Close examination of the termination point revealed small ducts traversing the epithelium of the ureter, suggesting that the larger duct releases product into the lumen of the ureter. These large glands stained differently than did the small glands. They stained blue in all specimens, and always showed the rosette development and grainy cytoplasm postulated to represent active cells.

In summary, lobsters posses two types of tegumental glands in the nephropore areas. The first, unicellular or individual rosettes, follows the molt cycle in activity. The second, a large mass of rosettes, seems to drain into the ureter via a common duct. It does not follow the molt cycle, appearing active in all specimens, although its large size in the post-molt female (Fig. 1) suggests some involvement in molting. Tegumental glands have been described that neither follow the molt cycle nor produce phenoloxidase, such as pleopodal cement glands (13). The large gland described here could be a novel type of tegumental gland, and is well positioned for production and release of a chemical signal, because any product would soon be excreted through the nephropore. It is possible, however, that the large gland serves another function, such as release of a bacteriostatic agent (14). Determination of function requires behavioral, chemical, and physiological testing, and work is under way in these areas.

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The Role of Chemical and Visual Cues in Agonistic Interactions of the American Lobster

Liat J. Kaplan, Courtney Lowrance, Jennifer Basil, and Jelle Atema
(Boston University Marine Program, Marine Biological Laboratory)

When two American lobsters (*Homarus americanus*) fight in a paired agonistic encounter, one will eventually exhibit more aggressive behavior than the other and establish dominance (1, 2). Chemical, mechanical, and visual senses contribute to the outcome of these interactions, but the relative importance of each sense is not known. We thus examined the roles of vision and chemical substances (*i.e.*, urine) in agonistic encounters between lobsters.

A dominant lobster is usually larger (1) and more aggressive than a subordinate lobster. Both of these characteristics are at least partly visual, and the extent to which they determine the winner of an encounter is unknown. We therefore examined the role of vision in initial establishment of dominance. In addition, lobsters may secrete a chemical substance into their urine that communicates dominance status during fights. After dominance has been established in an initial encounter between two lobsters, the subordinate lobster will be less aggressive in subsequent fights, resulting in a decrease in fight duration. We examined whether natural urine release is necessary for the decrease in second fight duration in encounters between previously matched lobsters.

General Procedures: Dominance interactions were examined by pairing two lobsters in a "boxing match." Two lobsters were placed into a 340-l "boxing tank" and their interactions were recorded on videotape for 20 min. The taped record was viewed in 5-s intervals. In each interval, a rank of aggression—from −2 (extremely submissive) to 4 (extremely aggressive)—was assigned to each lobster, based on stereotypical categories of behavior that it exhibited. Fight duration was defined as the time between first approach and the point at which the subordinate lobster stopped approaching the other animal. The percentage of intervals containing each aggression level was calculated for each fight.

Experiment 1: Twenty-four adult male lobsters were separated into 2 groups ("blindfold first" and "blindfold second") of 12 animals each. For the "blindfold first" group, two blindfolded lobsters were isolated in separate tanks for 48 h and then paired in a boxing match. Blindfolds were then removed and the lobsters were placed in separate communal tanks for two weeks so that their "memory" of each other would be erased (Karavanich, pers. comm.). The same pairs were then isolated for 48 h and were brought together for a second fight, without blindfolds. The "blindfold second" group underwent exactly the same procedure, except they fought first without blindfolds, then with blindfolds. Performances across groups were compared to determine whether there was a treatment order effect of blindfolding. To account for individual differences in behavior, a within-subject design was used, each animal serving as its own control.

Experiment 2: Four pairs of adult male lobsters were fitted with catheters attached to their nephropores (3). Each lobster was then fitted with a urine release device, and pairs were brought together for boxing matches. In first fights, the catheters were detached from the nephropores so each lobster could release its urine naturally. The lobsters (lobster A and lobster B) were then isolated from each other for 24 h; during this time their urine was collected for at least 12 h. Each pair was then matched a second time, with catheters attached to block natural urine release. The urine collected from each lobster before the second fight was diluted 20:1 with seawater to mimic the natural dilution of urine in the gill current. During the fight, this urine was released manually from syringes connected to the urine release devices. Fifteen seconds into the fight, 5 ml of diluted urine was released for 3 s from lobster A, but only when he was facing and within one body length of his opponent, regardless of the opponent's orientation. Fifteen seconds later the same procedure was followed for lobster B. This procedure continued for the entire 20-min duration of the fight. At no time were both lobsters releasing urinc simultaneously.

Results: In Experiment 1, there were significant differences (Kruskal-Wallis, $P < 0.05$) in aggression level 1 between groups in the nonblindfolded condition and in level 2 between groups in the blindfolded condition, indicating that there was an order effect. In the blindfolded fight of the "blindfold first" group, the average percentages of levels 0 and 1 were significantly higher, and the average percentage of level 2 was significantly lower, than in the nonblindfolded fight (Wilcoxon Signed Rank, $P < 0.05$), indicating that under blindfolded conditions there is diminished detection of the opponent. This could explain why the percentage of time they spent in physical contact (level 2) was lower than in nonblindfolded fights. We found no significant difference between aggression-level percentages in the first and second fights of the "blindfold second" group. No significant difference was found between the durations of first and second fights in the "blindfold first" group (first fight mean = 520 ± 348 s, second fight mean = 374 ± 167 s) or the "blindfold second" group (first fight mean = 577 ± 383 s, second fight mean = 378 ± 257 s). Finally, no significant difference was found in duration between groups for the nonblindfolded or the blindfolded condition. The finding that fight duration is not affected when lobsters are blindfolded, despite subtle differences in fighting behavior, suggests that vision is not important in initial agonistic encounters. Because lobsters are nocturnal and learn much of their fighting behavior under relatively dark conditions, vision may be less important than the other senses.

In Experiment 2, there were subtle changes in behavior between natural and manual urine release fights; later studies will explore these trends. Durations of first (natural urine release) and second (manual urine release) fights were not significantly different (first fight mean = 732 ± 354 s, second fight mean = 858 ± 259 s; Student's t-test, $P > 0.05$). These data indicate that the lobsters did not recognize each other, perhaps because natural urine release was blocked by catheters, in the second match of each trial. It may be that the timing of manual urine release did not mimic the natural timing. Alternatively, a cue necessary for communicating dominance may be released only during aggressive encounters and may therefore have been absent in the urine that was collected overnight and released manually. The presence of investigator-controlled squirts of the animal's nonfight urine appeared not to have a significant effect on fighting behavior.

We can therefore conclude that vision does not play an important role in the initial establishment of dominance and that natural urine release is necessary for recognition in repeated encounters.

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Agonistic Encounters in the American Lobster, *Homarus americanus*: Do They Remember Their Opponents?

Christy Karavanich and Jelle Atema (Boston University Marine Program, Marine Biological Laboratory)

Dominance is important in male lobsters for many reasons. Previous studies have demonstrated that female lobsters choose to mate with locally dominant males (1, 2, 3, 4). Dominant males also obtain more desirable shelters, which they need for protection (4, 5). The dominance of a particular lobster depends on its size, sex, molt state, and previous experience (6, 7). In aquaria, lobsters will form dominance hierarchies (6, 8, 9), and highly aggressive interactions can be observed during formation of these hierarchies. Subsequently, interactions are reduced to simple approach and retreat behaviors, similar to what is observed in the field (4). The mechanisms maintaining these hierarchies are unknown, but the alternatives are that subordinates recognize aggressive state and avoid all lobsters more dominant than themselves or lobsters recognize particular individuals and act dominant or submissive based on previous encounters.

Twenty pairs of size-matched, adult male lobsters were isolated for 48 h. Each pair was then allowed to interact in a 340-l tank for a 20-min videotaped match, during which a dominance relationship was established. After a postfight isolation of 24 h, 10 pairs were rematched against their original opponents in a second fight. In the other 10 pairs, the subordinates of the first fights were matched against an unfamiliar dominant. Each animal was assigned a relative aggression rank for each 5-s period on a scale of −2 to 4, ranked in whole number intervals. Negative numbers denoted submissive behaviors, and increasingly positive numbers indicated escalating aggression. The period necessary to establish