

Shelter sharing and chemical courtship signals in the lobster *Homarus americanus*

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Abstract: In a 3.7-m Y-maze flume study of social odor-mediated behavior of mature lobsters (*Homarus americanus*), females preferred male- but not female-occupied shelters over empty shelters: they detected them from a distance and spent much time trying to enter. Males did not show distant detection and preference for female shelters but did spend much time trying to enter female but not male shelters once nearby. Sheltered resident males showed strong aggression toward visiting males but only mild aggression to visiting females; intermolt and premolt females could enter resident male shelters, cohabit for at least 7 h, receive mating attempts, and sometimes mate. Premolt females or females with sperm plugs resisted mating attempts. Visiting females released more than four times and males more than seven times as much urine during a shelter approach compared with an equal time in isolation. Females with or without urine release entered male-occupied shelters successfully, but mating attempts rarely occurred when female urine release was blocked. Female urine block resulted in greatly increased resident male aggression toward her, reaching the same levels elicited by visiting males with or without urine block. The results show that female urine signals reduce male aggression and facilitate mating.

Résumé: Au cours d'une étude sur le comportement social régi par des stimuli olfactifs chez les homards à maturité, effectuée dans un labyrinthe en Y de 3,7 m, les femelles préféraient aux abris vides les abris occupés par des mâles mais non par des femelles : elles les détectaient à distance et passaient beaucoup de temps à essayer d'y entrer. On n'a pas observé chez les mâles de comportement à distance de détection et de préférence des abris des femelles; une fois à proximité, ils passaient cependant beaucoup de temps à essayer d'entrer dans les abris des femelles mais non dans ceux des autres mâles. Les mâles résidents des abris manifestaient une forte agressivité à l'égard des mâles visiteurs, mais une agressivité modérée à l'égard des femelles; les femelles en phases intermue et prémue pouvaient entrer dans les abris des mâles résidents, cohabiter avec eux pendant au moins 7 h, faire l'objet de tentatives d'accouplement, et parfois s'accoupler. Les femelles en prémue ou présentant un bouchon spermatique résistaient aux tentatives d'accouplement. Les femelles en visite libéraient plus de 4 fois plus, et les mâles plus de 7 fois plus, d'urine pendant l'approche d'un abri que pendant une période égale passée dans l'isolement. Les femelles avec ou sans émission d'urine entraient avec succès dans les abris occupés par les mâles, mais les tentatives d'accouplement avaient rarement lieu lorsque l'émission d'urine était bloquée chez les femelles. Le blocage de l'émission d'urine chez une femelle provoquait une hausse de l'agressivité du mâle résident à l'égard de la femelle, agressivité qui atteignait le niveau suscité par la visite de mâles, avec ou sans blocage de l'émission d'urine. Les résultats montrent que les signaux constitués par l'émission d'urine chez les femelles réduisent l'agressivité chez les mâles et facilitent l'accouplement. [Traduit par la Rédaction]

Introduction

Crustaceans display a wide range of mating systems and behaviors. Some species pair only for copulation (Yano et al. 1988; Kamiguchi 1972; Lipcius et al. 1983), while others form longer lasting pair bonds. Pair bonds include mate guarding by the male (Van Engel 1958; Anstensrud 1992) or guarding linked with male occupation and defense of a shelter (Shuster and Caldwell 1989; Borowsky 1983). A shelter-based mate guarding system is used by the lobster *Homarus americanus* (Atema et al. 1979).

Shelters are important for most aspects of lobster life, including courtship and mating. Male lobsters establish and defend

shelters, evicting adjacent males (Karnofsky and Price 1989; Karnofsky et al. 1989). Late-premolt females enter dominant-male mating shelters and cohabit with that male for approximately 2 weeks, during which time female molting and mating occur (Cowan and Atema 1990). Mating involves male deposition of a spermatophore in the seminal receptacle of the female, the outer portion forming a sperm plug covering the opening (Templeman 1934; Aiken and Waddy 1980). During cohabitation the male guards the shelter and the female. The female remains in the shelter until her new exoskeleton has hardened (Atema et al. 1979; Kamofsky et al. 1989). Shelter sharing has only been reported during this cohabitation mating; lobsters are otherwise thought to be solitary (Ennis 1984; Kamofsky et al. 1989).

A cohabitation mating system offers females protection during the molt, a vulnerable time in the life of a lobster. Animals molting without cohabitation have been observed blocking shelter entrances and sealing themselves in (Atema et al. 1979; Kamofsky et al. 1989). This system of mating immediately following molting also allows females to remain fertile for the greatest possible intermolt period: females with spermatophores can remain fertile for up to 3 years (Waddy and Aiken 1986), but they lose their spermatophore when they

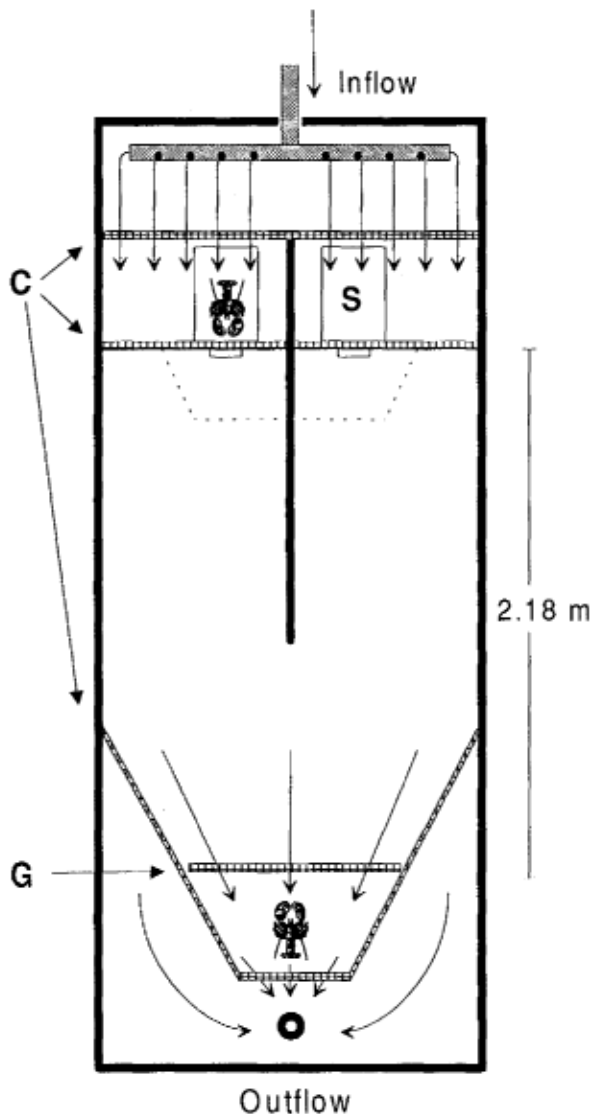
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Fig. 1. Diagram of flume used for all trials. Collimators (C) are screens of 1-cm³ mesh, used to smooth turbulent flow and direct current into the start position. Lobsters (approximately to scale) are shown in the start position and the left shelter. Arrows indicate general direction of water flow. S, artificial shelters; G, gate.



molt. In addition, cohabitation mating offers the male the important advantage of paternity insurance through mate guarding.

A less understood mating system exists involving intermolt females. Intermolt mating is thought to occur when females have molted without a mating opportunity. Such mating is of short duration and cohabitation does not occur. Females can then reproduce without waiting for the next molt period (Dunham and Skinner-Jacobs 1978; Waddy and Aiken 1990). It has been observed only in the laboratory, usually when shelter is poor or in short supply, and the natural context is unknown. However, its laboratory existence suggests that lobsters in nature may use multiple mating strategies (Waddy and Aiken 1990).

Chemical signals have been suspected to play a role in lobster mating for many years. Several workers have described

male attraction to tank water of freshly molted females (Hughes and Matthiessen 1962; McLeese 1970, 1973). In addition, Atema and Engstrom (1971) demonstrated that males showed reduced aggression when exposed to the tank water of freshly molted females. Atema and Cowan (1986) proposed urine as a carrier for lobster chemical signals and Cowan (1991) showed that ablation of the lateral antennules of either a cohabiting male or female leads to abnormal mating behaviors. However, Dunham (1979) did not observe male courtship behavior with water from freshly molted females, while Snyder et al. (1993) described mating occurring while male or female urine release was blocked. Therefore, the importance of urine and other chemical signals in lobster mating remains unclear.

For this study we hypothesized that females locate male-occupied shelters from a distance and release urine signals to facilitate entry and mating. We compared female and male behaviors, with or without urine release, as they approached sheltered males and females, and the behavioral responses of the sheltered animals. We also examined the influence of female molt stage and sperm plugs on female and male behaviors. A few preliminary results of this work have been reported (Bushman and Atema 1994).

Materials and methods

All lobsters in this study were adult, sexually mature males and females, 75–85 mm in carapace length, caught in the Woods Hole, Massachusetts, area by local lobstermen. They were kept in communal holding tanks for no longer than 3 weeks until use. Two males or two females of equal carapace length were paired and placed into one of two flow-through 1.84 x 0.51 x 0.30 m fiberglass tanks. Each tank contained one shelter. The pairs were allowed to establish a dominance relationship, evidenced by the dominant animal occupying the shelter. Pairs were allowed at least 1 week before use in an experiment. The lobsters paired in this way were termed resident males or females and were maintained throughout an experiment. Three days before an experiment other males or females were each placed individually into 1 of 10 flow-through 0.30 x 0.25 x 0.14 m plastic tanks. The lobsters placed into the individual tanks were termed visiting animals.

All tanks received unfiltered seawater from the general supply of the Marine Biological Laboratory in Woods Hole through individual seawater spigots. Outflow from the visiting animal tanks pooled and flowed collectively and equally into the tanks of the resident pairs, such that these tanks received the majority of their seawater from the individual tanks. In this way, the residents were chemically familiar with the visiting animals, while the visiting animals were not chemically familiar with the residents. The rationale for this arrangement was based upon the observations that male lobsters held in lengthy isolation exhibit increased aggression (Hoffman et al. 1975). Chemical awareness of other lobsters besides the tank mate was thought to represent a more natural condition and might prime the resident animals for mating behavior. No visual communication was possible between any tanks. All animals were housed in the same room, on a 14 h light : 10 h dark reversed phase light cycle. Experiments were performed in the dark phase, during the months of June–October of 1993 and 1994. Water temperature ranged from 15 to 24°C.

All experiments were conducted in a 3.7 x 1.4 x 0.30 m fiberglass flume, equipped with a flow-through seawater system (Fig. 1). A barrier split the upstream end of the flume into a Y. Two plastic containers (0.30 x 0.25 x 0.14 m) represented artificial lobster shelters and were placed at the upstream ends of each arm. Each shelter had several 1-cm upstream holes to permit water flow through the shelter

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and a downstream entrance constructed of 152-mm i.d. PVC pipe. The barrier prevented any water flow between shelters. The shelter entrances were either open or closed with two bars that prevented entry and exit but allowed visual, chemical, and tactile communication. The downstream end of the flume contained a start position 2.18 m from the shelter entrances. Seawater flowed through and around the shelters at 1 cm/s and drained through a standpipe directly behind the start position. Dye studies indicated that water flowing through the shelters pooled and mixed in the start position. Any animal in this position therefore received simultaneous chemical information from both shelters. Lobster behaviors and movements in the flume were recorded on videotape with a Panasonic WV-1850 low-light camera. The flume was illuminated by four 60-W incandescent bulbs dimmed to the lower limit of camera resolution.

A trial involved placing a resident, dominant animal in one of the shelters, while the other remained empty. Only dominants were used in this study because during cohabitation mating the dominant males are most attractive to females and are more likely to mate successfully (Atema et al. 1979; Cowan and Atema 1990). At least 1 h later, a visiting animal was placed in the start position. After 10 min acclimation, a trial began by dropping a gate allowing the visiting lobster to move freely about the flume. After 15 min the trial was ended and the visiting lobster removed. Thirty minutes were allowed between trials to clear the odor of the visiting animal. Dye tests showed complete water turnover in this time period. Each day no more than five visiting animals were tested in sequence. This would not be unusually high when compared with observations in naturalistic aquaria (Cowan and Atema 1990) and the field (Karnofsky et al. 1989).

The experiment was divided into two parts. Part 1 tested all possible combinations of males and females as visiting and resident animals to determine whether visiting animals would locate, approach, and attempt to enter resident animal shelters. Part 2 examined how urine release by visiting males and females influenced shelter entry and resident male mating behavior. Both parts followed the same general protocol, with variations as described below.

Part 1: attraction to sheltered lobsters

In this experiment, shelter entrances were barred to prevent entry or exit. Behaviors at each shelter entrance were recorded by videotape camera. Residents were switched between shelters each day to avoid bias owing to possible learning or intrinsic shelter preference. Animals were tested according to the following protocol: (i) one single resident male, 20 visiting females; (ii) one single resident male, 10 visiting males; (iii) one single resident female, 20 visiting females; and (iv) one single resident female, 10 visiting males.

Each condition was tested with different visiting and resident animals. Two parameters were examined. First approach was defined as the first shelter approached from the start position. A visiting animal crossing a line drawn 0.30 m from each shelter entrance was scored as having approached that shelter. Differences in first approach between the two shelters were evaluated using a χ^2 test. The second parameter was time spent entering. A visiting animal would often try to enter a shelter, although the bar prevented success. The time a visiting animal spent trying to enter was recorded and used as a measure of the visiting animal's motivation to enter the shelter of the resident. Differences in mean time spent entering between the two shelters were evaluated with a Mann—Whitney U test.

Part 2: shelter entry behavior

In this experiment a single dominant male was placed in a shelter and females ($N=20$) or males ($N=15$) were tested as visiting animals. Two dominant—subordinate male pairs were prepared. The shelter entrances were open, allowing entry. A low-light videotape camera (Panasonic WV-1850) was positioned over the shelters, which were fitted with 0.30 x 0.25 m transparent Plexiglas tops to allow observation. Shelters were screened from the flume incandescent lights and were illuminated by one red photographic safelight positioned 1 m

above the shelter tops.

Visiting animals were fitted with a nephropore catheter (Lindstrom 1991). This consisted of two 1-cm pieces of 1/8-in. i.d. (1 in. = 25.4 mm) Tygon latex tubing, the end of each glued over a nephropore so that the nephropore was fully enclosed by the tubing. The glue was a thick cyanoacrylate (Zap-a-gap), applied with an accelerator (Zip Kicker). A piece of 1/16-in. i.d. PVC tubing was inserted into the distal end of each piece of latex tubing and these PVC tubes led posteriorly to a Y connector glued to the dorsal portion of the carapace. A single piece of 1/16-in. i.d. PVC tubing led to a vented collecting bottle floating on the surface. In these experiments the catheters served two purposes. They prevented urine release into the environment, testing the effects of missing urine signals on the behaviors observed. By collecting urine they allowed measurement of urine release volume and the correlation of release rates with behavioral observations.

All males and females were tested with catheters in open and closed condition. In closed condition the catheters were fully connected. In open condition the PVC tubing between the Tygon tubing and the Y connector was removed, allowing normal urine release. Fifty percent of the visiting animals were tested in random sequence first with open, then with closed catheters, and the order was reversed for the remaining animals. The resident male was moved to the other shelter after every five trials to avoid shelter bias. Visiting females were molt staged by examination of pleopod tips for the formation of new cuticle (Aiken 1973) and checked before and after experimentation for the presence of a sperm plug in the seminal receptacle (Waddy and Aiken 1991).

Lobster aggression (Scrivener 1971), mating (Herrick 1896; Templeman 1934; Hughes and Matthiessen 1962; Atema and Engstrom 1971), and courtship (Atema et al. 1979; Atema and Cobb 1980; Cowan and Atema 1990) have been well documented. The behaviors used in this study were adapted from a recent review (Atema and Voigt 1995). Entering, eviction, and mating behavior were summed for all trials and compared between males and females and between open and closed catheter conditions using a χ^2 test. For those trials in which successful entering occurred, aggressive behavior by the resident toward visiting animals was recorded. These aggressive behaviors were summed for all trials and compared between males and females and open and closed catheter conditions using a Wilcoxon signed-rank test.

Behaviours used in the analysis are summarized in Table 1.

Results

Part 1: attraction to sheltered lobsters

Of all permutations tested, only the one in which females visited resident males produced both significant nonrandom first approach (Fig. 2A) and time spent entering (Fig. 2B). Visiting females showed a nonsignificant trend for approaching resident female shelters but rarely attempted to enter. Males did not display any ability to locate sheltered females but did show significantly nonrandom entering attempts once the shelter was encountered (Fig. 2B). Males showed no trend for approaching or entering resident male shelters.

Part 2: shelter entry behavior

Visiting female, visiting male, and resident male behavioral outcomes are compared in Table 2. Both females and males attempted to enter resident male shelters with no significant difference between female and male success rates. However, in all but one case successful male entry required eviction of the resident. Eviction success was correlated with visiting male

Table 1. Summary and definition of behaviors used in analysis.

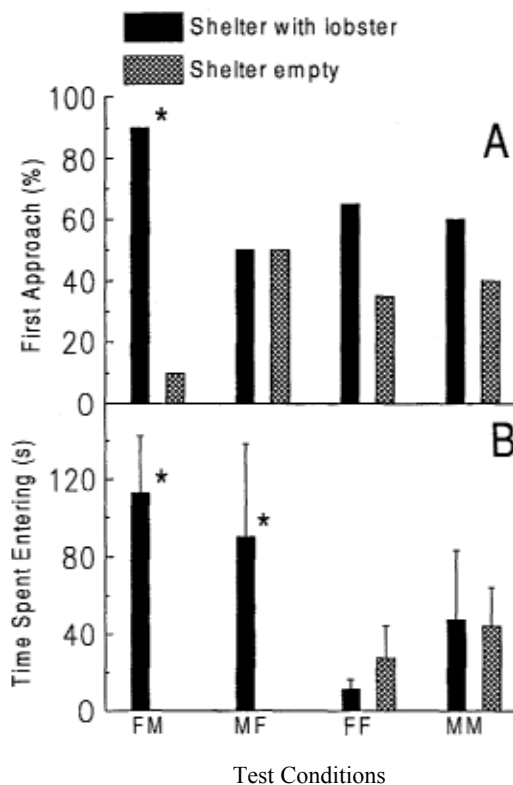
Term	Definition
Entering	Visiting animal pushes one or both chelae fully into the shelter entrance
Successful entering	Visiting animal enters shelter completely such that uropods and claws are fully within the shelter cavity
Eviction Attempted	Resident animal moves completely out of shelter
Successful mating	Resident male is above female, slightly behind and parallel to her; grasping the edge of her carapace with walking legs and lifting it
Successful mating	Female is upside down, claws forward and abdomen outstretched; male is parallel to and above her; confirmation of success required examination of the female for a new sperm plug after mating
Push	Pressing chelae against opponent animal and walking forward, with or without swimmeret current
Claw lock	Clamping of chelae onto opponent's chelae, either inside the open chelae or on the outside edge, or onto another body part
Scissor	Bringing the chelae from a laterally extend position rapidly inward in a scissoring motion directed toward opponent; may touch opponent in the process
Snap	Closing chelae quickly, directed toward opponent's body; may or may not actually seize opponent

carapace length (Spearman's $r = 0.69$, $p < 0.05$). In contrast, entering females never evicted the resident; instead, the resident male and visiting female shared the shelter for the duration of the trial.

The resident male behaved differently toward visiting females and males. In 10 of 14 successful shelter entries the resident attempted to mate with the female and was successful in 4 trials. Visiting males never received resident male mating attempts. Females that entered but received no mating attempt from the resident male were nonetheless allowed to remain in the shelter with little aggression directed toward them. Visiting males evoked aggressive behaviors from the resident male. These consisted mainly of pushing, with bouts of claw lock, scissor, and snap (Fig. 3). The males usually remained facing each other, pushing until the visiting animal was repulsed or gained entry into the shelter. The latter usually signaled eviction of the resident, who then abandoned the shelter. Female shelter entry began similarly, but the resident male responses were less aggressive, showing significantly fewer bouts of pushing and high-level aggression (Fig. 3). Once a female had gained entry, she always turned, presenting her abdomen to the male, and often flattened herself along one wall of the shelter, claws forward and outstretched. The resident male exhibited little aggression toward her at this point, and either attempted to mate or did not interact with her for the duration of the trial.

All females were molt staged and examined for the presence of a sperm plug before and after experimentation (Table 3). Females were grouped as either intermolt (stage C; 10 females) or premolt (stage D0 or D1; 10 females). No females of later molt stage were collected for use during this study. Seven females possessed sperm plugs, while 13 did not. Molt stage or sperm plug presence did not affect female

Fig. 2. (A) Shelter first approached by visiting males or females with resident males or females. Asterisks indicate statistically significant differences between shelters. FM, visiting female—resident male, $\chi^2 = 12.80$, $p < 0.05$; MF, visiting male resident female; FF, visiting female resident female; MM, visiting male resident male. (B) Mean time spent by visiting males or females attempting to enter shelters. Error bars are 1 SE. Asterisks indicate statistically significant differences between shelters. FM, Mann-Whitney U test, $z = 3.75$, $p < 0.05$; MF, Mann-Whitney U test, $z = 2.02$, $p < 0.05$.



attempted or successful entry. Resident male mating attempts were not influenced by molt stage or significantly by sperm plug presence, although there was a trend toward females without sperm plugs. All eight entering females without sperm plugs received mating attempts (Table 3). Females could resist mating attempts by spreading their chelae to prevent being rolled over. Premolt females and intermolt females with sperm plugs resisted mating, such that the four successful matings all involved intermolt (stage C) females without sperm plugs. Any other combination of female molt stage or sperm plug presence resulted in either no male solicitation or active female resistance. Resisting females did not mate during the trial period.

Visiting females and males were found to release significantly more urine during a 1 5-mm trial, compared with that collected during a 1 5-mm pretrial period in isolation (Fig. 4). Urine release by visiting females influenced resident male behaviors. Female urine block (catheters closed) did not affect the frequency of successful entry but did decrease the likelihood of mating attempts by the resident male (Fig. 5). Closing catheters also increased the frequency of occurrence of resident male aggression toward the visiting female. Pushing, the

Table 2. Behavioral outcomes for 20 females and 15 males allowed to approach and attempt to enter the shelter of a dominant male.

Outcome	Females (N= 20)		Males (N= 15)	
	Sum	%	Sum	%
Entering behavior				
Attempted entry	16	80	11	73
Successful entry	14	88	7	64
Resident eviction	0*	0	6*	86
Mating behavior				
Attempted mating	10*	71	0*	0
Successful mating	4	40	0	0

Note: The number or trials resulting in a particular behavioral outcome is presented, both as a sum and as a percentage of the trials in which the behavior occurred. For those animals that entered successfully, resident eviction and attempted mating were compared between females and males. Asterisks indicate statistically significant differences. Eviction: $\chi^2 = 12.2, p < 0.05$; attempted mating: $\chi^2 = 4.9, p < 0.05$.

most commonly observed behavior, as well as the more aggressive behaviors claw lock, scissor, and snapping were all elevated when female urine was blocked (Fig. 5).

Closing visiting male catheters, however, produced no significant differences. The occurrences of successful entry (seven) or eviction (six) when visiting male catheters were open were not significantly different from the closed-catheter condition (seven and seven, respectively). Resident male aggression toward open-catheter visiting males (16 counts of push; 17 counts of claw lock, scissor, or snap) also did not differ significantly from aggression elicited by closed-catheter visiting males (25 counts of push; 14 counts of claw lock, scissor, or snap). These aggression levels matched closely the behavior toward urine-blocked females (Fig. 5).

Discussion

In this study, intermolt and premolt female lobsters located male shelters from a distance of over 2 m and successfully entered with only mild resident male aggression. Although females had an overall tendency to approach any occupied shelter, they significantly preferred to approach and enter only male shelters (Fig. 2). Female urine release did not influence her shelter entry, but once she was inside it reduced resident male aggression and elicited male mating attempts (Fig. 5). Visiting males did not demonstrate a preference for locating sheltered animals, but they did spend much time attempting to enter female shelters (Fig. 2). Resident males responded to visiting male entering attempts with strong aggression (Fig. 3). Urine release by visiting males, although elevated during a visit (Fig. 4), did not influence entering success or the aggressive responses of the resident males.

Visiting animals were used only once per day and at most four times in all, while the two resident males were used repeatedly throughout the experiment. In the field (Karnofsky et al. 1989) and in large aquaria (Cowan and Atema 1990) all lobsters, and dominant males in particular, are visited regularly in their shelters. Repeated use of a single resident permitted more comparable observations of visiting animal behavior and had no discernible effect upon resident male behavior. The occurrences of attempted and successful male matings were not correlated with trial order during a day or with day order

Fig. 3. Summed occurrence of resident male aggressive behaviors for all trials for visiting open-catheter females and males. Behaviors are defined in Table 1 and were compared between females and males. Push, Wilcoxon signed-rank test, $z = 2.10, p < 0.05$; claw lock, scissor, snap, Wilcoxon signed-rank test, $z = 2.20, p < 0.05$.

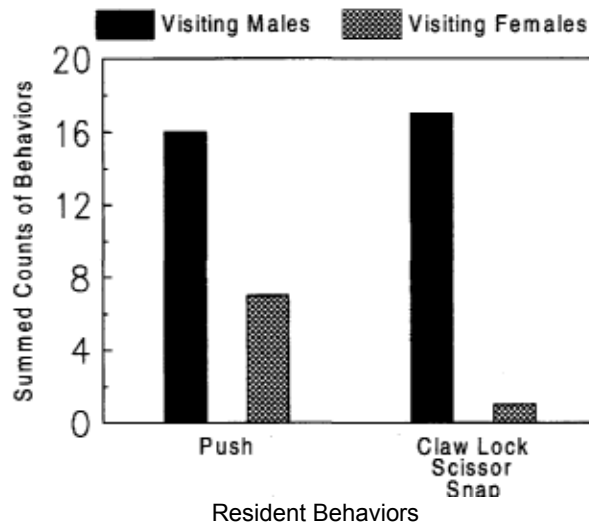


Table 3. Female molt stage and the presence of sperm plugs and their effects upon visiting female and resident male behavior.

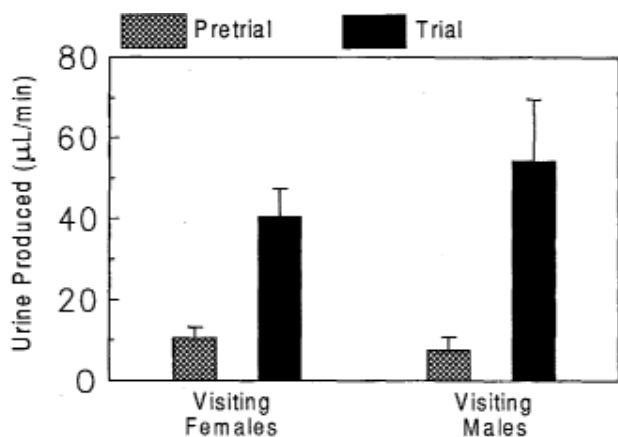
	Female condition (N= 20)			
	Intermolt	Premolt	Sperm plug	No sperm plug
Female totals	10	10	7	13
Female behavior				
Attempted entry	9	7	7	9
Successful entry	8	6	6	8
Male behavior				
Attempted mating	6	4	2	8
Successful mating	4	0	0	4

Note: Values are the number of females performing or eliciting a behavior.

during the experiment. Similarly, visiting male eviction success was related only to visiting male carapace length. However, with a small resident male sample size, conclusions concerning resident male behavior must be drawn with caution.

This study suggests that intermolt mating, observed previously without the provision of shelters of sufficient size for mating (Dunham and Skinner-Jacobs 1978; Waddy and Aiken 1990), may normally occur inside shelters. Lobsters are considered to be solitary and agonistic toward conspecifics (Ennis 1984; Karnofsky et al. 1989; Steneck 1991), and shelter sharing has not been observed in the field outside of cohabitation mating (Atema et al. 1979; Karnofsky et al. 1989). However, if intermolt mating occurs inside shelters soon after entry and is not accompanied by prolonged cohabitation, it would be difficult to observe in nature. Visiting animals in this study were unfamiliar with the resident animals and their immediate surroundings. These conditions may not be typical for lobsters in stable populations (Karnofsky et al. 1989) but may be similar to those experienced by transient animals, including females

Fig. 4. Mean urine release rates by visiting females and males with closed catheters during a 15-min trial and a 15-min pretrial isolation period. Error bars are 1 SE. Rates were compared between pretrial and trial conditions. Visiting females, Mann-Whitney U test, $z = 2.56$, $p < 0.05$; visiting males, Mann-Whitney U test, $z = 2.24$, $p < 0.05$.



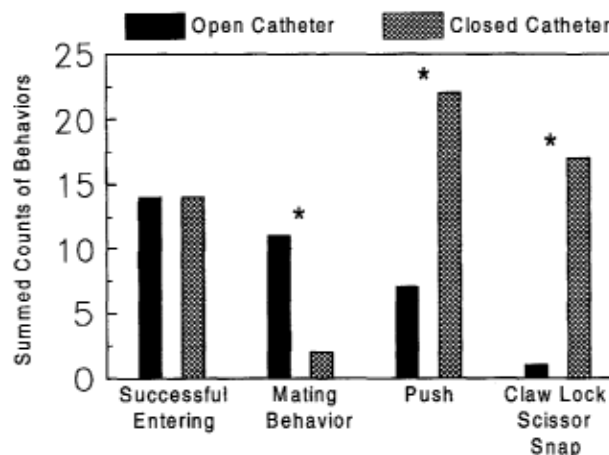
during migration (Campbell 1986; Pezzack and Duggan 1986). It may be useful for field workers to examine these migratory events for evidence of intermolt mating or shelter sharing.

Females with sperm plugs and in premolt resisted mating attempts yet successfully entered and remained in the resident male shelters (Table 3). Shelter sharing with these females precluded resident male mating during that period. This apparent male cost suggests that prior to shelter entry, males cannot determine female receptivity, either through molt stage or sperm plugs. By not providing this information, females gain access to shelter, a phenomenon described in stomatopod crustaceans (Caldwell 1986). Males could still benefit overall if receptive intermolt females occasionally entered and mated with the resident. Field observations of intermolt female entry into male shelters would provide evidence for the existence of intermolt mating in nature. Without any mating possibility it is difficult to see why males would allow intermolt females to enter and remain in their shelters.

Because females were removed at the end of 15-min trials the full duration of shelter sharing was not measured. In a preliminary test, four females were allowed to remain in the male shelter after entry for 2, 3, or 7 h. All females and resident males were still in the shelter at the end of each period. If a female entering at night remained until daylight, shelter sharing would likely last at least until the following night, as lobsters are unlikely at least in shallow water to leave shelters during the day (Karnofsky et al. 1989).

Female chemical signals carried in urine did not influence shelter entry, but after entry female urine reduced resident male aggression and increased the likelihood of male mating attempts (Fig. 5). Indeed, resident males treated urine-blocked females similarly to males with or without urine. These results confirm earlier reports (Atema and Engstrom 1971; McLeese 1973; Atema and Cowan 1986) but appear to be at odds with some recent work in which normal mating was observed in catheterized lobsters (Snyder et al. 1993). However, in the latter study animals were tested in open arenas, with no shelters provided. There is considerable evidence from the laboratory

Fig. 5. Summed occurrence of successful female entering and resident male mating and aggressive behaviors for visiting females with open or closed catheters. Asterisks indicate statistically significant differences between open and closed catheter conditions. Mating behavior, $\chi^2 = 5.20$, $p < 0.05$; push, Wilcoxon signed-rank test, $z = 2.24$, $p < 0.05$; claw lock, scissor, snap, Wilcoxon signed-rank test, $z = 2.31$, $p < 0.05$.



and field to suggest that shelters are important for lobster survival and much of lobster behavior (Scarratt 1968; Cobb 1971; Atema et al. 1979; Karnofsky et al. 1989). Lobster behavior is quite context specific, and often a stimulus will not generate a response unless the behavioral context is correct (Atema and Cowan 1986). Effects of female urine release upon male aggression and mating were seen here inside the shelter of a dominant resident male, but these effects may not be expressed in other contexts. Conversely, the observation of visiting male urine having no effect on resident male behavior does not imply that male urine has no effect upon male lobsters in other contexts, such as boxing matches outside of shelters (Karavanich and Atema 1991; Breithaupt and Atema 1993).

Although loss of female urine signals through catheter closure resulted in elevated male aggression, closed-catheter females were able to remain in the male shelter. Moreover, males with closed catheters still invoked high resident male aggression. Clearly the resident males were receiving information in addition to urine signals that influenced their reactions to visiting females and males. One likely source of information was the posture of the visiting animal. Females always adopted a crouching posture and turned around with their claws facing away from the male, as described in Atema et al. (1979). This female posture resulted in less resident male aggression. Visiting males faced the resident males, spreading their chelae and (or) raising their bodies from the substrate. This may have evoked resident male shelter defense behavior regardless of any urine signal. The single male that entered and remained in a resident male's shelter without eviction immediately adopted the crouching posture exhibited by females and retained it for the duration of the trial.

This study provides evidence that female urine signals play an essential role in facilitating intermolt mating. Loss of chemical signal reception in resident males through antennule ablation has been shown to lead to increased female injury during cohabitation mating (Cowan 1991). Together, these

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studies suggest that lobsters rely heavily on chemical communication during courtship and mating. This is not surprising in an almost exclusively nocturnal animal. Therefore, lobsters may be vulnerable to even low levels of chemical pollution if those chemicals disrupt signal reception by damaging the antennular chemoreceptors or if they mimic or mask the biological signal (Atema et al. 1973). Understanding the role of chemical signaling in lobster social behavior and the interactions of chemical and other sensory signals is important for accurate predictions of lobster mating success and population dynamics.

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