: 665-671.

——, 1968. Size relationship and aggressive behavior of the hermit crab Clibanarius vittatus (Decapoda, Paguridea). Zeitschr. Tierpsychol., **25**: 608-614.

——, 1970. The effect of shell size and weight on the agonistic behavior of a hermit crab. Zeitschr. Tierpsychol., **27**: 369-374.

HAZLETT, B. A. & W. H. BOSSERT, 1975. A statistical analysis of the aggressive communication systems of some hermit crabs. Anim. Behaviour, **13**: 358-373.

HAZLETT, B. A. & G. F. ESTABROOK, 1974. Examination of agonistic behavior by character analysis. 1. The spider crab Microphrys bicornutus. Behaviour, **48**: 131-144.

HECKENLIVELY, D. B., 1970. Intensity of aggression in the crayfish Orconectes virilis (Hagen). Nature, London, **225**: 180-181.

KUMMER, H., 1968. Social organisation in Hamadryas baboons. A field study. Bibliotheca Primatologica, **6**: 1-189.

MANNING, A. 1972. An introduction to animal behavior: 1-294. (Addison-Wesley Publishing Co., Reading, London).

MARLER, P., 1956. Studies of fighting in chaffinches. 3. Proximity as a cause of aggression. Brit. Journ. Animal Behaviour, **4**: 23-30.

RUBENSTEIN, D. I. & B. A. HAZLETT, 1974. Analysis of the aggressive behavior of the crayfish Orconectes virilis by character analysis. Behaviour, **50**: 193-216.

SCHENKEL, R., 1967. Submission: Its features and function in the wolf and dog. American Zoologist, **7**: 319-329.

SCRIVENER, J. C. E., unpublished. Agonistic behaviour of the American lobster Homarus americanus (Milne-Edwards). M.Sc. Thesis, 1970, University of Victoria.

Received for publication 5 April 1976.