Field Observations of Social Behavior, Shelter Use, and Foraging in the Lobster, *Homarus americanus*

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Abstract. Over a three-year period (1978–1981) behavioral observations of the lobster, *Homarus americanus*, were made by snorkeling in a shallow cove. Three hundred and thirty-four (334) animals were individually marked and this was the only time they were disturbed. In summer, the resident population numbered about 30 animals. The size composition, activity patterns, and habitat use of this population are described in a companion paper (Karnofsky *et al.*, 1989).

Shelters are of prime importance in the life of the lobster. Lobsters spent most of their time in shelters, leaving only at night. They dug shelters under eelgrass, rocks, and boulders; shelter locations appeared clustered. Some animals changed shelters frequently whereas others occupied the same shelters for up to 10 weeks. Premolt behavior was characterized by multiple shelter use. Cohabitation in the same shelter occurred only during periods of pair formation: when a mature female shared a male's shelter prior to and following her molt. We report the only field evidence for such courtship cohabitation.

Food foraging behavior was rare (0.35 instances/observation hour); most foraging involved live prey. Similarly, intraspecific interactions were surprisingly infrequent (0.2 instances/observation hour) and most, by far, did not involve physical contact. Although puncture wounds suggested intraspecific aggression, actual observations of escalating fights were rare. Premolt residents were involved in 65% of the interactions observed. In 70% of the interactions the larger animal won. However, smaller males and females could successfully defend their shelters against larger females. We report results from three homing experiments. The results suggest that much of the time that resident lobsters spend outside

shelters is used to remain familiar with their constantly changing physical and social environment.

Introduction

Most studies on individual behavior of the lobster, *Homarus americanus*, have been made under tightly controlled laboratory conditions and most were concerned with aggressive behavior, dominance, and shelter use (Scrivener, 1971; reviewed by Dunham, 1978; 1987; Atema and Cobb, 1980; Sastry and Ehinger, 1980; Finley and Haley, 1983). Controlled experimental situations are necessary when looking into behavioral mechanisms. However, such experiments cannot tell how relevant this behavior is in the behavioral ecology of a lobster. Without further knowledge of context the results from controlled studies cannot be interpreted. Feeding behavior of *Homarus americanus* has been observed in the laboratory (McLeese, 1970; Derby and Atema, 1982; Devine and Atema, 1982), but not in the field. Controlled and manipulative field studies on this species have addressed aspects of shelter use and population structure (Stewart, 1972; Richards and Cobb, 1986; Hudon, 1987). Some field studies have indicated possible territoriality in shelter use (Ennis, 1984).

Nonmanipulative studies in semi-natural environments in large aquaria circumvent some of the disadvantages of highly controlled environments and manipulative field studies. They have provided detailed knowledge about aggressive behavior, feeding behavior, courtship, pair formation, and the timing of molting and mating (Stein *et al.*, 1975; Atema *et al.*, 1979; Karnofsky and Price, 1989). However, even these conditions remain artificial, as it is impossible to imitate realistic emigration and immigration, the threat of predation, and the fluctuations in climate, shelters, and food. Controversies

concerning the lobster's social behavior, such as the existence of a dominance hierarchy, territorial defense, or the incidence of escalated fights, and theories about mate selection, habitat utilization, and competition cannot be addressed without knowledge of behavioral relationships in the natural context. Only field studies can provide answers to these questions. To minimize human bias and misinterpretations due to human interference, a first study of this sort must be observational and nonmanipulative.

For such reasons we began a three-year (1979–1981) field study of *Homarus americanus*. The first year and a half we developed methods of marking and observation that would maximize the yield of data and minimize the interference with the animals' natural behavior. During the last 19 months we collected data in a standardized format. The results are reported in two papers, the first, a quantitative description of the population structure of lobsters found in this shallow habitat (Karnofsky *et al.*, 1989). This second paper is a description of the behavioral activities of that population.

Since the purpose of this behavioral study was to learn how lobsters live under natural conditions, undisturbed by human manipulation, we chose a site away from human activities and fishing: there is no lobstering in such shallow areas. For the same reason we limited our own manipulation to the absolute minimum necessary: individual marking of lobsters and their shelters. We were particularly interested in various aspects of shelter use, feeding, and social behavior. Because of our studies of courtship and pheromones in the laboratory (see Atema, 1986, for review) we were also interested in field evidence of courtship, male and female dominance orders, and mate choice strategies. These field data have allowed us a first glimpse of the natural behavior of this species. This information on behavior in an unrestricted population serves as a reference source against which results from manipulative field studies and controlled laboratory studies can be measured.

Materials and Methods

The study area was a shallow cove along a tidal channel on the southern edge of Buzzards Bay, Massachusetts (Figs. 1, 2). The substrate was divided between eelgrass beds, sandy spots, and an area called the "rock garden," containing small boulders covered with macroalgae. At low tide, water depth ranged from 0.3 to 1.5 m. Throughout the seasons water temperature ranged from 0 to 24°C.

All animals over 50 mm carapace length (CL) were marked with numbered claw bands and "pleural clips" (cut ventral tips of abdominal pleura) allowing recovery of both molt shells and molted animals. Bands were placed behind the dactyl so as not to interfere with claw use. Shelters were marked by placing numbered stones near them. To minimize interference with lobster behavior no other manipulation was performed.

The lobster population consisted of individuals ranging in size from 23 to 92 mm CL and most were subadults (<70 mm CL). The male-female sex ratio was approximately 2. Residents were defined as animals observed on more than one night; transients were defined as animals seen only during one night. During summer about 30 animals 50 mm CL and larger resided in the study area, while about 15 of these probably overwintered there. Lobsters, mostly smaller animals, were found even in areas with less than 0.5 m water depth. Turnover was considerable although some animals remained present for at least 13 months (Karnofsky *et al.*, 1989).

Observations were made during the nocturnal activity period using snorkel, a dim flash light, and a note sheet. Slow and gentle movements such as floating slowly over the study area using flippers or pulling ourselves along rocks caused no obvious changes in lobster behavior although occasionally the edge of a flashlight beam would startle them. Whenever possible we avoided shining the beam directly toward the lobsters. During most observations we scanned the area noting each animal's activities and location when encountered. The central study area was surveyed regularly (once or twice per observation night). Sometimes an observer would follow an individual animal for a longer period (a few minutes to an hour). Instances of cohabitation, agonistic interactions, and feeding were observed in more detail. Observation frequency ranged from 1–4 h per night, 1–6 nights per week, depending on temperature and visibility, totalling 333 hours of observation. Further details are given in Karnofsky *et al.* (1989).

Three homing experiments were conducted in September 1980. These were the only exceptions to the nonmanipulation rule. For these a battery pack with a periodically flashing, light-emitting diode was attached with cyanoacrylate glue to the part of the dorsal carapace that lobsters are unable to reach and groom with their walking legs. The two lobsters used were long-term residents with known and stable burrows. They were caught near their homes and brought to a boat dock where the pack was attached; this procedure took about 30 min. They were then released from the dock and followed by snorkeling without lights. For the first trials (7 Sept.) we used a 56-mm CL male who consistently occupied a shelter in the rock garden. For the second trial (16 Sept.) we used a 51 mm CL female whose shelter was in the same general area. For the third trial (23 Sept.) the male from the first trial who had lost his pack a few days after the first trial was again caught and refitted with a new pack.
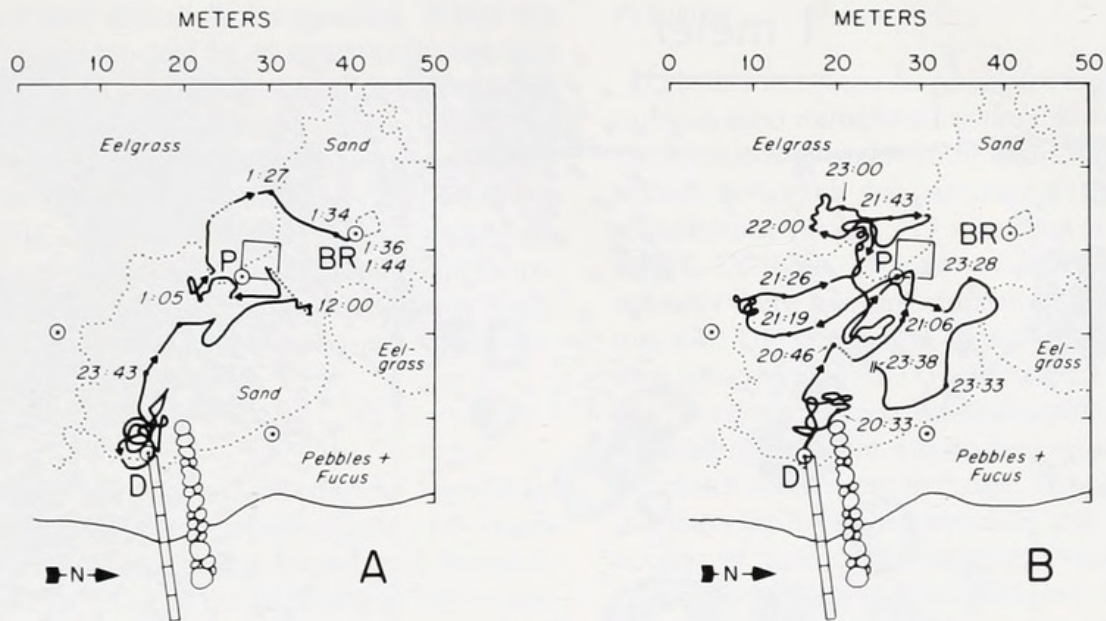
Figure 1. Detail of the field site map showing homing tracks of two lobsters, both stable residents of shelters near BR. A. On 7 September, a 56-mm CL male was released at the dock (D) at 23:24 h; he returned home (near BR) in 2 h, 12 min and remained there for at least 8 min, when observations were terminated; he continued to use his home shelter for several more weeks. B. On 16 September, a 51-mm CL female was released at D at 20:28 h; she did not return home (near BR) in the observation time (3 h, 10 min), but was found there the next day. She continued to be a stable resident in her home shelter. Dotted line: track lost. P indicates the 4 × 4 m chain link plot also seen in Figure 2. Circled points are fixed locations from which maps were drawn by triangulation.

Results and Discussion

In an attempt to determine if the animals were disturbed by our manipulations during marking, we compared the amount of time a lobster remained in the study site if it was caught at its shelter entrance *versus* caught when away from its shelter; we assumed that being caught near the shelter might pose a greater threat than being caught elsewhere. Disturbing the lobster near its shelter did not change the probability of its remaining in the study site nor the length of its stay (Chi-square, $P > 0.05$, d.f. = 369). In two cases animals involved in pair formation prior to mating (see *Courtship*) were caught and marked. In both cases the animals continued cohabitation without any obvious disturbance. Also, resident animals fitted with battery packs for homing studies continued to live in the same shelters. We concluded that our marking did not interfere seriously with lobster behavior.

Shelter use

In this shallow habitat, shelter appears to be critical since all animals spent much time inside shelter. During the day no lobsters were observed outside shelters. At night they were often seen bulldozing sand and debris out of their shelters, especially following storms. Eelgrass shelters almost always had two openings: one major entrance and a smaller "escape door." This has been seen

in a variety of experimental and observational studies (Cobb, 1971). The number of entrances of rock shelters was more difficult to determine.

Lobsters would often barricade entrances to their shelters with a variety of objects, but particularly rocks, which they pushed or pulled with their (closed) claws, walking legs, and maxillipeds. Often such shelters would remain closed for up to two weeks. This may be related to molting as seen in the laboratory, where lobsters have been observed barricading their shelters for periods centered around their molt (unpub. obs.)

For the 66 molts recorded in the field we analyzed shelter-use in 2-week blocks prior to each molt date. The average number of different shelters occupied by a premolt animal increased steadily from 1, during the period 7–8 weeks before the molt, to 1.9 during the period 2 weeks before the molt. Moreover, during the early (7–8 week) premolt period, only 7 (10%) of the animals were seen in 3 or more shelters; this number increased to 21 (33%) during the 2-week period just prior to molting. The increased number of shelters frequented 1–2 weeks prior to molting may reflect increased aggression, in addition to increased activity seen in premolt lobsters (Tamm and Cobb, 1978; Atema *et al.*, unpub.). We speculate that spending time in several shelters may make a lobster's place of molt less obvious to competitors and discourage other lobsters from inhabiting the immediate vicinity.
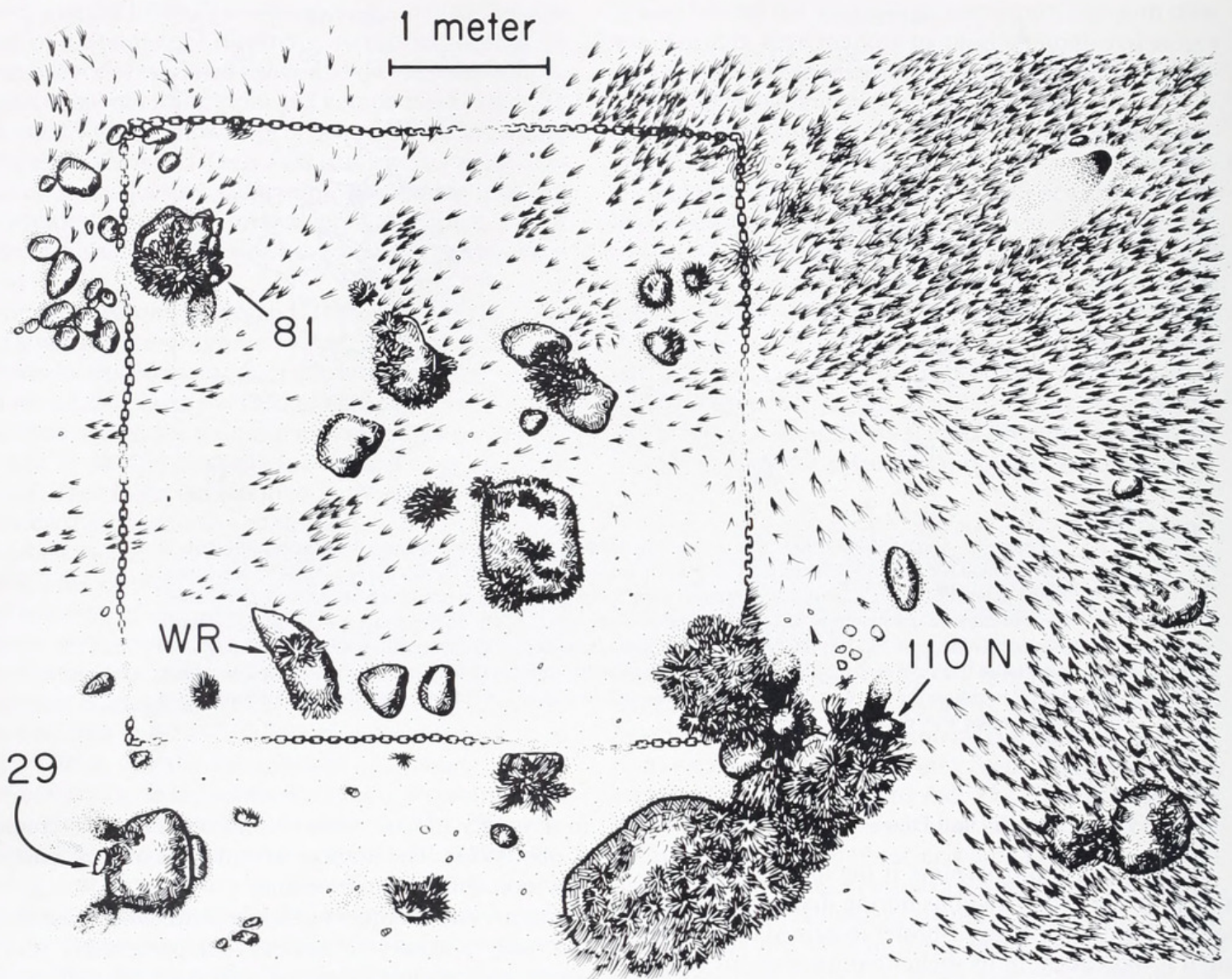
Figure 2. Further detail of field site showing lobster shelters dug in eelgrass (top right, unmarked) and under rocks. Many larger rocks were covered with macroalgae. Shelter #29 was a mating shelter in 1979; its resident male evicted the resident male of shelter #110N. Courting females often stood near WR from where they made approaches to #29. A lobster living in shelter #81 rarely emerged and did not interact with other animals. Chain marks area 4 × 4 m.

There were individual differences in shelter fidelity: some residents were rarely observed away from their shelters and occupied the same shelter consistently for several weeks or even months (n = 34), whereas others were never seen in any shelter (n = 26). Residents who were never seen in a shelter were also rarely seen in the site (an average of only 2–3 times); they must have had shelters just outside the observation area, because no animals were seen during the day. Ennis (1984) also reported differences in shelter fidelity.

Except for mated pairs, lobsters lived alone in shelters. Shelters appeared to be clustered (Karnofsky *et al.*, 1989: Fig. 1). Substrate features such as scars in the eelgrass, where it is easy to start digging under the roots, and rocky areas where shelters can be dug out under the rocks, may have encouraged clumping. Substrate features such as large boulders could also act as natural barriers setting apart shelter openings that were actually close in distance. The concentration of shelters in the rock garden could be explained by the large number of suitable rocks to burrow under. However, given that there were many rocks that were not used, and others that were used and then abandoned at some distance from the main shelter concentration, a social reason for shelter clumping seems possible. In the first figure in Ennis (1984) one can also observe shelter clumping, but it is unknown if this is related to habitat features or social behavior.

Lobsters seemed to have a good knowledge of their environment. When chased, as would happen occasionally for marking purposes, they would "tail flip" backwards

directly toward and into a shelter opening. When the nearest opening was blocked by an observer the animals would tail flip into an alternative shelter or hiding place (this behavior has also been seen in the spiny lobster *Panulirus*). For example, the dominant male of shelter #29 could walk 5 m directly toward shelter #110N and evict the male (see Fig. 2). Females at WR (Fig. 2) walked directly to #29, 1.5 m away. Since accurate vision is unlikely (Fine-Levy, unpub. obs.), such observations imply that lobsters know their physical environment, as do various insects (Burk, 1988).

Homing

To gain further insight about the lobsters' knowledge of their physical environment, we conducted a few short-range homing experiments. Upon release from the dock, both the male (Fig. 1A) and the female (Fig. 1B) turned a few circles and meandered about the release site; both animals left in the general direction of their homes; both animals began to turn back in the area halfway to their home. The male turned a large loop through the eelgrass area and, upon leaving the grass, headed straight for home over sand. The female did not return home for over 3 h. The next night her back-pack was found detached but flashing in front of her home where she was also seen. The second time the male was released from the dock he went into a nearby shelter for 20 min and then disappeared; he could not be located despite an extensive search. The following night he was seen in the rock garden, having recently molted. On the third night the pack was found still attached to the molted carapace, flashing in front of his former home. Apparently the lobster had molted in his home shelter and was subsequently evicted (as is usual for newly molted lobsters in the laboratory, unpub. obs.). The next occupant then probably pushed the molt carapace out. In all three homing trials the lobsters returned to their home shelters within 24 h of capture, and probably between 2 and 6 h (*i.e.*, well before sunrise), since in this shallow site lobsters were never observed out of the shelter during the day. Our homing trials not only showed familiarity with the environment but also the importance of the home shelter: the male who molted within 24 h of the homing trial returned to his shelter for molting rather than staying in the closest unoccupied shelter.

Long-distance homing in *Homarus americanus* has been shown using tag-recapture methods (Pezzack and Duggan, 1986). Over a period of months lobsters were recaptured more than 100 km from the tagging site and then subsequently were captured again at the tagging site. However, these animals did not return to a particular shelter. Ennis (1984) described evidence for homing when a lobster that had been absent for some time was again seen in a burrow in which it had been seen earlier.

Foraging

Lobsters were seen searching for food as well as killing, carrying, and manipulating prey. However, considering the hundreds of observation hours, the number of food-related behaviors was surprisingly low. Over the 19-month study period, 117 instances of foraging were observed. Of these, 77 involved marked animals; the remainder were unmarked animals, mostly less than 50 mm CL. The proportion of males and females that were seen foraging (M63:F37) reflected the higher proportion of males in the population (Karnofsky *et al.*, 1989).

Foraging behavior was divided into four categories: (i) attacking or carrying live prey, (ii) carrying dead prey, (iii) carrying molt shell remains, and (iv) miscellaneous actions of unknown nutritional value. Live prey was much more common than dead prey. Of the 44 instances of attacking or carrying live prey, 14 attacks were not successful. Live prey items included snails (*Littorina littorea*), crabs (*Callinectes sapidus, Carcinus maenas, Ovalipes ocellatus,* and *Libinia* sp.), hermit crabs (*Pagurus* sp.), molluscs (razor clams, *Ensis americanus, Modiolus modiolus, Crepidula fornicata,* and *Placopecten irradians*), fish (sandlance, *Ammodytes* sp.), and polychaete worms (*Nereis vulgaris*). Preference for live prey was found previously (Squires, 1970; Weiss, 1970; Miller *et al.*, 1971). Lobsters were seen carrying dead prey in eight instances, including old fish carcasses used to bait traps and the remains of juvenile silversides (*Menidia menidia*) after bluefish attack. One lobster was seen manipulating a pork bone. Carrying molt shell remains, both of lobster and crab, was observed 19 times. Miscellaneous actions of unclear nutritional value were observed in 46 instances. These actions included digging, shell and pebble manipulation, probing with dactyls, and manipulations of algae and blades of eel grass.

Lobsters spent much time combing through various types of algae. They may have been gleaning small invertebrates. Although there is no strong evidence that they digest or feed on algae, lobster stomachs do contain algae (Herrick, 1911; Squires, 1970; Weiss, 1970; Ennis, 1973) and improved growth and survival of lobsters maintained in the laboratory have been shown when their diet includes small amounts of the alga, *Ascophyllum* sp. (Leavitt and Aiken, pers. comm.).

Some observations suggest that lobsters may actively hunt for buried sandlance. In fall, lobsters were seen feeding on sandlance that were half buried in the sand. Two weeks earlier, four lobsters had been seen digging large craters in open sand flats. The lobsters first dug down in the sand to a depth of about 10 cm and then continued to plow forward. Perhaps they were digging for buried fish that we could not discern.

Food burial as described by Smith (1976) and in natu-

ralistic tanks (Atema and Leavitt, unpub.) was not seen during the study. Diet appeared to change with food availability. Lobsters continued to feed at low temperatures (5–10°C) well into the fall.

Agonistic interactions

Despite the lobster's reputation for being aggressive, only 71 instances of intraspecific interactions were observed (0.2 instances per observation hour). The interactions involved 52 animals, of which only 4 were transients. In most encounters, no physical contact occurred; only 5 (7%) included high level aggression such as "scissor, snap, attack, lunge" (definitions in Atema and Cobb, 1980) and 13 (18%) resulted in "tail flip." No wounds were inflicted. In a 30 m round pool tank with a population density similar to the rock garden, 6% of the interactions involved high level aggression (Karnofsky and Price, 1989). In a 7 m narrow tank with a higher population density, 17% of the interactive units recorded were high level aggression (Atema *et al.*, unpub.). In the same tank, Cowan and Atema (unpub. obs.) observed even higher levels of aggression when several mature males were present. The hypothesis emerges that most high-level aggression is related to the mature males attempting to establish a mating shelter and local dominance (see further evidence below and in following sections).

The ratio of males and females involved in agonistic interactions (2.2) was similar to the sex ratio (1.8) of the whole population. The number of *inter*sexual (19) and *intra*sexual (20) interactions were equal, and not significantly different (Chi-square, $P > 0.05$) from the expected value (22:17) given the sex ratio of the population. The larger animal won in 70% of all interactions. This has been well documented in laboratory experiments (review Atema and Cobb, 1980). Size-based dominance is characteristic for lobsters, but sex differences are important exceptions (see below).

Many interactions (24/71) involved animals defending their shelters, often successfully (16 successful defenses). Larger animals were usually successful in evicting smaller animals, but smaller ones were able to defend their shelters as well; in six (5M, 1F) of the nine instances in which smaller lobsters won a shelter defense, the smaller animal was defending its shelter against a larger female. In eight shelter approaches there were evictions (*i.e.*, the resident left and the challenging animal entered the shelter), usually between animals of the same sex; the winner was always the larger animal. Of the six evicted lobsters for which sex was known, four left the study area within a week of eviction. An equal number of males and females approached shelters (M8:F9). Males approached mostly males in shelters (M7:F1) which may reflect intrasexual competition in males (see *Courtship*). Females approached both sexes equally (M5:F4) in spite of the male biased population composition.

Naturalistic laboratory studies (Atema, 1986; Cowan and Atema, unpub.) suggest that male-female shelter interactions and evictions are the basis for intrasexual male dominance related to courtship. Based on the fact that in the field escalated fights were rare, we hypothesize that with few exceptions the 71 observed interactions were not direct dominance encounters, as suggested by staged laboratory fights (Scrivener, 1971), but served mainly to familiarize a lobster with its social environment. It stands to reason that social familiarity, as well as environmental familiarity (as described in *Shelter use* and *Homing*) would be advantageous particularly at the time of molting, both to avoid competition and predation, and, for mature animals, to secure mating partners. However, mature males may engage in dominance fights as observed in laboratory courtship studies (Cowan and Atema, unpub.; Karnofsky and Price, 1989). During this study we observed a male leaving shelter #29 (Fig. 2), running to a shelter 5 m away, and evicting its occupant, a large male. After evicting (presumably his competitor) he returned directly home. The evicted animal eventually returned to his shelter briefly, but subsequently left the area. In the laboratory such evictions are seen regularly. The eviction sequence itself has been described in detail (O'Neill and Cobb, 1979). These instances may be indications of territoriality or the expression of local dominance by one male (Kaufman, 1983; Karnofsky and Price, 1989).

Occasionally new lobsters were observed in a shelter originally occupied by another lobster. If the original occupant had not molted and was still in the study site, the second animal may have evicted it. In the rock garden, larger lobsters evicted smaller ones more often than the reverse (13:2) (Chi-square, $P < 0.05$). In the rest of the study area smaller and larger lobsters were equally likely (30:34) to be evictors. Thus, since lobsters show size related dominance, this may imply that the rock garden, but not other areas, contained preferred shelters. Rock shelters probably afford better protection and may be easier to defend. In addition, rock shelters are less modifiable than eelgrass shelters and thus properly sized rock shelters must be found and, if necessary, captured.

We observed a disproportionate number of interactions involving residents that molted in the study area (*t*-test, $P < 0.05$): 67 of the 103 interacting residents molted (65%), whereas only 6 of the 71 noninteracting residents molted (8%). Interactions may thus be related to impending molt. Since most interactions consisted of simple approach-avoidance behavior, this may reflect increased activity rather than increased aggression or both. Mature and subadult premolt lobsters in a semi-natural environment in the laboratory showed a distinct activity

peak in the four days before their molt, and the dominant male showed increased aggression in addition to greatly increased activity (Atema *et al.*, unpub.). In staged fight experiments, a premolt aggression peak (during molt stages D_1 and D_2) has been shown for juvenile (10th and 11th stage) lobsters (Tamm and Cobb, 1978).

Based on these overall results, we hypothesize that high-level aggression is displayed by mature males establishing a mating shelter area, and that low-level aggression is generally related to premolt increase in activity.

Courtship

We observed four situations with evidence of courtship and pairing. Because data are rare and difficult to obtain (one cannot look into most shelters) we describe the observations in detail. Unfortunately, the most complete observations presented themselves in the preparatory phase of the field studies in 1979 before animals were marked with individual numbers. However, body size and left (L) or right (R) handed crusher (C) or seizer (S) claw can give partial identification.

In 1979 it was possible to look partially into shelter #29 (Fig. 2). We infer that the resident male of that shelter cohabited and mated with two females in sequence over a two-week period based on the following evidence. A banded resident male and an unbanded, one-clawed, left-seizer (LS) lobster were seen together inside this shelter occasionally "pushing" and "boxing," a common behavior for cohabiting pairs in the laboratory (Atema *et al.*, 1979; Atema, 1986). Two nights later an unbanded lobster with a normal seizer claw on the left side and a regenerating right crusher was seen with the same male in the same shelter. They were seen together for six nights. On the seventh night a two-clawed, banded, RC female was seen in the shelter with the same male. That same night the left seizer claw of a molt shell was found near the shelter. After two nights a large two-clawed, unbanded, RC lobster was seen with the male and stayed in the shelter for four more nights.

Laboratory observations in semi-natural conditions (Atema *et al.*, 1979; Atema, 1986; Cowan and Atema, unpub.; Karnofsky and Price, 1989) have shown that only mature males cohabit with mature females and then only for several days surrounding the female molt. In these laboratory studies dominant males retained their shelters during successive matings with different females. Therefore, we assume that both animals seen with the same male in shelter #29 were females. The molt remains of the left seizer claw and the sighting of an unbanded LS animal with a regenerating right crusher claw imply that the first LS animal was a female that molted during cohabitation. The subsequent sighting of a cohabiting, larger, unbanded RC lobster two nights after sighting a

cohabiting banded RC female suggests that this second female also molted during cohabitation. Based on our laboratory observations, we infer that molting and mating occurred in both of these instances, and that the cohabitations of the one-clawed LS female and the two-clawed RC female with the same male followed each other almost immediately.

A number of additional observations showed that during this period the "mating" shelter #29 might have been unusually attractive to other lobsters. A small (<30 mm CL) lobster was seen regularly under an adjacent rock but was never approached by the inhabitants of shelter #29. A large male was seen digging at the back of the mating shelter; he subsequently approached the entrance, turned, and ran away. Two banded females (50 and 65 mm CL) were seen within 2 m of the shelter near WR (Fig. 2) on several consecutive nights. The larger made several approaches to the entrance of #29. The resident male appeared with a threat display (meral spread), stood outside and the approaching female left. Such shelter checking behavior by females is also common in laboratory observed courtship (Atema, 1986; Cowan and Atema, unpub.).

Some nights later a new banded male was seen in shelter #29. During the same night we caught a large newly molted male, perhaps the original male occupant, after he had approached the shelter and then fled. During the next few days several females, including the visitors mentioned above, inspected the shelter but cohabitation was not observed again. Subsequently, different males were seen in the shelter but none established long-term residence. Gradually fewer lobsters approached the shelter.

More indirect evidence for pair formation was obtained in 1980 and 1981. In 1980 a large, marked male (77 mm CL) and a new, initially unmarked female (80 mm CL) were seen in a shelter together. Two nights later the male was seen there again and subsequently a female molt claw and carapace were found in front of the shelter. The male left this shelter but remained in the area, where he was seen "bulldozing" in front of another shelter. The female was never seen again. In 1981 an initially unmarked male (77 mm CL) was caught and marked at a shelter where a marked female (61 mm CL) was also present. When he was returned after marking she stood near the entrance and both entered together. During subsequent observations they were seen together at the entrance. Two weeks later both were gone. The male was later seen elsewhere. In none of these latter cases could one look inside the shelters to gain more direct evidence for pairing.

While observations alone can never prove causality, observations in the field can provide both context and relevance for manipulative experiments in the laboratory and in the field. These observations of individually

marked lobsters in their natural habitat provide valuable information on shelter use, foraging, homing, and agonistic behavior, and on cohabitation between males and females before and after the female's molt. These data are particularly useful because more detailed information was obtained from naturalistic environments in the laboratory. However, without the context of field studies, one must always doubt the validity of laboratory studies for natural behavior.

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