

7. Interobserver agreement for the three scorers was 93 percent and 94 percent on judgments of location contacted. The infants would frequently contact the display with both hands. If one hand contacted the display 1/2 second or more before the other hand, the location of the first contact was scored. If one hand touched the middle region while the other hand simultaneously (within 1/2 second) contacted a side, the reach to the side was scored. If the infant simultaneously contacted both the large and small regions, the reach was classified with responses to the middle region.
8. Data on an additional three infants, one from the binocularly viewing group and two from the monocular group, was excluded from analysis because of insufficient reaching.
9. W. Schriever, *Sehen. Z. Psychol.* 96, 113 (1925).
10. A high percentage of infants in the 20- to 22-

week-old group failed to reach six times. The 26 infants in each condition remained after eliminating data on 44 infants because of insufficient reaching; 25 were from the group viewing the real window and 11 were from the group viewing the trapezoidal window.

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Behavior and the Crustacean Molt Cycle: Changes in Aggression of *Homarus americanus*

Abstract. *The phase of the molt cycle affects dominance status and the performance of agonistic acts in individual juvenile lobsters (Homarus americanus). Lobsters in the midphase of proecdysis are more aggressive than those in intermolt; the latter are more aggressive than lobsters in early or late proecdysis and those in postecdysis.*

Although most crustaceans are subject to continual periodic ecdysis throughout their lives, aggression has not been fully examined in the context of the molt cycle. Such diverse physiological processes as hormone production, calcium deposition, limb regeneration, and protein metabolism (1) all undergo profound changes during the molt cycle. Concomitant changes in a crustacean's behavior should also be expected. Food selection and intake vary with the molt cycle in lobsters (2), and locomotor activity and aggression vary with the stage of the molt cycle in stomatopods (3).

Numerous factors affect aggression. Most previous studies focused on size, sex, food, and shelter availability (4). In this report, we describe variation in the agonistic behavior of the American lobster during its molt cycle.

The crustacean molt cycle can be subdivided into phases (molt states) correlated with known physiological and behavioral events (5-7). In this study, lobsters that had molted within 12 hours were operationally defined as being in state A; those 48 to 96 hours postmolt were considered in state B. These times fall within the ranges given by Passano (7). Hard-shelled lobsters were differentiated as C, D₀, D₁, D₂, and D₃ by Aiken's technique of examining setal development in the pleopods (5).

Juvenile lobsters, 10 and 11 molts from hatching (about 6 months), all in apparent good health and not missing appendages, were chosen for this experiment. The subjects had been cultured in a controlled seawater system and maintained in physical isolation for at least three

molt cycles. The sex, wet weight, and molt state of all subjects were determined (8). Pairs consisting of a control (state C) and a target lobster in one of the seven molt states were selected. They were of the same stage (10 or 11), sex, and approximate weight (9). Control and target lobsters were used only once.

Paired lobsters were placed into 7.6-liter aquariums (one pair per tank) on the day of the molt-state determination. Individuals were separated by an opaque divider, and allowed to acclimate to the tank for 24 to 28 hours. A shorter acclimation period (8 to 10 hours) was necessary for A-C and D₃-C pairs because of the brief duration of the A and D₃ molt states. Animals were not fed after the molt state was determined, nor during the observations. Shelter was not provided, but a 3-cm layer of silica sand covered the bottoms of the aquariums. Temperature and photoperiod were maintained as in the previous holding

conditions (22°C; 14 hours of light in 24 hours, turned on at 0400 hours).

Fifteen-minute observations on pairs were conducted after the lights went out, between 1830 and 2130 hours. Observations were made from behind a blind, under red illumination. Three aspects of agonistic behavior were studied: (i) the type and duration of encounters, (ii) the frequency and duration of acts within these encounters, and (iii) the intra-individual act sequences. Data were simultaneously recorded onto an event recorder (Esterline-Angus) and an audio-tape. The data presented here are for the target lobsters only.

Each agonistic encounter was classified as either "won" (control lobster withdrew), "lost" (target lobster withdrew), or "even" (both withdrew), and its duration was noted. A target lobster that spent significantly more than 50 percent of its total agonistic time in one of these three types of encounters was assigned the appropriate social rank (dominant, subordinate, or equal). Characterization was clear in all cases, with 84 percent of the target lobsters involved in a single class encounter in excess of 75 percent of their total agonistic time. Molt state had an obvious effect on dominance (Table 1) ($\chi^2 = 44.96$, d.f. = 12, $P < .001$). Target lobsters in D₁ and D₂ were dominant or equal, but in A, B, and D₃ they were subordinate to control animals. There was no significant difference in the distribution of social ranks between C and D₀ target lobsters when this behavioral measure was used ($\chi^2 = 1.71$, d.f. = 2, $P > .05$).

During agonistic encounters ten acts were scored: approach, meral spread, antenna touch, claw touch, fight, freeze, back, slow withdrawal, rapid withdrawal, and abdominal flex (10). A two-way analysis of variance tested the effects of molt state and sex on the frequency and duration of each act. We will address only the effect of molt state in this report. In eight of the ten acts, there was a significant difference ($\alpha = .05$) attributable to the molt state in the mean frequency [meral spread: $F(6, 49) = 8.45$; abdominal flex: $F(6, 49) = 8.11$] or duration [approach: $F(6, 49) = 7.46$; rapid withdrawal: $F(6, 49) = 15.27$] (Fig. 1). Only claw touch and slow withdrawal did not statistically differ with molt state. The Student-Newman-Keuls test for multiple comparisons among means based on unequal sample sizes was used to determine where differences existed (which molt states were to be grouped). Each act varied uniquely with molt state, but there were several typical trends in the data (Fig. 1). During the

Table 1. Number of target lobsters in seven molt states grouped by social rank on the basis of an individual's time spent in winning, even, or losing agonistic encounters with state C (control) lobsters.

Molt state	Social rank		
	Dominant	Equal	Subordinate
A	0	0	5
B	0	0	10
C	4	3	7
D ₀	1	3	8
D ₁	9	1	1
D ₂	4	3	0
D ₃	0	0	7

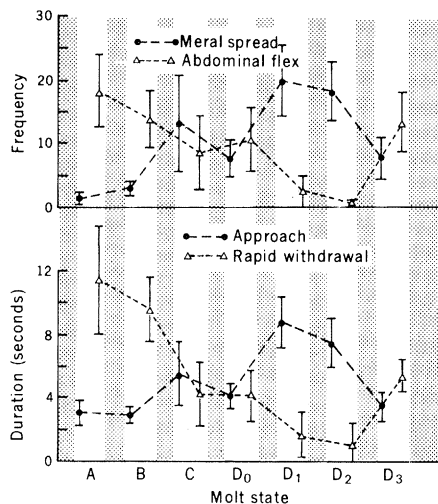


Fig. 1. Two common trends for the frequency and duration of agonistic acts for target lobsters. Measures were recorded for individuals; values were pooled for individuals within a given molt state. A mean \pm 2 standard errors was computed from the pooled data. Trend lines are added as an aid in visualizing the relationships.

midphase of proecdysis, approach and meral spread, a threat posture, were observed for greater durations and more frequently, while there was a corresponding marked decrease in the frequency and duration of such avoidance acts as abdominal flex and rapid withdrawal.

Agonistic encounters consisted of sequence of acts. Sequences were subdivided into two-act sets called dyads. The second act of one dyad was also considered the initial act of the next dyad. Dyads were categorized as aggressive and submissive (Fig. 2), and their distribution was tested for independence of molt state. The D₀ lobsters were significantly less aggressive than target lobsters in state C ($\chi^2 = 16.29$, d.f. = 1, $P < .001$).

Additional observations of a descriptive nature support these findings. Lobsters in postecdysis states A and B primarily displayed evasive actions when encountering their state C opponents. Fights were rarely initiated, never won, and, for state A animals, usually resulted in appendage loss and death. In C-C pairs, dominance was often closely contested: subordinates did not consistently lose encounters, and fights were frequently slowly enacted and stylized in form, suggesting ritualized behavior (11). Antenna whipping, which we interpret as another threat posture, was commonly observed. The D₀ lobsters characteristically displayed an "ambivalent" agonistic behavior, such as repeated sequences of approach→antenna or claw touch→back→freeze→back→approach. Lob-

sters in D₀ also exhibited occasional abdominal flexes, apparently in vacuo. There was a dramatic change in agonistic behavior with the onset of D₁. These animals approached, charged, and followed control lobsters. During these episodes, D₁ lobsters often maintained an exaggerated meral spread, a greatly elevated stance with the chelae held very high and widely separated. The D₂ lobsters responded similarly, but their agonistic behavior seemed less directed. Instead, D₂ animals would rush toward and then past their opponent and wander around the tank displaying a meral spread. Fights, when they occurred in D₂-C pairs, were customarily lengthy. In early encounters, D₃ lobsters appeared aggressive, displaying meral spreads and charging opponents. However, fights were usually terminated by the often abrupt withdrawal of the target animal. After several such encounters, fights became rare and D₃ lobsters displayed an "ambivalent" response similar to that described for D₀ lobsters. Abdomen flexing, in vacuo, was again often observed. One D₃ animal displayed a bout of 14 successive abdominal flexes.

We suspect that the submissiveness of A, B, and D₃ lobsters was attributed, to a large extent, to limited shell hardness. In postecdysis, calcification is incomplete, and in D₃ the cuticle is decalcifying, especially in the joints (5-7). In D₀, many of the processes preparatory for ecdysis are initiated (5-7). Perhaps the surprising submissiveness of D₀ lobsters indicates their rapidly changing internal state. During D₁ and D₂, there is a great increase of ecdysones in serum titers in *H. americanus* as well as in other crustaceans (2, 12). These hormones are generally thought of as the molting hormones in crustaceans, but injections of an ecdysone may also affect the aggressive behavior of stomatopods (13).

The adaptive significance of changing aggressive states with respect to molt condition in wild populations of *H. americanus* has yet to be determined. In the laboratory, lobsters molt inside shelter, if provided, and remain inactive, avoiding contact with conspecifics until their integument hardens (14). The same is to be expected for wild populations. The heightened aggressive state in D₁ and D₂ probably reflects the behavior necessary for the acquisition and defense of optimum shelter before ecdysis. By D₃, lobsters are obviously preparing for the imminent molt. Their feeding ceases or is greatly reduced (15) and activities such as burrowing and grooming occupy much of their time. As we have shown, their aggressiveness is minimal. In the

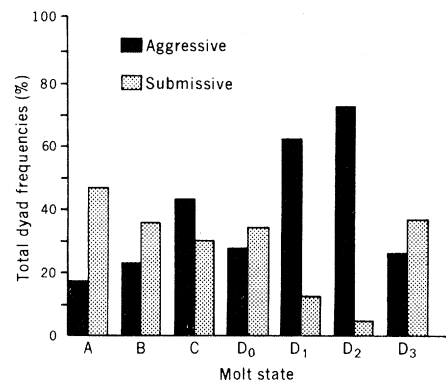


Fig. 2. Aggressive and submissive dyad frequencies for target lobsters. An aggressive dyad was considered an act of fight, meral spread, claw touch, antenna touch, or approach followed by another act from this group. Subordinate dyads included all acts of freeze, slow withdrawal, back, rapid withdrawal, and abdomen flex followed by another act from this group. Frequencies were expressed as a percentage of agonistic dyads observed for all target lobsters within a given molt state.

field, individuals in late proecdysis presumably would be inside their burrows awaiting ecdysis.

Behavioral scaling of aggression has been reported in response to changes in population density, habitat quality, food availability, and season or life stage (16). To our knowledge, this is the first documentation of such behavioral scaling in relation to the molt cycle of a crustacean. Often in studies of crustacean behavior, it is simply stated that the subjects were "hard-shelled" or "inter-molt." Our observations indicate that this description may not be sufficient and may explain some of the variability reported in other studies of crustacean agonistic behavior.

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Behavioral Thermoregulation: Orientation Toward the Sun in Herring Gulls

Abstract. *Orientation toward the sun combined with postural changes minimized the net radiation gain on the adult herring gull during the breeding season. The decrease in absorbed solar radiation was due to reduced surface area exposed to direct sunlight and to reduced absorptivity since, when the bird orients toward the sun, the angle of incidence is such that only the white surfaces receive direct sunlight. At low wind velocities (0 to 0.6 meter per second) and ambient temperatures above the lower critical temperature, the birds rotated 180 degrees during the day, always facing the sun.*

The ability to select or construct a favorable thermal environment is an important aspect of thermoregulation in birds. This is especially true during the breeding season, since a minimum of thermal stress from temperature, wind, and solar radiation is extremely important to the eggs, the nestlings, and the incubating adult. Various behavior patterns in response to thermal stress during the breeding season have been observed in the wild. Desert birds have been observed to build nests in the shade (1), to build roofed nests in exposed situations (2), or to orient the nest to avoid mid-day sun (3). Calder (4) has shown that hummingbirds build their nests under branches, thus avoiding radiation loss to the cold night sky. Except for a few studies (5), investigations to date deal with birds that build protective nests or that nest in a sheltered area. The synergistic effects of wind, solar radiation, and ambient temperature on the energetics of birds nesting in open areas with little nest construction need further investigation.

This report deals with the effects of wind, solar radiation, and ambient temperature on the energetics of the herring gull (*Larus argentatus*). Four basic questions were asked. (i) Which is more stressful to the gull, low ambient temperature (T_a) or high T_a ? (ii) What effect does solar radiation have on the energetics? (iii) Can plumage color affect the use of solar radiation? (iv) What behavioral and physiological mechanisms

can the gull use to overcome thermal stress?

We studied a herring gull colony during the 1977 breeding season, at the U.S. Steel calcite quarry in Rogers City, Michigan. The birds were on the territory from the first of April through July. The environmental parameters measured in the field were solar radiation (R_s), diffuse radiation (R_d), atmospheric radiation (R_a), ground radiation (R_g), reflected radiation (R_r), wind velocity, ambient temperature, ground temperature (T_g), and sky temperature (6). We also monitored the dorsal and ventral surface temperatures of the birds when they were facing toward and away from the sun (7). Standard metabolic rate, body temperature, and foot temperature were measured in the laboratory over an ambient

temperature range of -10° to 35°C (8).

The lower critical temperature (T_{LC}), not sharply defined, lies between 5° and 10°C ; the metabolic rate at ambient temperatures between T_{LC} and -10°C increases only 1.7-fold (Fig. 1). This suggests that the adult gulls (1000 g) are well adapted to a cold climate. In general, birds can increase their metabolism three to five times basal by shivering thermogenesis. A threefold increase would mean that the herring gull could maintain its body temperature without solar radiation at an ambient temperature of approximately -45°C .

During April and May in the field, at T_a 's between 5° and 12°C , birds sitting on the nest in direct sunlight panted, which indicates that the upper critical temperature (30°C without sunlight) was shifted down. Birds standing at T_a 's between 5° and 12°C were not observed to pant. This is explained by the fact that the feet are important avenues of heat loss, the foot temperature exceeding the T_a at all temperatures above the T_{LC} (Fig. 1). Other investigators (9) have shown that the feet of the herring gulls are important to heat loss.

It is known from previous studies by Lustick (10) and Hamilton and Heppner (11) that dark plumage absorbs more solar radiation than light plumage. In the visible spectrum, where 40 percent of the solar energy lies, white plumage absorbs approximately 10 percent (10) of the solar energy while the gray plumage absorbs approximately 50 percent (12). Thus, if the darker surface of the gulls were facing toward the sun the birds would gain more heat from radiation than if they faced the sun with their white surfaces. In direct sunlight, the surface temperature of the gray plumage increased to as much as 15°C above T_a , compared to 4°C above T_a for the white plumage (Fig. 2). The temperatures of the surfaces not receiving direct sunlight

Fig. 1. The relationship of metabolic rate (solid circles), mean foot temperature (f), and mean body temperature (b) to ambient temperature (T_a). The regression line relating metabolism to T_a was fitted by the method of least squares ($\text{W/kg} = 6.63 - 0.174 T_a$). The dashed line is the temperature equilibration line. A total of six adult gulls were used in this study.

