BEHAVIORAL COMPONENTS OF SOCIAL INTERACTIONS IN THE CRAYFISH *PROCAMBARUS GRACILIS* (BUNDY) (DECAPODA, CAMBARIDAE)

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Eight apparently innate components of social interactions are described for the primary burrowing crayfish, *Procambarus gracilis*. These are alert, approach, threat (low and high intensity), combat (low, high and maximum intensity), submission, avoidance, escape, and courtship. Ritualization was noted in combat. Relationships of individual components and their importance in crayfish social behavior are described.

Procambarus gracilis is an obligate burrowing crayfish common in areas adjacent to seasonal water bodies in eastern Oklahoma. Individuals construct relatively simple burrows with or without short chimneys. The burrow occupant generally leaves the burrow only during rainy periods or on warm humid nights. In eastern Oklahoma, greatest social activity appears to occur from late April through late June or early July. During this period many adult individuals leave their burrows shortly after sunset and move about the populated area. Aggressive and sexual encounters are apparently common, resulting in occupation of prime burrow sites by dominant breeding pairs (one form I male and one adult female per burrow).

Although many observations of social interactions in the natural habitat were made, it was necessary to observe activities of captive individuals in aquaria to accurately describe postures and action patterns. Social interactions are defined as any activities occurring between conspecifics.

Several authors have studied crayfish behavior (1-7), but, none have described postures and action patterns of individual species systematically for comparisons of behavioral components between species. This report will systematically describe social behavioral components of adult *Procambarus gracilis*, providing a basis for similar analysis of other crayfish species.

METHODS

Most field observations were made between early May and early July, 1972. The study area was a seasonally wet meadow and shallow roadside ditch 4¼ mi east of the junction of Highways 33 and 66, Wagoner County, Oklahoma. *Procambarus gracilis* was fairly abundant in this area.

Field observations were originally made for approximately three hours after sunset and two hours before dawn, since individuals were secretive during the day. Early morning observation was abandoned after the population was found to be active from shortly before, until one hour after sundown. Nocturnal observations were made with a dim head-lamp. It soon became apparent that laboratory observations of captive individuals would be necessary for accurate recording of behavioral components. Comparisons with field observations showed no apparent difference.

Individuals were collected by hand from the study site on June 9, 1972, during the nocturnal activity period. Six males (form I) and four females were taken. All were maintained in a ten-gallon aquarium (water level 3 cm) and allowed to acclimate for four hours before observations were begun. Observations were made for one or more hours daily until July 1, 1972. All activities between individuals were noted and individual components of behavior were observed and recorded verbally, photographically and by drawings.

RESULTS

Many behavioral patterns of *P. gracilis* show marked similarities to those of fiddler crabs (8-10) and other crab species (11, 12). Visual and tactile senses are important during social contact. Crayfish see throughout a range of 360° (2) with peak sensi-

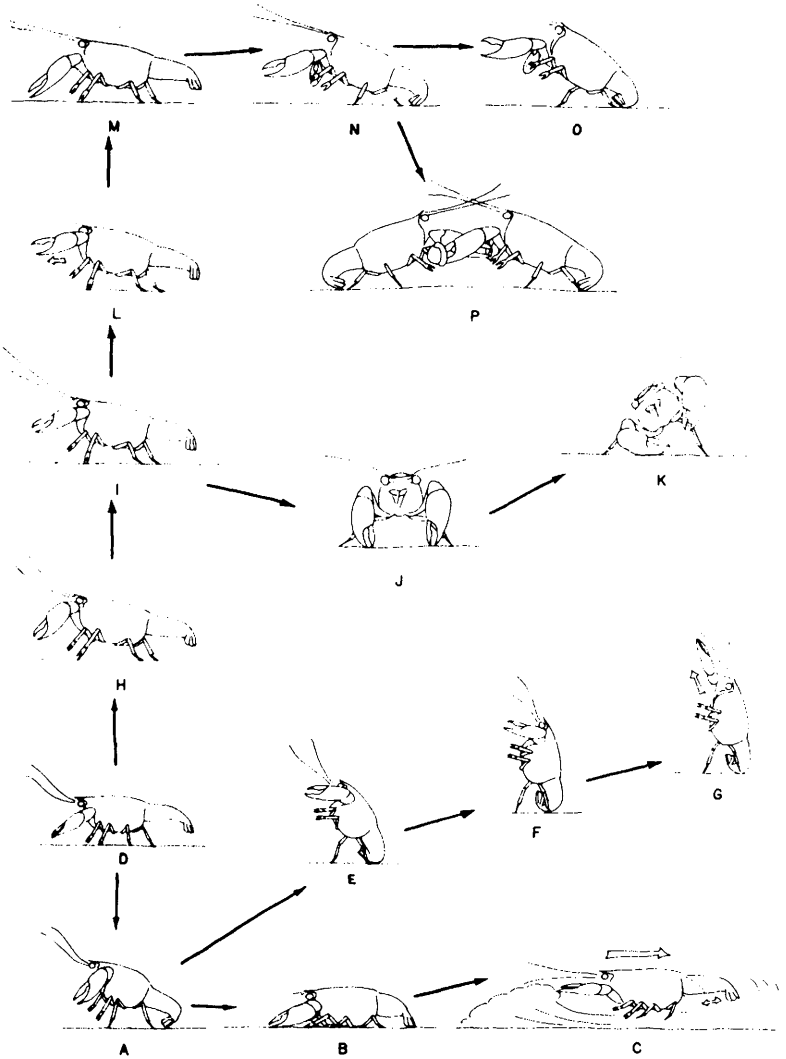

FIGURE 1. Behavioral component postures of *Procambarus gracilis*: A, avoidance; B, submission; C, escape; D, alert; E, low intensity predator response posture (PRP); F, high intensity PRP; G, maximum intensity PRP; H, approach; I, low intensity threat; J, courtship; K, courtship turning; L, high intensity threat; M, low intensity combat; N, high intensity (ritualized) combat; O, maximum intensity combat; and P, opponents engaged in ritualized combat.

tivity to visible light at 5700 Å (yellow) in *Procambarus clarkii* (13). In normal crayfish, touch and vision are coordinated to give normal, well-organized responses. Without vision, touch is sufficient. Absence of both results in behavioral disintegration. Lack of the additional operative sense of olfaction is indicated (2). *P. gracilis* uses visual presentation, touch, and sound production during social interactions.

Visual presentation involves body postures and chelae positions. Touch is involved in both aggressive and sexual activities. Sound is produced by air bubble emission from efferent branchial channels as in fiddler crabs (10). This appears to be a signal, but its purpose is unknown.

Eight behavioral components have been observed for the activities of *P. gracilis* during social interactions: 1) alert, 2) approach, 3) threat, 4) combat, 5) submission, 6) avoidance, 7) escape, and 8) courtship. Only slight variations in these components were observed. The normal stance is described for each.

The alert posture (Fig. 1, D) is assumed by an individual during normal activity when not affected by any specific external stimulus. The body is held horizontally, usually raised slightly above the substrate, and supported by the walking legs. The tail is held with the distal end below horizontal. Chelae are held close to the body, moderately flexed, with fingers slightly below horizontal and separated slightly. Tips of chelae are directed medially well below horizontal.

The approach posture (Fig. 1, H) is assumed when an individual moves toward another. The body, supported by the walking legs with the front of the carapace raised slightly, is oriented toward the other individual. The tail, held with the distal end below horizontal, often touches the substrate. The chelae are held forward and laterally, moderately flexed, with fingers moderately separated. Tips of chelae are directed medially well below horizontal.

The threat component is divisible by intensity into two subcomponents. The low intensity threat posture (Fig. 1, I) is assumed by a dominant individual when nearing another. The body and tail are held as in approach. Chelae are flexed less, with tips oriented more directly at the opponent. Fingers are widely separated. Tips of chelae are directed medially and below horizontal.

The high intensity threat posture (Fig. 1, L), a modification of low intensity posture, is initiated at close proximity to the opponent. The body is raised higher than in low intensity threat and readied for maximum intensity threat action—strike (1, 2).

Combat is partially ritualized in *P. gracilis*. Usually, low intensity combat follows threat with the crayfish assuming a posture as in Fig. 1, M. The body is elevated on the last three pairs of walking legs with the anterior of the cephalothorax slightly above horizontal and oriented toward the other individual. The tail is held almost horizontally with uropods spread. Chelae are held in chelae-forward display (12), with fingers slightly spread. Combating individuals face each other with chelae tips touching or overlapping. Increased intensity results in each trying to grasp the other's chelae or rostrum. This usually leads to ritualized high intensity combat (Fig. 1, N and P). In high intensity combat, the anterior portion of the body is held even higher, supported by the last two or three pairs of walking legs. The tail is semiflexed. Chelae are held in a ritualized position—right chela flexed, shielding the body, left forward grasping the immovable finger of the opponent's shield chela (less often, the mirror image of this posture is displayed). Tuberculations on inner surfaces of fingers prevent maximum interlocking of chelae during normal ritualized combat. With extreme aggression in one or both combatants, chelae may slip past tuberculations and engage maximally. Maximum intensity combat (Fig. 1, O), wild fights, appears to be extremely dangerous to individuals involved, with injury or death often occurring. Evidence of wild fights are crush-marks on chelae of captured specimens. Wild fights are fairly uncommon. Most combat ends in retreat of one opponent after low or high intensity battles without severe injury.

Preceding courtship, the male approaches the female and initiates typical threat activities. If she becomes submissive or avoids he will adopt a chelae-forward courtship display similar to low intensity threat but with chelae held almost vertically (Fig. 1, J). Upon nearing the submissive female's side, he adopts a turning posture (Fig. 1, K), turns her over and mounts.

Avoidance (Fig. 1, A) is an interesting posture due to the combination of elements evidenced in it. The body is often held moderately high as in threat but the chelae are strongly flexed in front of the mouth as in submission. The posture is usually combined with turning away from the stimulus which initiated it (i.e., a dominant male). It appears to result from interaction of fright and aggression. Combat, submission, or escape may result if the individual is stimulated further.

Submission (Fig. 1, B) is the antithesis of threat. This posture occurs when a subdominant male or a female is approached by a dominant male. This apparently hides or significantly reduces threat value of display color or form, thus lowering the dominant's aggression. In this posture, the body is held flat against the substrate with walking legs other than the last pair pointing forward and partially appressed. The last pair of walking legs are usually held laterally. The tail is either spread and held flat against the substrate or folded back beneath itself and helps to force the anterior end of the cephalothorax below horizontal. Chelae are held forward with fingers only slightly spread and pointing medially.

Escape (Fig. 1, C) is the family's characteristic backward swim. The posture is roughly the same as submission except for tail movement. This posture streamlines the crayfish for rapid movement.

The predator response pattern (Fig. 1, A, E, F, and G), although not actually an aspect of social interaction, is shown here due to similarities in chelae postures and intensity relations to normal intraspecific threat. Although illustrated here, this pattern will be discussed in detail in a later paper.

DISCUSSION

In *P. gracilis*, posturing by aggressive individuals increases their apparent size to respondent crayfish. Color patterns and movement may accentuate aggressive postures. Generally larger size and brighter localized coloration of males' chelae may serve to enhance their effectiveness during display.

The submissive posture of *P. gracilis* decreases the individual's apparent size and may hide important display elements. This "signal" change presented to an aggressive individual usually results in change of response (i.e., loss of aggression and initation of courtship behavior in a male when presented with a submissive female).

Any behavior between males involving contact of chelipeds may be considered combat (combat also occurs between females and mixed pairs). Preliminary to combat is exhibition of threat postures. Low intensity threat may be followed by high intensity threat and maximally with a strike by an aggressive individual (2). The purpose of threat is to frighten the opponent.

Submissive postures are the antithesis of threat with the body and chelae lowered, legs appressed and fingers only slightly separated. The purpose of submission is to lower aggression in the opponent and initiate sexuality.

Fighting components were defined more distinctly than in the studies by Bovbjerg (1). Separate components, resembling those described in fiddler crabs by Crane (10), are low intensity, high intensity, and maximum intensity combat. During low intensity combat, opponents face each other, chelae raised as in high intensity threat, with fingers only moderately separated. Tips of chelae usually touch or grasp the opponent's chelae. High intensity combat shows ritualization with characteristic stereotyped postures. Normally, left chelae are presented, right are flexed. The chelae of each are linked with the opponent's with tuberculations acting to assist in positioning. Opponents may remain motionless or see-saw back and forth trying to displace the other by shoving. In maximum intensity combat, chelae are fully linked with the opponent's, their bases in contact. This position occurs when chelae slip past tuberculations which normally prevent such engagement during normal high intensity combat. This form of fighting is often violent with one or both individuals being injured. Opponents may have difficulty in disengaging.

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