uated, it was decided to compare parasitemias on day 5 in animals from four of the groups: thymectomized animals treated with antilymphocyte serum were compared with those in the sham-operated group treated with normal serum; also, the group treated with antilymphocyte serum alone was compared with that treated only with normal rabbit serum (Table 1). There was a significant ($P < .02$, Wilcoxon test) depression of parasitemia in each of the groups treated with antilymphocyte serum as compared with its appropriate control.

These studies demonstrate the protective effect of the administration of antilymphocyte serum on *P. berghei* infection in mice. It appears that adult thymectomy, in this system, has little additive effect. This fact suggests that the suppression of humoral immune mechanisms may be more important than the inhibition of cellular immunity in the observed protection, for adult thymectomy seems mainly to potentiate the effect of antilymphocyte serum on cellular immune mechanisms (*6*). With regard to the role of humoral immune factors in malaria, McGhee (*4*) presented evidence that the development of the anemia in ducklings with malaria could not be correlated with parasitemia, and he speculated that at least part of the observed destruction of erythrocytes might be due to the concomitant development of an autoimmune reaction to host erythrocytes. Similarly, the thrombocytopenia regularly seen in malaria (*8*) seems also related in some way to the development of the immune response (*9*).

Thus, the results of our experiments might be interpreted as follows. Impairment of the immune response is actually of transient benefit to the host with a fulminating plasmodial infection in that it permits longer circulation of erythrocytes and ultimate prolongation of survival. If such were the case, one might expect that the degree of parasitemia in the immunosuppressed animals should be equal to that in the control group; but we have shown that parasitemia is suppressed (Table 1). Hence, antilymphocyte serum may have an intrinsic antiparasitic effect.

Using a different model system, Wright (*10*) has described the effect of neonatal thymectomy in hamsters infected with *P. berghei*. In this species, the infection is usually fatal in 6 to 12 days. Animals thymectomized at birth survived significantly longer (death occurring between 19 and 25 days), even though their hemoglobin concentrations and parasite levels were similar to those of nonthymectomized animals earlier in the course of the infection. Wright proposed that neonatal thymectomy inhibited or delayed production of immune responses which lead, in control animals, to microembolization of the cerebral capillaries with agglutinated parasitized erythrocytes.

Brown *et al.* (*11*) described the effect of neonatal thymectomy on the course of *P. berghei* infection in rats. In the rat, immunity to *P. berghei* develops rapidly, and clearing of parasitemia occurs with ultimate survival of most animals. Among adult rats that were thymectomized at birth the mortality was higher and the duration of parasitemia was longer. Since cell-mediated immunity is most strikingly depressed by neonatal thymectomy, Brown *et al.* postulated that such immune mechanisms may play a part in the resolution of malarial infections.

Thus, these studies show that the immune response itself contributes significantly to the death of animals undergoing a fulminating malarial infection. But, in those infections where the immune response eventually brings about control of the parasitemia, immunosuppression is deleterious.

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References and Notes

1. J. P. Thurston, *Exp. Parasitol.* **2**, 311 (1953).
2. B. T. Wellde, N. T. Briggs, E. H. Sadun, *Mil. Med.* **131**, 859 (1966).
3. H. W. Cox, *ibid.*, p. 1195; J. N. George, E. F. Stokes, D. J. Wicker, M. E. Conrad, *ibid.*, p. 1217.
4. A. B. McGhee, *J. Infec. Dis.* **107**, 410 (1960); *Amer. J. Trop. Med. Hyg.* **13**, 219 (1964).
5. A. Zuckerman, *Nature* **185**, 189 (1960); *Mil. Med.* **131**, 1201 (1966).
6. A. P. Monaco, M. L. Wood, P. S. Russell, *Science* **149**, 432 (1965).
7. L. K. Martin, A. Einheber, E. H. Sadun, R. E. Wren, *Exp. Parasitol.* **20**, 186 (1967); R. R. MacGregor, J. N. Sheagren, S. M. Wolff, *J. Immunol.* **102**, 131 (1969).
8. G. J. Hill, V. Knight, G. M. Jeffery, *Lancet* **1964-I**, 240 (1964).
9. J. N. Sheagren, N. R. Shulman, W. A. Sodeman, Jr., *Clin. Res.* **16**, 313 (1968).
10. D. H. Wright, *Brit. J. Exp. Pathol.* **49**, 33 (1968).
11. I. N. Brown, A. C. Allison, R. B. Taylor, *Nature* **219**, 242 (1968).
12. The technical assistance of I. Barrett, J. Edelin, and D. Lawless is acknowledged. Dr. D. Alling assisted with the statistical analyses.

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Queuing Behavior of Spiny Lobsters

Abstract. *Autumnal mass migrations of spiny lobsters,* Panulirus argus, *involve diurnal movements of thousands of individuals in single-file queues. Initiation, posture, and alignment of a queue can be effected entirely by tactile cues received through antennular inner rami, pereiopods, and antennae. Since spiny lobsters queue when deprived of shelter, this behavior may serve a defensive function. Specimens captured while migrating maintain the queue indoors for up to several weeks, whereas at other times the queue lasts only a few hours. Hence, the migratory behavior probably depends in part upon environmentally induced neurohormonal changes.*

The occurrence of "columns" or "trains" of spiny lobsters, *Panulirus argus*, moving over open areas was reported as early as 1922 (*1–3*), but the extent and significance of the phenomenon has remained inadequately described. In autumn, thousands of lobsters migrate diurnally in parallel single-file queues across shallow areas near Bimini, Bahamas, and the Florida east coast (*4, 5*). This activity is remarkable since spiny lobsters are usually seclusive by day, remaining in crevices on the reef and emerging at night to feed.

The widespread occurrence, periodicity, and large numbers of individuals involved, as well as the stereotyped behavioral character of the queues, clearly defines this phenomenon and suggests previously unrecognized significance of these migrations in the life history of the species. Furthermore, the mode of mass movement, which outwardly resembles migrations of army ants and certain bird flocks, and its abrupt nature make it unique among benthic marine crustaceans (*3*). I now present some major behavioral characteristics of the single-file formation, evidence for internal influences, and offer hypotheses to explain causal and functional aspects of the migrations.

The following analysis of postural and behavioral elements was derived from observations of 325 queues involving 20 captive lobsters (7.0 to 12.0 cm carapace length) in a 2 m diameter vinyl-lined pool. Particular attention was directed at determining the mode of queue formation and mechanism of queue maintenance.

Normal appearing lobsters with all appendages intact most often queued by approaching the posterior of another moving individual until antennal contact was made (Figs. 1 and 2a). Such behavior suggested initial visual orientation during queue formation. The approaching lobster then turned until both antennular inner rami touched the other's abdomen, thus completing alignment. Constant physical contact was maintained with the preceding individual by either the antennular inner rami, anterior pereiopods, or antennae (Figs. 1 and 2b). The antennular inner rami were most often involved (88 percent) and made intermittent contact every few seconds for the duration of the queue (*6*). The pereiopods either touched or hooked around the telson of the lobster ahead in 51 percent of queuing individuals and always during the times the antennules were not in contact. In 19 percent of the cases one or both antennae were brought into contact for several seconds but were otherwise held slightly forward of a line perpendicular to the direction of movement. I did not observe normal lobsters maintaining alignment without physical contact.

The relative importance of visual versus tactile stimuli was further investigated on specimens blinded by opaque tape. After an acclimation period of several hours, the blinded lobsters readily queued but only after their antennae or antennules were touched by another lobster (Fig. 2c). After initial contact, a blinded individual turned neatly into alignment and maintained appendicular contact, posture, and position equivalent to that of unblinded specimens (Fig. 2d). These results tended to rule out the influence of waterborne chemicals in queue formation and emphasized the importance of tactile stimuli.

The effect of loss of the extensively used antennules was investigated by taping them to the posterior surface of the antennae. Individuals so treated queued in the same way as normal lobsters (Fig. 2e), but they aligned themselves by hooking the anteriormost pereiopods around the telson of the preceding lobster and usually maintained contact in this way for the duration of the queue (Fig. 2f, 92 percent). Position was maintained as long as the path was reasonably straight but misalignment occurred during sharp turns when the pereiopods often lost contact. Hence, either pereiopod or antennular contact was necessary for proper queue maintenance although the antennules alone were more effective than the walking legs.

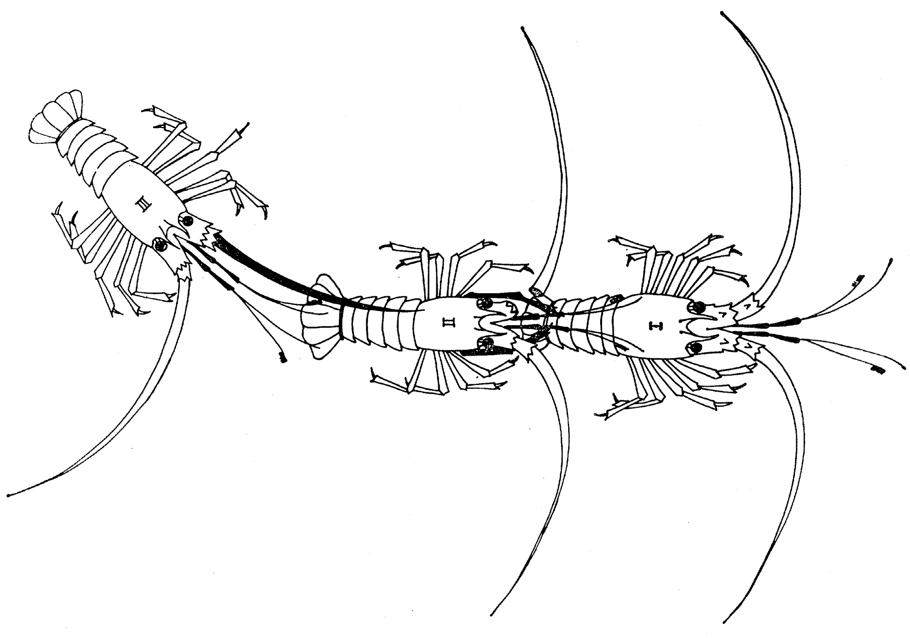

Fig. 1. Illustration of appendicular usage in queuing behavior of the spiny lobster *Panulirus argus*; appendages involved are blacked in. Lobster III joins the queue after touching lobster II with an extended antenna and turning until both antennular inner rami touch the sides of II. Lobster II maintains queue alignment either by frequent intermittent flicks of the antennules against lobster I, grasping or touching I with extended anterior pereiopods, or both. Antennae, antennular inner rami, and pereiopod tips are sensitive to tactile stimulation.

Evidence presented thus far suggests that queuing in light was apparently initiated most frequently by visual cues associated with movement of other lobsters within the visual field of an individual. Supplementary experiments indicated that acoustic or waterborne olfactory cues were not responsible for queue formation or maintenance (*7*). Tactile stimuli, taste or touch or both, seemed necessary for proper maintenance of the queue at all times and also served to initiate column formation in the absence of visual cues. This suggests that spiny lobsters are able to effectively form and maintain the single file at night and under conditions of poor visibility such as during the autumnal mass migrations when the water is often cloudy.

Appendicular-receptor usage in the queue was hierarchially arranged with antennular inner rami playing the major role, followed by the anterior pereiopods and the antennae (Fig. 2). Accordingly, deprivation of antennular sensitivity resulted in substitution by the pereiopods while removal of each pair of anterior pereiopods was followed by substitution of the next posterior pair. Loss of antennae or vision, seldom used by normal specimens, had little effect.

Lobsters captured during nonmigratory periods, as well as those captured from migrating columns, queued under controlled conditions. However, the overall activity patterns and responses to certain stimuli differed markedly between the two groups.

One dozen nonmigratory lobsters (7 to 12 cm carapace length) in rectangular tanks tended to gather in the corners, or other sheltered areas, and became inactive. However, when released in a large circular vinyl pool (2 m diameter, 20 cm depth), they immediately formed queues of two to six individuals. The queues moved over the open sand substrate in tortuous paths or around the perimeter for periods averaging about 40 seconds. Individuals then broke away and wandered to join other queues or became inactive for several minutes. The frequency of queue formation decreased after 1 hour until most of the lobsters gathered in stationary clusters along the pool perimeter. However, queuing could be reinitiated by transferring the animals for several hours to tanks providing shelter, then reintroducing them to the pool.

Lobsters captured during a mass migration (transported within 3 hours to a pool) also queued but, in contrast to the nonmigratory specimens, continued this activity for an extensive period. Four lobsters (7.0 to 10.0 cm carapace length) continuously marched around the perimeter at a rate of approximately 6 m/min for the first 6 hours after introduction. Subsequent monitoring at various intervals each day revealed that these lobsters filed nearly continuously for 33 days, both during the day and at night (in dim light).

Responses to food and shelter by the migrating lobsters were markedly different from those of nonmigratory individuals. The latter readily took up residence in concrete block shelters and fed heavily after several days of starvation. By contrast, the migratory specimens ate part of the cut shrimp provided or briefly investigated the concrete blocks, then resumed the queue. They finally took up residence in the shelters on the 33rd day after a gradual increase over the final 2 weeks in periods of erratic individual wandering and quiescence.

The function and causation of queuing behavior and of the mass single-file migrations cannot, as yet, be explained fully although the available evidence yields several conclusions and suggests reasonable hypotheses. Field observations and the above information from captive specimens indicate that spiny lobsters are induced to queue when moving over relatively open areas. At such times the formation may serve a defensive function. The vulnerable abdomen, ordinarily protected while a lobster faces outward from a crevice, is "protected" in the queue by the spinous cephalothorax of each trailing individual (with the obvious exception of the last in line). The defensive function of the file may be particularly important during the mass migrations when the lobsters are exposed for extensive periods.

Internal physiological changes are probably responsible, at least in part, for the mass movements as indicated by the contrast in the behavior between captive migratory and nonmigratory individuals under similar external conditions. The continuous file activity is interpreted as a form of migratory restlessness (Zugunruhe), usually associated with captive birds. This migratory internal state may be brought on by developmental processes (such as growth or molt) or by seasonal changes in daylength, temperature, or other bioenvironmental factors. However, the actual migratory movement in a locality is probably induced by the abrupt changes in physical conditions accompanying storms which immediately precede the migrations.

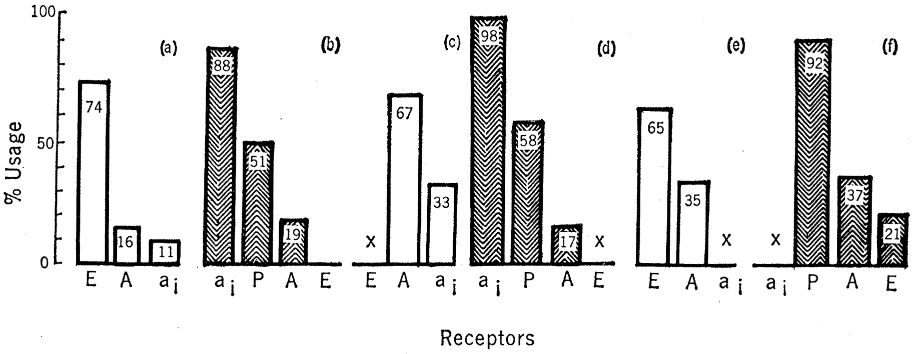

Fig. 2. Histograms showing the proportion of appendicular-receptor usage by captive spiny lobsters during queue formation (unshaded) and maintenance (shaded). (a) Normal lobsters during queue formation (number observed, $n = 19$); (b) maintenance ($n = 87$). (c) Blinded lobsters during queue formation ($n = 18$); (d) maintenance ($n = 60$). (e) Antennule-deprived lobsters during queue formation ($n = 20$); (f) maintenance ($n = 72$). *E*, Eyes-vision; *A*, antennae; a_i, antennule inner rami; *P*, anterior pereiopods; and x, receptor sensitivity eliminated.

The direction of migration seems characteristic for a given population; for example, files moved southwest at Bimini and northeast at Boca Raton. Each individual in the population may be initially capable of orienting in this heading, as in the case of escape movements by fiddler crabs (*8*), or directional information may be communicated by the queuing behavior. In any event, individuals other than the leader adopted the original bearing after the foremost lobster was removed.

This question of orientation by a benthic animal is of special interest since the directional movements occurred when the sky was overcast, the sea surface turbulent, and currents and bottom slope variable. Such conditions complicate postulating orientation mechanisms such as a celestial-compass, chemorheotaxy, pressure perception, or sound localization used to explain migrations in birds, fishes, and turtles (*9*). The single-file migratory behavior may share the navigational capabilities indicated by homing experiments in which 20 percent of released lobsters returned to a home area from distances of up to 2 miles and depths of more than 500 m (*10*).

The adaptive significance of autumnal mass migrations has not been determined. Available evidence argues against a reproductive function since females do not carry spermatophores until spring (*11*). Possible functions being examined are: attainment of better feeding grounds (*2*), attainment of maximum shelter for molting (*12*), local dispersal, and reduction of population pressure.

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References and Notes

1. D. E. Crawford and W. J. J. DeSmidt, *Bull. U.S. Bur. Fish.* **38**, 28, 281 (1922).
2. C. E. Dawson and C. P. Idyll, *Fla. State Board Conserv. Tech. Ser.* No. 2, 39 (1951).
3. R. Bainbridge, in *The Physiology of Crustacea*, T. Waterman, Ed. (Academic Press, New York, 1961), vol. 2, pp. 431–463.
4. W. F. Herrnkind and W. C. Cummings, *Bull. Mar. Sci.* **14**, 123 (1964).
5. I witnessed a mass migration on 22 October 1965, near Hilsboro lighthouse and was reliably informed by individuals from the Bureau of Commercial Fisheries of another occurrence at Boynton Beach on 1 October 1965. Another migration occurred near Boca Raton in the fall of 1966.
6. D. M. Maynard and H. Dingle, *Z. Vergl. Physiol.* **46**, 515 (1963).
7. W. Herrnkind, in preparation.
8. ———, *Amer. Zool.* **8**, 585 (1968).
9. R. M. Storm, Ed., *Animal Orientation and Navigation* (Oregon State Univ. Press, Corvallis, 1967).
10. E. P. Creaser and D. Travis, *Science* **112**, 169 (1950).
11. A. B. Williams, *U.S. Dep. Interior Fish. Bull.* **65**, 91 (1965).
12. C. Von Bonde, *Fla. State Board Conserv. Tech. Ser.* No. 2, 29 (1951).
13. I thank Dr. A. A. Myrberg, Jr., P. B. Wright, S. Ha, and J. D. Richard of the Institute of Marine Science, University of Miami, Florida, for aid and facilities. I appreciate the assistance of Dr. R. Mariscal in preparation of the manuscript. Miss L. Spence prepared the illustrations.

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