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Foraging and agonistic activity co-occur in free-ranging blue crabs (*Callinectes sapidus*): observation of animals by ultrasonic telemetry

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Abstract

To define the temporal and spatial patterns of agonism and foraging activity in blue crabs (*Callinectes sapidus*), we monitored five free-ranging animals in the Rhode River subestuary of the central Chesapeake Bay by ultrasonic telemetry during the summers of 1991–93. The interdependence between the two activities was of special interest. High crab densities have been associated with more frequent aggressive interactions and decreased foraging success in previous laboratory studies. High crab population density is correlated with increased frequency of aggression-related injury (autotomy) and cannibalism in the field. Consequently, we predicted that as crabs aggregate to clam patches during feeding periods in the field, the level of aggressive interactions would increase. In early trials, we collected data on location and agonistic activity (the stereotypical spreading of the chelae in the 'meral spread' threat display) of crabs moving freely in the estuary by using single-channel telemetry transmitters. With subsequent technological advancements, we received simultaneous data on agonism and feeding.

Crabs exhibited a diel pattern of agonism with peaks in threat display occurring in mornings and sometimes in evenings. Crabs fitted with single-channel telemetry transmitters were observed interacting aggressively most often at times previously identified as feeding periods, although the highest levels of agonism came slightly later than periods associated with the highest levels of feeding. Simultaneous telemetry of the two behaviors indicated that periods of increased agonism and feeding overlapped. Feeding activity tended to wane as threat activity increased, consistent with the hypothesis that aggressive interference impairs foraging.

Keywords: Agonism; *Callinectes sapidus*; Chesapeake Bay; Foraging; Ultrasonic telemetry

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1. Introduction

Animals showing a high degree of intraspecific aggression generally meet three criteria (Dingle, 1983). First, the animal utilizes a resource that merits defense (Brown, 1964). Examples include food, space, shelter, and mates. Prey resources that are difficult to detect or capture, requiring protracted searching by predators, may especially promote competitive interactions among predators. Second, the animal has the behavioral and morphological traits (e.g., sufficient body size, weapons) needed to defend the resource (Parker, 1974). Third, the animal uses a resource that occupies a limited space, so as to permit defense. In this light, animals in marine and estuarine systems seem good models for studying the function and effects of agonistic activity. Given the patchiness of many prey in these systems, predators could be expected to aggregate and reach high densities on the best prey patches (McClatchie et al., 1989; Piatt et al., 1989). Moreover, crustaceans, a common predatory taxon in these systems, appear excellent subjects for studying the role of agonism. Many of these species possess weapons (claws, chelae, spines), making them formidable opponents in contests for resources (Dingle and Caldwell, 1978; Vannini and Gherardi, 1988). Resources needed by these animals, such as home sites and prey items, are often contested and occupy discrete, defensible spaces (Vannini and Gherardi, 1988; Peeke et al., 1995). Finally, owing to the vigorous activity of many species, large amounts of data can be collected in a short time. However, the study of agonistic interactions in crustaceans or any other predators moving freely in marine and estuarine systems has been limited by the wide scale of patchiness and by turbidity of estuarine water. The former demands long-term continuous observation to understand behavior of animals moving among prey patches. The latter often precludes direct observation of animals.

We endeavored to surmount these difficulties, using the ecologically and commercially important blue crab (*Callinectes sapidus*). Since its habitat is too turbid for visual observation at our study site (the Rhode River subestuary of the central Chesapeake Bay), we developed a series of ultrasonic behavioral telemetry systems for long-term continuous tracking and monitoring of agonism and foraging activity. High-frequency sonic beacons ('pingers') have been used for over 20 years to track movements of many marine animals at fine spatial and temporal scales (Stasko and Pincock, 1977), including another portunid crab (*Scylla serrata*) in an Australian estuary (Hill, 1978). We integrated beacon signals for long-term (up to several months) continuous tracking, with sensors and encoding circuitry to telemeter one or more behaviors. Single-channel behavioral transmitters have provided data on either ecdysis or feeding of blue crabs (Wolcott and Hines, 1989, 1990; Shirley and Wolcott, 1991). Multi-channel transmitters now allow us for the first time to collect simultaneous data on feeding and agonistic posturing in an estuarine system.

In the blue crab, spreading of the chelae (the 'meral spread' threat display) was telemetered as a surrogate of intraspecific agonistic activity (in the Rhode River, almost all agonism by blue crabs will be intraspecific). The meral spread posture is part of a threat display common to many decapods (Jachowski, 1974; Dingle, 1983). The posture is probably employed to extend the animal's chemo-and tactile sensory range, to increase the apparent size of a combatant, and to display defensive structures. The

display may also be part of a 'bluffing' ploy to forestall outright combat (Caldwell and Dingle, 1979). Analogous behaviors in vertebrates include presentation of beaks and fangs. In some crustaceans, the meral spread display may be part of a ritualized behavioral repertoire that seldom leads to physical contact between opponents. Ritualized behavior is marked by decreased variability of movement and a predictable sequence of movements (Hazlett, 1972). Threat displays meeting criteria for ritualization have been demonstrated in hermit crabs and stomatopods (Dingle, 1972; Hazlett, 1972). In blue crabs, the degree to which threat behavior is ritualized has not yet been quantified; however, it is apparent that outright combat is frequent when crab density is high (Smith, 1990; Mansour and Lipcius, 1991; Smith and Hines, 1991). Consequences of aggressive interactions among crabs can be serious in terms of physical damage and energy loss (Smith, 1990; Smith and Hines, 1991; Smith and Taylor, 1993; Juanes and Smith, 1995; Smith, 1995), and – when there is a large size differential between combatants – even fatal (Dittel et al., 1995; Hines and Ruiz, 1995).

The blue crab is a particularly appropriate model organism for studying the relationship of intraspecific agonism to foraging activity. Blue crabs appear to aggregate at high densities while foraging; they feed primarily on patchy resources (clams) and appear able to detect these patches from at least 10 to 15 meters (Clark, 1997; Hines, Terwin, and Thrush, unpublished data). Once on a patch, they generally remain there long enough to consume multiple prey (Nye, 1989; Wolcott and Hines, 1989). Both laboratory studies and indirect field evidence indicate a high level of intraspecific agonism as crab density increases (Smith, 1990; Mansour and Lipcius, 1991; Smith and Hines, 1991). Under laboratory conditions, these aggressive interactions among crabs impair foraging success (Mansour and Lipcius, 1991; Dittel et al., 1995; Hines and Ruiz, 1995). Considering these relationships, we hypothesized that, in nature, aggression will increase as crabs aggregate on clam patches to feed; we used telemetry to collect the necessary data from an environment in which direct observation is impossible. Because we were interested in establishing whether feeding activity and aggressive interactions tend to co-occur in individuals, we elected to observe a few 'focal' animals intensively rather than to spot-sample many animals.

Blue crabs are abundant and hardy, and make favorable experimental subjects for telemetry. They have a rigid exoskeleton, permitting attachment of external packages and sensors as well as easy fixation of transcutaneous electrodes for sensing muscle potentials. Individuals with a carapace width of 140 mm carry our transmitter packages without evident alterations in behaviors like feeding and moving around in laboratory aquaria. Instrumented animals also seem to maintain normal behaviors in the field (as far as direct observations permit), moving freely, swimming to escape when startled, and in one case, mating.

The Rhode River has several advantages for studying predator–prey relationships. The estuary's simple predator–prey complex of six abundant species (Hines et al., 1990) allows manipulation of predators and prey under controlled conditions. In this ecosystem, crabs are the sole predators on whole clams, and may take them as 50% of their diets (Hines et al., 1990). Thus, factors affecting crab foraging success on clam patches have explained much about patterns of clam survivorship in the field (Lipcius and Hines, 1986; Eggleston et al., 1992). The other major predators on clams in the system are

fishes (spot, *Leiostomus xanthurus*; croaker, *Micropogonius undulatus*; and hogchoker, *Trinectes maculatus*) that only graze clam siphons (Hines et al., 1990).

Hypotheses that our novel biotelemetry system allowed us to test were as follows:

1. Aggressive behavior tends to occur mostly during feeding periods. The null hypothesis, that feeding and agonism are temporally independent, would be rejected if peaks in agonism co-occurred with peaks in feeding that had been observed in previous studies of free-ranging crabs (Nye, 1989).
2. Agonism reduces feeding activity in blue crabs. We expected that as crabs feed on patches, chemical cues (from clam flesh or hemolymph) would attract additional crabs. We predicted that as crabs congregated on prey patches, intraspecific agonism would rise and eventually interfere with foraging. Consequently, we expected that peaks of agonism would lag peaks of feeding. The null hypothesis, that agonism does not impair foraging, would be rejected if peaks in agonism occured after peaks in feeding activity.

2. Methods

2. *Study*

During the summers of 1991–93, we tracked a total of five free-ranging crabs, using ultrasonic telemetry in the Rhode River (38°51' N, 76°32' W), a 485-hectare subestuary of the central Chesapeake Bay (Fig. 1). The river is shallow (maximum depth ≈ 4 meters). Bottom substrate is primarily fine, silty mud with some patches of sand near shore, and was devoid of submerged aquatic vegetation at the time of our study. The Rhode River is mesohaline (annual range = 4–18 ppt), with summer salinities typically 12 to 18 ppt.

Crabs were collected by trap and otter trawl. Intermolt adult male crabs (> 140 mm carapace width) having all limbs were selected for instrumentation with telemetry transmitters. Prior to transmitter attachment, crabs were held in 2000 l outdoor tanks with flowing estuarine water at a depth of 10 centimeters, and observed periodically for about 48 h to verify health and vigor. Crabs were fed *ad libitum* with clams and frozen fish up until 24 h before they were fitted with telemetry transmitters.

2.2. *Telemetry system*

The telemetry system used during the summers of 1991–92 permitted us to monitor crab location while signaling the occurrence of one behavior (meral spread threat display) by an increase in the speed of the tracking pulse. These transmitters were derived from a design used to detect molting (Wolcott and Hines, 1990; Shirley and Wolcott, 1991). The multi-channel system deployed in 1993 relied on 8-bit digital encoding to telemeter simultaneously meral spread, feeding, and individual identification codes (Wolcott, 1995; Wolcott and Hines, 1996).

Multi-channel telemetry allowed us to test more sophisticated hypotheses about the

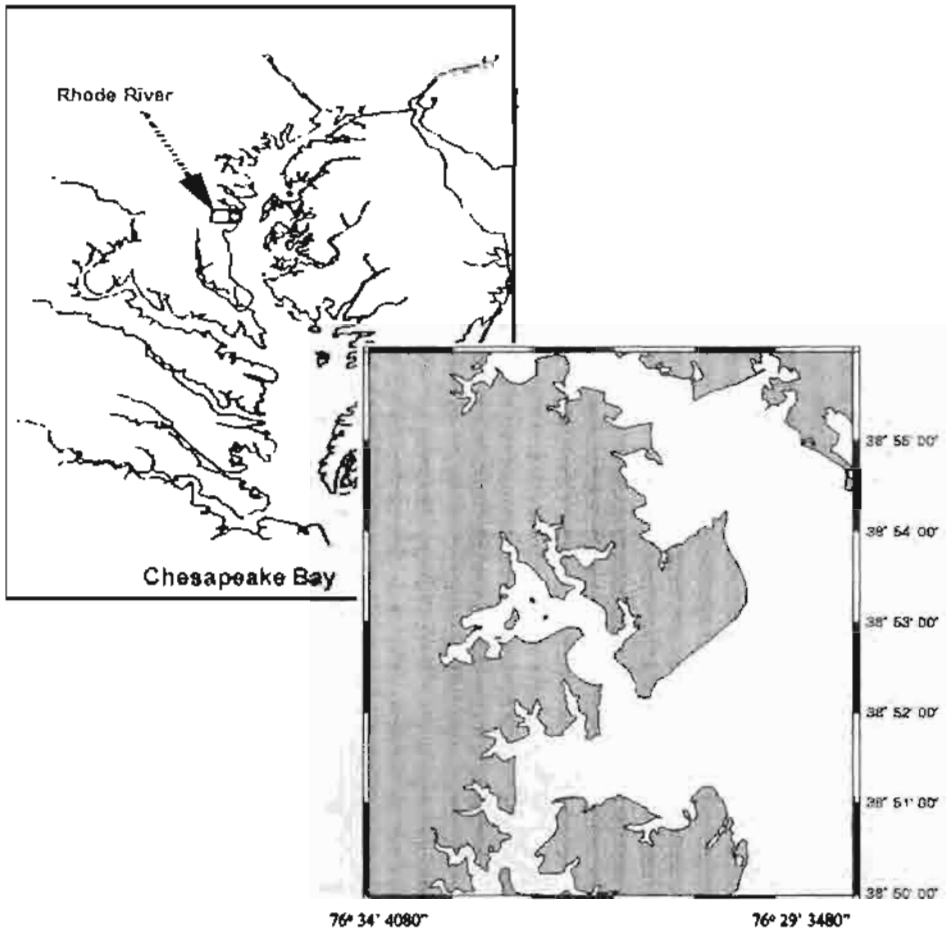

Fig. Chesapeake Bay map, with inset of the Rhode River study site.

direct impact of agonism on feeding of individual crabs. However, data from the multi-channel system were not always directly comparable to those from the single-channel system because reflections and refraction (especially when the water had a thermal gradient) could cause errors (false positives for meral spread or feeding) in the reception of the multi-channel signal. The transmitters signaled the onset or end of a behavior immediately, while continuing to transmit tracking pulses at a fixed interval. Consequently, we were able to screen for errors by disregarding records of meral spread/feeding that occurred at exact multiples of the tracking pulse, and by shortening any unreasonably long bites or threat displays to the longest previously observed in the laboratory or with the earlier telemetry equipment (1 s for a single bite, and 5 min for a single threat display). Because of this data editing, we considered activity estimates using the multi-channel data to be conservative, and therefore analyzed the two types of data separately as well as by pooling.

2.3. Preparation of telemetry subjects

Feeding was telemetered by sensing biopotentials of the crab's mandibular (chewing) muscle (Wolcott and Hines, 1989). Electrode sites were cleaned with acetone, drilled nearly through the calcified exoskeleton, and covered with a rubber membrane (dental dam) affixed with cyanoacrylate glue (Hysol® 2-C-500). Stainless steel electrodes (Teflon®-insulated No. 40 (AWG), diameter ≈ 0.008 cm) with an approximately 3 mm long, bared tip were inserted through the membrane, which prevented bleeding, and a second layer of rubber added as a waterproof covering. Flexible leads connected the electrodes to the preamplifier in the electronics package.

The meral spread threat display was signaled only when both chelae were extended, to distinguish it from other postures (swimming, feeding) in which extension of one chela is common, but extension of both is rare. This display was sensed with waterproofed magnetic reed switches fastened to the dorso-medial surfaces of the merus of each chela with dental dam and cyanoacrylate glue. On each carpus, we positioned magnets so that they would energize the adjacent switch when the chela was extended. The two switches were wired in series, closing the circuit only if both chelae were extended (Fig. 2).

The electronics were packaged in electrical sleeving, contoured to conform to the

Fig. 2. Photograph of crab outfitted with multi-channel transmitter, showing preparations to monitor feeding and threat display activity (meral spread). Right side of crab's 'face' (i.e., left side of photo): dental-dam patch, which is covering electrodes, is visible. On crab's chelae: reed-switches are secured to dorsum of each merus, and magnets to each carpus.

dorsal carapace (to minimize drag), and filled with corn oil to couple sound from the transducer to the water. Transmitters were lashed transversely on the dorsal carapace using No. 18 (AWG) copper wire twisted around the lateral spines. Single-and multi-channel transmitters weighed approximately 7 g and 15 g in water, respectively. These weights corresponded to roughly 5 to 10% of the weight of telemetered crabs.

Operation of completed behavioral preparations (transmitters on 'behaving' crabs) was verified in laboratory tanks. Crabs carried the transmitters without evidence of disturbance to routine behaviors such as feeding or locomotion in the laboratory. The crabs were then held in 15 gallon laboratory tanks, without food, for approximately 24 h before being released into the estuary.

2.4. Data collection

For continuous 96 h periods (06:00 Monday to 06:00 Friday), shifts of observers tracked transmitter-equipped crabs moving freely in the Rhode River, and recorded the time and location of behaviors. They worked from a small boat, using an ultrasonic receiver (Sonotronics® USR-5) to monitor the tracking pulses ($\approx$75 KHz) with omnidirectional hydrophones, and to map locations of crabs onto a chart of the river by triangulating with directional hydrophones.

Agonistic activity of three crabs was monitored using single-channel transmitters: Crab #1 (carapace width = 140 mm) starting at 06:50, July 22, 1991, until 06:50, July 26, 1991; Crab #2 (carapace width = 160 mm) from June 15 (06:00) until June 19 (06:00), 1992; and Crab #3 (carapace width = 186 mm) from August 10 (06:00) until August 14 (06:00), 1992. These transmitters signalled a meral spread display by increasing the frequency of the tracking pulse from 1 pulse/sec to 2 pulses/sec. Time, duration and location of these events were recorded manually by observers.

Simultaneous logging of both agonistic and feeding behaviors of two additional crabs depended on digital encoding that required a microcontroller-based interface and a lap-top computer. Crab #4 (carapace width = 145 mm) was tracked starting at 17:00, July 26, 1993, until 18:45, July 29, 1993; and Crab #5 (carapace width = 165 mm) from August 9 (11:00) until August 13 (06:00), 1993. Delays from the scheduled 0600 start time were caused by equipment malfunctions, and Crab #4 was caught on a baited line approximately 11 h before the track's scheduled end.

2.5. Data analysis

To verify that movements of crabs were qualitatively consistent with those from previous field tracking experiments (Nye, 1989; Wolcott and Hines, 1989, Wolcott and Hines, 1990; Hines et al., 1995), we mapped each crab's track onto a chart of the river. Quantitative comparisons were made by calculating velocity of movement (mean, SE, and range) for each crab and for the pooled data from all five crabs.

The mean activity (feeding and agonistic episodes) for each crab during a given hourly clock-time interval was calculated by summing activity during that interval over all study days, and dividing the sum by the number of study days. For each crab, we generally had observations for 96 hourly intervals (i.e., 24 hourly clock-time intervals x

4 study days). Activity measurements are presented as the percentage of time (out of an hourly interval) devoted to the activity.

To identify hourly clock-time intervals that had activity levels significantly above background level, we contrasted the mean activity level during each of the 24 clock-time hourly intervals against the grand mean of all hours. Hours that were significantly greater than background were defined as 'peaks', and are identified in Section 3. Pooled datasets across multiple crabs were used for the contrasts. We created these datasets by pooling data from the three crabs outfitted with the single-channel transmitter, from the two crabs outfitted with the multi-channel transmitter, and from all five crabs. Because of unequal variances among treatment levels (i.e., among hourly clock-time intervals), Satterwaite's Approximation was used to synthesize the denominator degrees of freedom and mean square error used in contrast F-tests (Satterwaite, 1946). As a secondary means of identifying peak periods of aggressive activity using the pooled dataset from all five crabs, we contrasted each hourly clock-time interval against every other interval (Duncan's Multiple Range Test, Duncan, 1955). The error term for both models included the variability due to hour and to individual crab.

Finally, we tested hypotheses regarding the relationship between agonistic activity and feeding in individual crabs outfitted with the multi-channel transmitter. To test whether feeding and the probable resultant aggregation of more crabs to the feeding site leads to increased agonism during a given feeding period (reflected by peaks in threat activity following shortly after peaks in feeding activity), we regressed hourly threat activity against the hourly feeding activity 1 or 2 h earlier (i.e., threat display activity lagged by 1 or 2 h versus feeding activity).

3. Results

3.1. Movement

Crabs moved in patterns similar to those observed in previous field tracking experiments, meandering on scales of 50 to 100 meters for several hours to days, but sometimes moving on a fairly constant course at rates exceeding 300 m/h. The data pooled over all five crabs yielded a mean velocity of 11.94 m/h (SE = 2.02), similar to the 12 m/h reported by Wolcott and Hines (1989). Mean velocity of individual crabs ranged from 0.77 to 36.23 m/h (Table 1).

Table 1
Mean hourly movement rate (m/h) of individual crabs

Crab ID #	Mean movement rate (m/h)	Standard error	Range
	14.26	3.14	0–150
	36.23	8.84	0–370.91
	4.43	0.93	0–33
4	3.47	2.08	0–150
5	0.77	0.45	0–30

3.2. Feeding activity

Feeding activity occurred in crepuscular peaks, consistent with observations from previous tracking studies. A total of 165 hourly observations were collected (i.e., where an observation is defined as the summation of activity within an hourly interval). Both crabs monitored with multi-channel transmitters were most active in early-to mid-morning and in the evening, with activity during the 05:00-06:00 interval (F-test; $F(1,117) = 5.16$, $p < 0.05$) and during the 19:00-20:00 interval (F-test; $F(1,117) = 3.82$, $p = 0.05$) well above background in the pooled dataset (Fig. 3). Crabs fed in areas where they meandered slowly for several hours.

3.3. Aggressive activity

Each of the five free-ranging crabs we monitored generally demonstrated a high intensity of aggressive posturing (meral spread) in the early-to mid-morning. All peaks in agonism observed in the three pooled datasets occurred during this time period, or (in

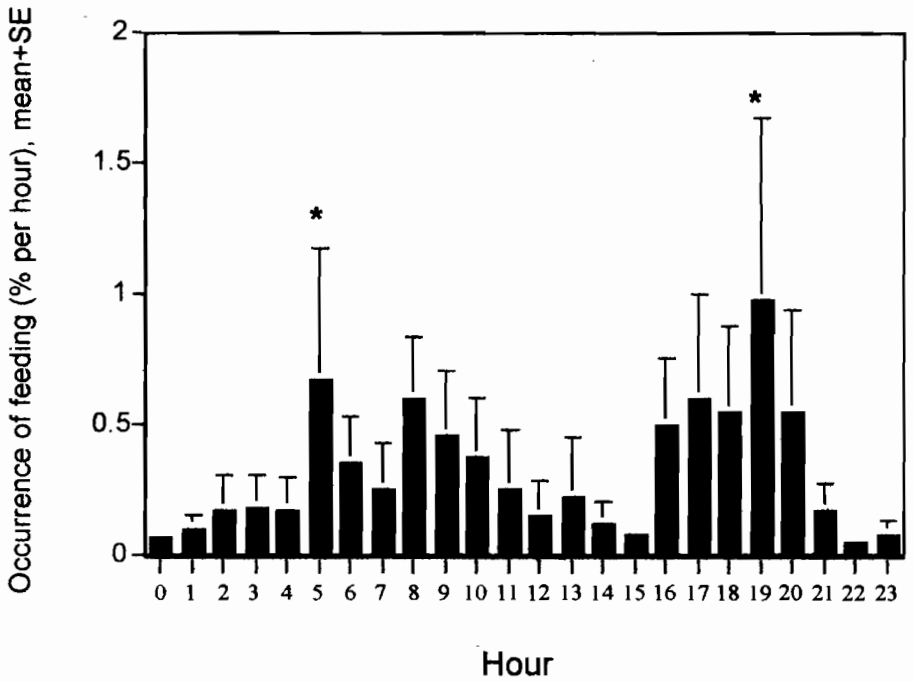

Fig. 3. Mean hourly occurrence of feeding activity (% of time in an hourly interval): data from multi-channel transmitter. Observations were made on two crabs, with each hourly interval assessed on 4 to 5 days for each crab. Vertical bars are mean + SE, where SE shows the variation of the two crabs' means around the grand mean. Asterisk indicates difference from the grand mean (grand mean = 0.37%/hour) is significant at 0.05 level (t-test). Each hour listed on the x-axis represents the hourly clock-time interval beginning with that hour (e.g., 6 represents the 6–7 AM interval).

the multi-channel dataset) during the early evening, suggesting that aggression is associated with feeding periods. Totals of 275, 165, and 440 hourly observations were collected with the single-channel, multi-channel, and combined telemetry, respectively. In analyses of data pooled from the three crabs with single-channel transmitters, periods of significantly increased threat activity, relative to the grand mean, occurred during the 06:00–07:00 (F-test; $F(1,203) = 7.30$, $P < 0.01$), 07:00–08:00 (F-test; $F(1,203) = 7.90$, $P < 0.01$), and 08:00–09:00 (F-test; $F(1,203) = 12.33$, $P < 0.001$) intervals (Fig. 4). During the 08:00–09:00 interval, crabs spent an average of 9.94% of their time in agonistic activity (i.e., mean of 5.96 min during this clock-time interval). Using data pooled from both crabs with multi-channel transmitters, significantly increased threat activity, versus the grand mean, appeared during the 09:00 –10:00 (F-test; $F(1,117) = 5.19$, $P < 0.05$) and 20:00–21:00 (F-test; $F(1,117) = 5.02$, $P < 0.05$) intervals (Fig. 5). Finally, when data from all five crabs were pooled, hourly measurements that were significantly above background emerged during the 07:00–08:00 (F-test; $F(1,320) = 5.46$, $P < 0.05$), 08:00–09:00 (F-test; $F(1,320) = 10.76$, $P = 0.001$), and 09:00–10:00 (F-test; $F(1,320) = 6.69$, $P = 0.01$) intervals (Fig. 6). During the 08:00–09:00 interval, crabs spent an average of 7.37% of their time in agonistic activity (i.e., mean of 4.42 min during this clock-time interval).

The threat display data pooled over all five crabs yielded a mean occurrence of 2.02%

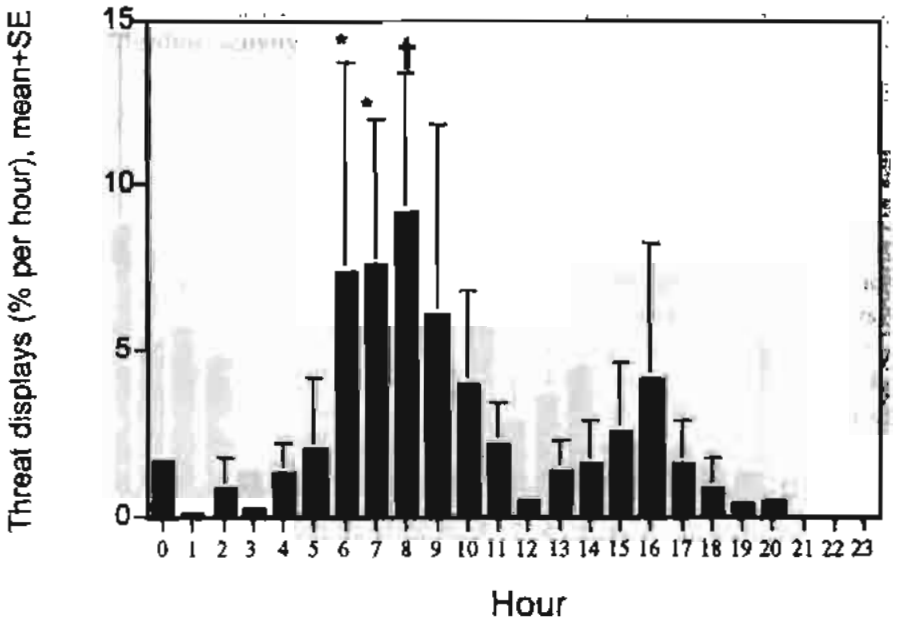

Fig. 4. Mean hourly occurrence of threat displays (% of time in an hourly interval): data from single-channel transmitter. Observations were made on three crabs, with each hourly interval assessed on 4 to 5 days for each crab. Vertical bars are mean + SE, where SE shows the variation of the three crabs' means around the grand mean. Asterisk indicates difference from the grand mean (grand mean = 2.3%/hour) is significant at 0.01 level, dagger at 0.001 level (t-test). Each hour listed on the x-axis represents the hourly clock-time interval beginning with that hour (e.g., 6 represents the 6–7 AM interval).

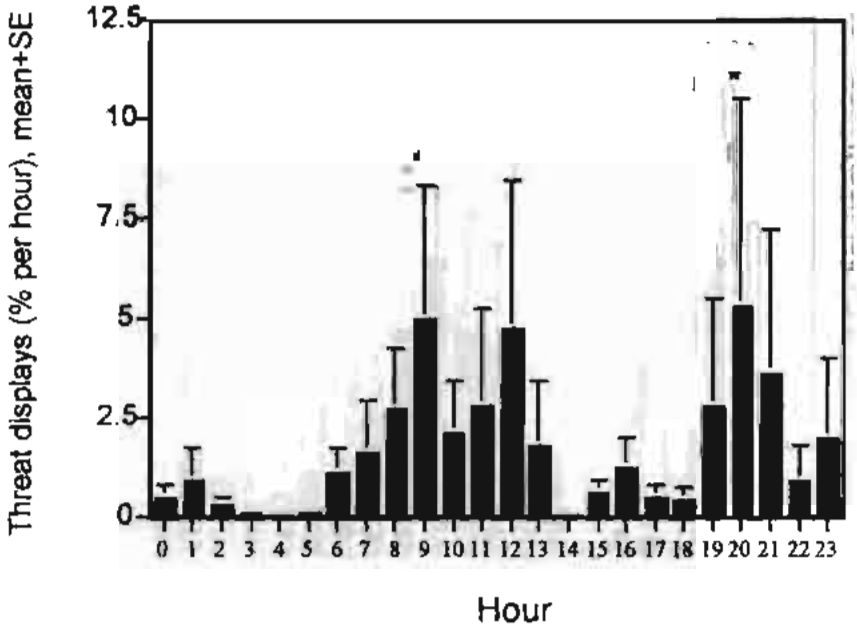

Fig. 5. Mean hourly occurrence of threat displays (% of time in an hourly interval): data from multi-channel transmitter. Observations were made on two crabs, with each hourly interval assessed on 4 to 5 days for each crab. Vertical bars are mean + SE, where SE shows the variation of the two crabs' means around the grand mean. Asterisk indicates difference from the grand mean (grand mean = 1.67%/hour) is significant at 0.05 level (t-test). Each hour listed on the x-axis represents the hourly clock-time interval beginning with that hour (e.g., 6 represents the 6–7 AM interval).

of the total time that crabs were observed (i.e., mean of 1.46 min per h). Agonism intensities among individual crabs were highly variable (Table 2). The maximum hourly occurrence of individual crabs ranged from 2.43% to 39.87% of observation time (i.e., 1.46 to 23.92 min per h). Within individuals, the amount of agonistic activity also varied greatly throughout any given day, with hourly occurrences of agonism often near zero from midnight until dawn and at the highest values in early-to mid-morning and/or in the late afternoon through early evening.

3.4. Relationship between agonism and feeding

Peaks of threat display activity often lagged the peaks of feeding activity in crabs that we monitored with multi-channel transmitters. This trend is illustrated qualitatively in Fig. 7. Fig. 7 overlays the feeding and threat display activity presented in Figs. 3 and 5, respectively. (To present both types of observations on the same scale, we converted them to percentages of total activity occurring during each hourly clock-time interval, i.e., as distinguished from percentage of a clock-time interval spent in the activity). This pattern is consistent with continuing aggregation of crabs during feeding periods, resulting in more frequent aggressive interactions and decreased ingestion of prey. Further, we reasoned that the most extended bouts of feeding (presumably on the best

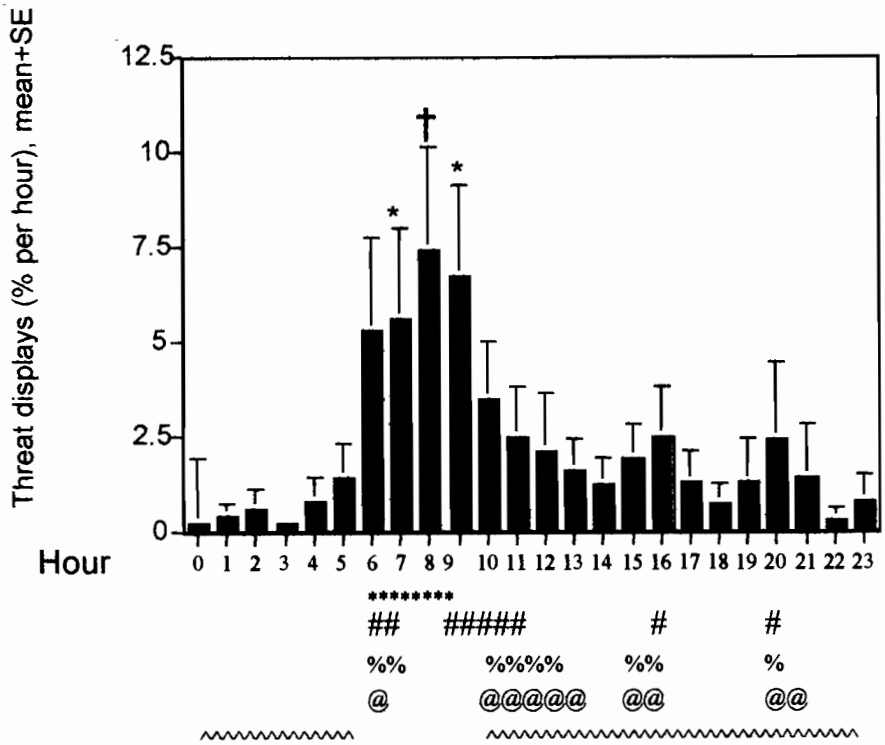

Fig. 6. Mean hourly occurrence of threat displays (% of time in an hourly interval): all crabs. Observations were made on five crabs, with each hourly interval assessed on 4 to 5 days for each crab. Vertical bars are mean + SE, where SE shows the variation of the five crabs' means around the grand mean. Asterisk indicates difference from the grand mean (grand mean = 2.02%/hour) is significant at 0.05 level, dagger at 0.01 level (t-test). Means with the same symbol (shown under x-axis) are not significantly different ($p > 0.05$) from each other (Duncan's Multiple Range Test). Each hour listed on the x-axis represents the hourly clock-time interval beginning with that hour (e.g., 6 represents the 6–7 AM interval).

Table 2
Mean hourly agonism occurrence (% of time spent in meral spread posture) of individual crabs

Crab ID #	Mean agonism occurrence (% of hour spent in meral spread posture)	Standard error	Range
	5.15	0.91	0–39.87
	0.38	0.09	0–4.08
	1.18	0.48	0–35.42
	0.18	0.05	0–2.43
	2.88	0.68	0–36.73

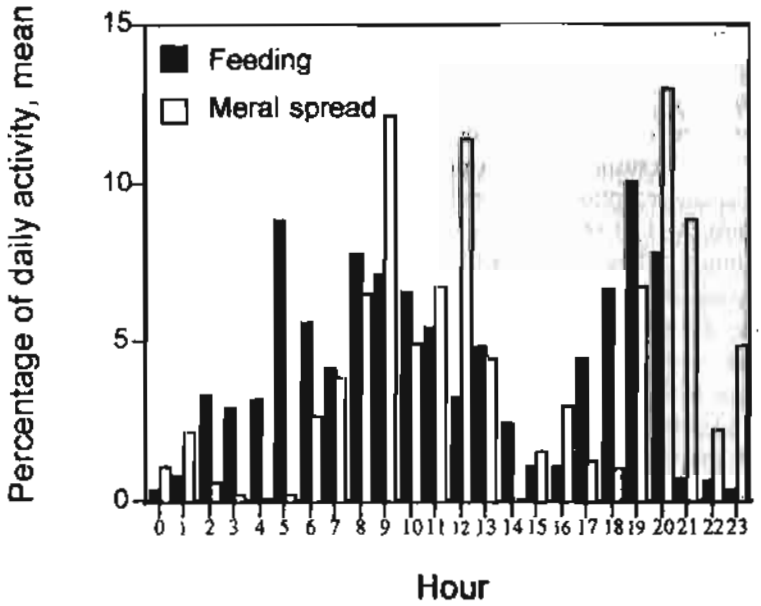

Fig. 7. Mean percentage of total daily feeding and agonistic activity that occurred during each hour: data from multi-channel transmitter. Observations were made on two crabs, with each hourly interval assessed on 4 to 5 days for each crab. Each hour listed on the x-axis represents the hourly clock-time interval beginning with that hour (e.g., 6 represents the 6–7 AM interval).

prey patches) would draw in many other crabs and ultimately be followed by the highest occurrences of fighting among crabs. However, quantitative tests indicated only a weak correlation between the amount of feeding that occurred in a given hourly interval and the intensity of agonism that occurred in the hourly interval 1 to 2 h later (F-test, $F(1,161) = 4.70$, $P < 0.05$, $R^2 = 0.03$; and $F(1,161) = 23.41$, $P < 0.0001$, $R^2 = 0.13$, respectively). The very low correlation coefficients were perhaps due to the fact that lag times between feeding and agonism peaks varied widely among feeding periods.

4. Discussion

Blue crabs exhibited a diel pattern of agonism, with morning and sometimes evening peaks in threat display. Morning periods of increased agonism (7–9 AM) tended to come later than periods of increased feeding (6–7 AM) identified in past telemetry studies (Nye, 1989). Simultaneous telemetry of both behaviors indicated that periods of increased agonism and feeding often overlapped. Feeding activity tended to wane as threat activity increased, consistent with the hypothesis that aggressive interference impairs foraging. We infer that crabs continue to aggregate onto clam patches during feeding periods, although we did not have sufficient telemetry data to test this explicitly. Crabs telemetered in previous experiments tended to remain moving slowly for hours in

areas where they fed (Nye, 1989). Crabs might enter a clam patch in response to waterborne cues (e.g., amino acids from torn clam flesh) and then meander within the patch for multiple feeding bouts. In the murky water of the Rhode River, crabs are predicted to rely heavily, if not exclusively, on chemosensory foraging. Blue crabs possess sensitive olfactory receptors, especially on the antennules, and respond to concentrations of crushed clam extract as low as 10^{-15} M (Pearson and Olla, 1977). They use chemoreception for foraging in laboratory studies (Zimmer-Faust, 1989; Zimmer-Faust et al., 1995). In field experiments, they appear to detect additional prey patches within a radius of 10 to 15 m, displaying shorter patch visits (Clark, 1997) and better foraging success than when feeding on isolated patches (Clark, 1997; Hines, Terwin, and Thrush, unpublished data on file at SERC). A related brachyuran (*Scylla serrata*) also acts as though it follows scent trails in the field, making directional 'sprints' up-current (Hill, 1978).

The time-course of crab aggregation onto patches during feeding periods could account for the observed variability in time-lags between the peaks of feeding and of threat displays (or the absence of any burst of agonism). When the density of crabs in the vicinity of a patch is high, feeding by the first successful forager could quickly attract enough additional crabs to cause increased agonistic interactions and subsequent interference with foraging. Conversely, in an area more sparsely populated with crabs, aggregations dense enough to cause interference presumably would occur more slowly if at all.

An alternative explanation for the time-lag between maxima of feeding and aggression is based on diel changes in light level. If the meral spread threat display were primarily visual, its delay after the early-morning feeding peak could simply reflect its increasing effectiveness as light intensity rises. However, this cannot account for the lag of peak threat intensity after the feeding peak in the afternoon and evening, when light intensity is declining, nor for the variation in time-lag between feeding and agonism peaks. It is difficult to imagine that visual displays alone are very effective in waters as turbid as the Rhode River, where nearly complete darkness prevails at depths below 1 meter, and it seems possible that displays in blue crabs also include a chemical component, as has previously been suggested – if not conclusively demonstrated – in other decapods (Hazlett, 1985; Smith and Taylor, 1993).

The diel pattern of crab foraging and attendant agonistic interactions may be a vestige of foraging behaviors adaptive for crabs in less turbid waters. In systems where visual foraging is important, crepuscular foraging activity is often selected (Howard, 1989). At low light levels, crabs (with their acute sensitivity to light–dark contrast) might detect siphons of their bivalve prey, but be undetectable to their predators (e.g., wading birds). Although this bimodal foraging pattern confers no obvious advantage to crabs in the Rhode River, the local crab population may experience sufficient gene mixing with other estuaries for this behavior to persist (McMillen-Jackson et al., 1994).

Blue crabs spent an overall mean of roughly 2% of their time in agonistic activity, in line with that reported for other arthropods contesting resources (e.g., fiddler crabs and spider mites competing for mates, and fiddler crabs competing for burrows) (Christy, 1988; Enders, 1993). That blue crabs spent up to nearly 40% of some hourly observation intervals in meral spread posturing, among the highest occurrence of threat display

reported for arthropods, underlines the bellicose nature of the species. This amount of aggressive activity seems especially impressive given that the summers of 1991 through 1993, when experimental subjects were tracked, were seasons of low crab densities in the Rhode River (approximately 0.01 to 0.1 crab/m^2). For comparison, densities in more plentiful summers can reach 0.4 to 0.5 crab/m^2.

Although the temporal and spatial pattern of agonism was similar among crabs, the percentage of time spent in agonistic activity varied widely. The maximum percentage of time spent in agonistic encounters within an hourly interval ranged from 2.43% to 39.87% among crabs. The degree of variability that we observed was not unexpected given the high individual variability previously observed among blue crabs in a variety of other behaviors including movement, feeding, and molting of free-ranging crabs in the field, as well as in agonistic activity in large field enclosures (Nye, 1989; Shirley et al., 1990; Clark, 1997). One factor that can account for differences in threat display activity is the status of individuals within a dominance hierarchy. American lobsters (*Homarus americanus*), which are relatively sedentary compared with blue crabs, demonstrate recognition of individual conspecifics and dominance status in contests for home sites (Atema, 1995). Stomatopods (*Gonodactylus bredini*) also form dominant-subordinate relationships, which affect agonistic behavior (Dingle, 1972). However, repeated encounters among individual blue crabs, sufficient to establish a dominance hierarchy, are unlikely given the high mobility of these crabs. A second possible explanation for the variable occurrence of threat display is competitive 'class' of an individual. In a range of brachyurans, anomurans, and macrurans, the outcome of aggressive contests can be predicted by factors such as size, sex, hunger status, and molt stage of individuals (Dingle, 1983). In fact, large blue crabs generally dominate over smaller ones, and males over females (Jachowski, 1974). However, given that all of our telemetered crabs were large (140 mm carapace width) intermolt males, potential for a class effect is low. It seems most likely that the variable occurrence of threat displays reflects spatial and temporal differences in crab abundance, although no quantitative correlation emerged between amount of agonistic activity and monthly crab density in the Rhode River as estimated from trawl catch. However, trawl estimates are averages and do not account for local differences in conspecific densities experienced by telemetered crabs.

Factors that determine the foraging success of blue crabs may have far-reaching impacts. Blue crabs have important direct predatory effects on the infaunal community of the Chesapeake Bay, generally reducing abundance of bivalves as well as overall diversity of the benthos (Holland et al., 1980; Hines et al., 1990). Crabs also have indirect effects on community structure, destabilizing the sediment while digging for prey (Hines et al., 1990) and consequently favoring deposit-feeding animals at the expense of suspension feeders (Woodin, 1976). Factors, such as sediment type and prey density, that affect success of crabs foraging on bivalves in the laboratory have already been shown to explain much about bivalve survival in the field (Sponaugle and Lawton, 1990; Eggleston et al., 1992). Crabs at high density seem to forage poorly and to disperse throughout a patchy habitat presumably minimizing costly agonistic encounters (Micheli, 1995). Factors such as crab density and distribution of prey patches probably interact to affect crab foraging success and could ultimately explain more about patterns

of bivalve abundance and benthic community diversity. For example, if crabs normally disperse among prey patches thereby reducing agonistic encounters, they probably forage less successfully when crowded onto relatively isolated patches. Thus, the highest prey abundances and diversity levels might be expected on such isolated prey patches. Indeed, a recent study of crabs foraging in large field enclosures suggests this (Clark, 1997). As another example, if crabs are frequently moving among neighboring prey patches to sample patch quality (consistent with optimal foraging theory) and/or to disperse from areas of high predator density, they probably partition their foraging efforts among multiple patches rather than concentrating efforts on one patch until that patch is depleted. Thus, the abundance and diversity of the benthic community among non-isolated bivalve patches in one locality would be expected to be similar at any given time, rather than being a mosaic of widely differing abundances and diversities. Ultimately, if density of blue crabs and distribution of prey patches interact to affect the foraging behavior of crabs and subsequent survival of bivalve prey, we may expect our findings to generalize to crustacean-bivalve interactions in many other systems (Sponaugle and Lawton, 1990; Hsueh et al., 1992; Barbeau and Scheibling, 1994). Our study, the first to telemeter agonistic activity in a free-ranging marine invertebrate, has given us insights into blue crab behavior that have strong implications for benthic community structure, and has led us to further explore the effects of crab density and distribution of prey patches on crab behavior (Clark, 1997).

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