al. (2) also noted effects of both repeated and alternated events and related their results to the "unexpectedness" of the outcome.

24. The discriminant score is a combined measure of the N200, P300, and SW components of the ERP at the three electrode sites that was developed according to a stepwise discriminant analysis procedure (*26*), which optimally discriminates between ERP's elicited by rare and frequent stimuli (*3, 4*). The use of such a statistic has certain advantages; since it is a combined measure of several ERP amplitudes, it is less susceptible to EEG noise than individual base-to-peak amplitudes, it includes more waveform information, and it is a measure that can be applied to any subject's data without adjustment. The latencies at which ERP amplitudes were taken for inclusion in the discriminant score were 104, 188, 248, 320, 356, and 380 msec for F_z; 128, 236, 332, 356, 380, and 668 msec for C_z; and 224, 344, 380, 476, 536, and 572 msec for P_z.
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26. Combining data across stimuli was justified, because the tree structures for each were essentially identical. A repeated measures analysis of variance yielded a significant sequence effect [$F(30,180) = 106.5$, $P < .001$], but the effect of differing signals was nonsignificant, as was the signal by sequence interaction. High-pitched tones (counted by the subject), however, tended to yield larger discriminant scores than the low-pitched tones. This counting effect was significant ($P < .01$) when we tested it using difference scores for matched pairs of fifth-order sequences, but it was small relative to the sequence effect.

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Drag Reduction by Formation Movement in Spiny Lobsters

Abstract. *Movements of spiny lobsters (*Panulirus argus*) in formation reduce drag during locomotion; such movement is of particular significance during mass migration. Queues (single-file lines) of spiny lobsters sustain less drag per individual than do individual lobsters moving at the same speed. It is proposed that queuing behavior conserves energy and is a consequence of the evolutionary role of migration in this particular species.*

A wide variety of animals assemble in stable aggregations or formations, either stationary or moving. The immediate adaptive significance of such formations is often far from obvious, despite its self-evident germaneness to current concern with the evolution of social behavior.

Schooling of fish, herding of mammals, flocking of birds, and swarming of insects seem to provide protection against predation (*1*). Other advantages of aggregation relate to thermoregulation, mating efficiency, finding food, pooling of orientational information, learning, and reducing aggression. An advantage occasionally suggested but infrequently demonstrated is that energy is saved during long-distance locomotion, for example, that V formations of geese and some other birds reduce drag and increase lift; this hypothesis is supported by mathematical models but remains unconfirmed (*2*). We now present experimental evidence that precise, single-file line formations or queues conserve energy by reducing drag during group migratory movements of the spiny lobster, *Panulirus argus* (*3*).

Queuing is most prevalent during autumnal mass migrations during which thousands of spiny lobsters traverse open bottom, day and night, for periods of at least several days (*4, 5*). Queues of as many as 65 individuals are maintained through tactile contact by the antennular rami and first pereiopods of each lobster with the extended abdomen of the lobster ahead. Queuing and clustering of lobsters may deter predatory fish by presenting them with a barrier of antennae. Queuing may also facilitate the pooling of orientational information and the leadership by the best-oriented individuals at any instant. But a basic physical advantage may result from improved hydrodynamic performance through reducing drag.

From an analysis of film and field data, we constructed a model of a typical queue. Walking speed, proper interlobster positioning, and posture were determined from 35-mm color slides and 16-mm color cine film taken during mass migrations near Bimini, Bahamas. Measures of queue size and length of migratory lobsters were based on field data (*4, 5*). Carapace lengths (CL) of migrating lobsters at Bimini ranged from 55 to 126 mm with a mean of approximately 83 mm (1969, 84.6 mm; 1971, 82.1 mm). There was no apparent correlation between lobster size and position within a queue. The interlobster distance was measured between the trailing edge of the lead lobster carapace and the base of the rostral horns of the following lobster (range, 7 to 34 cm; $\bar{X} = 16$ cm). This distance is limited by the length of the inner rami of the follower's antennules and the length of the abdomen of the lobster ahead. The angle between antennae, which the slowly moving lobsters constantly waved, was approximately inversely proportional to queue speed ($\bar{X} = 150°$ at 15 cm/sec; $\bar{X} = 92°$ at 28 cm/sec; minimum recorded angle, 30° at 28 cm/sec).

Queues ranged from 2 to 65 individuals during migrations, although isolated individuals and small queues (fewer than six lobsters) often resulted when long queues were fragmented by intense fishing with nets by lobstermen. Lobsters maintained larger queues in undisturbed areas. While marching on level substrate, lobsters stand erect, with the body axis held horizontal approximately 5 cm (85 mm CL lobster) above the substrate.

Lobsters migrate at a rate that ranges from 15 cm/sec for queues just forming to 35 cm/sec for well-formed queues moving over open areas ($\bar{X} = 28$ cm/sec). During ultrasonic tracking studies, average walking speeds of 28 cm/sec were recorded for individual lobsters over distances up to several kilometers. Individual lobsters walked at maximum rates of 30 to 34 cm/sec for 10 to 30 m during orientation experiments ($\bar{X} = 21$ cm/sec, $N = 23$).

A plywood tow tank (10 m long by 1 m wide by 0.75 m deep) filled with freshwater was used to test the drag-reduction hypothesis. A variable-speed electric capstan was used to pull preserved lobsters on a nylon monofilament line (0.6 mm diameter). A weighted pendulum with an idler pulley, through which the towline was threaded, measured force in degrees of deflection, which was then converted to newtons (*6*).

For test models, lobsters with all appendages were preserved in 10 percent solution of formalin in seawater. Pieces of Styrofoam were placed inside the carapace dorsal to the approximate center of gravity so that the average density of each lobster was slightly greater than that of freshwater, and friction with the tank floor was essentially eliminated. Lobsters of the appropriate size range were connected in queues with thin stainless steel wire.

Two sources of error arose from using preserved specimens. We could not determine the drag associated with movements of the walking legs or antennae during locomotion, and our models could not make instantaneous trim adjustments, which, in living animals, might normally influence both lift and drag. However, neither of the inaccuracies seems sufficiently large to influence the interpretation of the data.

In initial experiments, we measured both individual drag and queue drag at varying speeds, keeping antennal angle and interlobster distance constant at

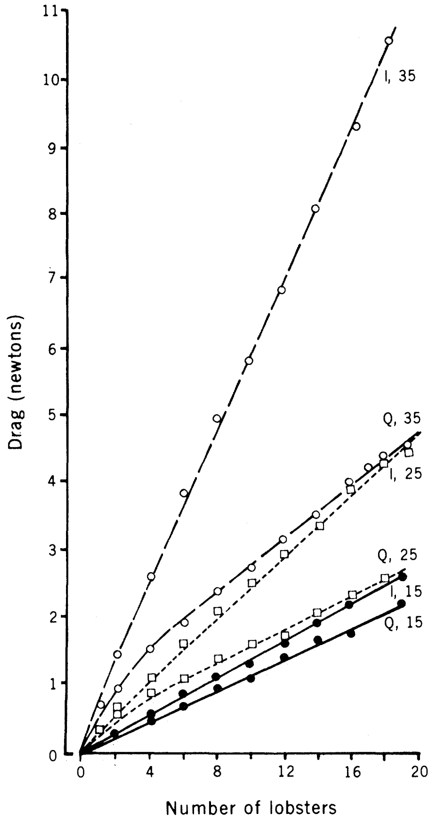

Fig. 1. Results of experiments in a tow tank with individuals and queues of preserved spiny lobsters towed at 15 (○), 25 (□), and 35 (●) cm/sec. Proportional drag reduction for queues compared with the cumulated value for the same lobsters towed individually is apparent at all three speeds, but it was most prominent at 35 cm/sec, a speed that approximates the maximum sustained walking speed of queuing migrant lobsters. Abbreviations: *I*, individuals; *Q*, queues.

their measured means. Each lobster was towed individually at 15, 25, and 35 cm/sec (N = 19; range 70 to 108 mm CL; $\bar{X}$ = 89.8 mm). Drag was summed for the individuals and compared with that for queues reconstructed from the same individuals towed at the same speeds (Fig. 1).

Hydrodynamic performance is improved by queuing, and the benefit of queuing varies directly with speed. At 35 cm/sec, a queue of 19 lobsters reduces drag by 65 percent compared with that of 19 lobsters tested individually; at 15 cm/sec, drag is reduced by only 10 percent. In effect, a moving envelope of water behind a moving lobster surrounds a follower, which thus experiences reduced drag (*7*).

The greater the spread of the antennae, the greater is the drag (Fig. 2). The observed mean (92°) is not the most economical. For example, at 33 cm/sec the reduction of antennal spread in a queue of five from 92° to 40° reduced the drag from 1.7 to 1.4 newtons. Thus, the decrease in angle between antennae as migrants increased speed yields a substantial drag reduction. The spacing of queue members also influences drag. For a queue of five moving at 35 cm/sec, drag does not significantly increase between the mean interlobster distance of 16 cm and about 30 cm; at greater interlobster distances, drag increases markedly. Individual size affects drag as expected; the larger the lobster, the greater the drag. The drag of a lobster essentially doubles between 70 mm CL and 108 mm CL at tow speeds of 15, 25, and 35 cm/sec (antennal angle constant).

The behavioral features of queuing are appropriate to the proposed function of energy conservation. Queue leadership changes spontaneously during migration as a result of splitting or joining of queues and because of external disruptions; such changes spread the high-drag positions among the group and reduce leader fatigue (*8*). Maintaining a queue tactually ensures appropriate interlobster distances. The tendency to maintain constant contact during path changes reduces the possibility that the lobsters will separate farther than the most effective interlobster distance. Such separations might cost considerable energy by requiring that the separated lobster move faster in order to rejoin the group.

As a result of the strong tendency for migrants to aggregate, most of the populations we studied move in queues of six or more individuals (77.8 percent in 1969, 88.9 percent in 1971). Although our data suggest no upper limit to queue size, two opposing factors may operate. First, as queue size increases, the average drag per individual decreases, since each spends less time in the lead position. However, very long queues may be subject to more breaks in rank as a result of topographic irregularities or other disturbances. We observed long queues (40 lobsters per queue) only over level, unobstructed sand substrate.

The observed reduction in antennal angle at increased queue speeds decreases drag even though the angle generally exceeds the minimal drag position (30° or less). Our photographs show that the antennal tips of walking lobsters always cover a frontal distance approximating or exceeding the lateral spread of the legs during locomotion. Spreading the antennae may serve either to stabilize the lobster as it is buffeted by waves or as an adaptation for tactually sensing objects ahead when visibility is reduced.

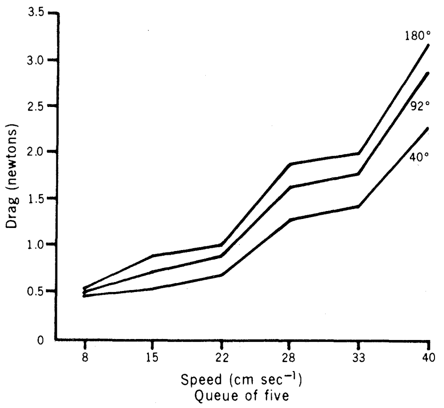

Fig. 2. Influence of the angle between antennae on drag of a queue of five preserved spiny lobsters at different speeds. Reduction of drag with decreasing antennal angle becomes more significant at higher speeds, a result consistent with the antennal posture of migrants observed in the field.

Queuing is particularly evident during autumnal mass migrations. Queuing coincided with striking population increases at Bimini over periods of several weeks in late October and early November during each year of observation (1969, 1971 to 1975). Of lobsters observed in mass locomotion, 98 percent queued in 1969 and 1971 (*4*). Queuing migrants maintain nearly continuous locomotion for periods exceeding several hours. In captivity, nearly constant queuing occurred for periods as long as 14 hours per day in groups of seven to ten migrants in pools 2 m in diameter (*9*). Spiny lobsters apparently queue for well over half of the day at the peak of migration.

Our data suggest that queuing increases the distance covered for a given metabolic cost. For example, lobsters in a queue of 19 can maintain a pace of 35 cm/sec at the same drag as lobsters walking individually at only 25 cm/sec. An additional advantage may accrue from drag reduction when the migrants head into currents or the bottom surge from swells, both prevalent hydrodynamic features of the migratory pathway at Bimini. We roughly measured current speeds of 5 to 15 cm/sec and surge velocities of approximately 30 cm/sec at the time of migration. Thus, migrants walking into the current and wave path may encounter maximum water speeds exceeding 75 cm/sec. Another possible advantage might be an increase in walking speed of slower lobsters (for example, small individuals or those with missing pereiopods).

These initial results support the hypothesis that the curious queuing phenomenon in *P. argus* reduces drag and thereby increases speed or conserves energy during group locomotion. Field observations suggest that queuing is especially significant during autumnal mass migrations. Because queuing behavior during mass migration is thus far known only in *P. argus*, it seems that this species was subject to some selective pressures different from its congeners, which was directed toward increasing locomotor efficiency (*10*). Other, less easily measured phenomena may serve similar functions in formation movements of other aquatic, terrestrial, and aerial species. While continuing to investigate both the hydrodynamic mechanism and the evolutionary significance of queuing, we suggest that it potentially serves other important biological functions, for example, in defense against predation and for group orientation. However, such functions are considerably more difficult to examine experimentally.

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8. Naturally queuing lobsters commonly changed the lead spontaneously, although the behavior was not rigorously quantified because some queue members looked alike. However, time-lapse photographs taken in circular pools 2 m in diameter showed leadership shared by all members of groups of four to seven marked lobsters (P. Kanciruk, in preparation).
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10. Migration is characteristic of certain other *Panulirus argus* congeners including *P. japonicus, P. longipes,* and *P. interruptus* [J. A. Allen, *Oceanogr. Mar. Biol. Ann. Rev.* **4**, 247 (1966); C. H. Turner, E. Ebert, R. Given, *Calif. Dep. Fish Game Fish Bull.* **146**, 99 (1969)]. Of these, *P. interruptus* was observed by divers to make mass movements and to form tightly packed resting clusters in open areas; queues were not reported. Head-to-tail clustering similar to the queuing posture was observed in *Palinurus delagoae* on open bottom, although locomotion was not involved [P. F. Berry, S. Afr. Assoc. Mar. Biol. Res., Investigational Report No. 27 of the Oceanographic Research Institute (1971), p. 1. W.F.H. has on file various personal statements from divers and scattered published material of unknown origin reporting group formations or group movements in *Jasus edwardsii* and *Palinurus vulgaris* (both Palinuridae) and even *Homarus americanus*. No information available suggests group movement or extensive migration by *Panulirus guttatus* or *P. laevicauda*, sympatric congeners of *P. argus*.
11. We thank N. Schuh and R. Ball of the Naval Coastal Systems Laboratory, Panama City, Florida, for technical assistance; and W. Tschinkel, P. Hamilton, and R. Krishnamurti of Florida State University for a critique of the manuscript. The work was funded by grants to W.F.H. from Florida State University and the National Science Foundation (BMS 74–22276). We appreciate the continued support of the Psychobiology Program at Florida State University.

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Handedness in a Chinese Population: Biological, Social, and Pathological Factors

Abstract. *A questionnaire survey of 4143 Chinese was conducted. Social pressure for right-handed writing and eating was effective on these two target skills but showed little indirect influence on hand use in other activities. Neither primiparous birth nor birth to older mothers affected handedness. Twinning, however, seemed to be associated with both decreased right-handedness and lower intelligence.*

It is commonly acknowledged that human handedness is genetically predisposed, but its expression can be modified by either social pressure or brain damage (*1*). The extent of social influence on handedness has not been studied directly and cannot be examined readily in most present-day Western societies because of the current tolerant attitude toward left-handedness. Primiparous birth, birth to older mothers, and twinning have been proposed as circumstances that may result in brain damage and consequent altered handedness, but the results have been inconsistent (*2*).

We conducted a questionnaire survey on handedness in a Chinese population in Taiwan, where social pressure for right-handed writing and eating is still strong. One of our purposes was to examine the extent to which social influence affects hand use in these two "target" skills, as well as in ten other activities of little social concern. The relations between handedness and each of the three high-risk birth conditions mentioned above were also studied. Social pressure was found to be highly effective in changing hand use in the target skills, yet it showed little transfer effect on hand use in other activities. Handedness was found to be totally unrelated to either primiparous birth or birth to older mothers. Conversely, twinning seemed to be associated with both decreased right-handedness and lower intelligence.

Our sample consisted of 1048 boys and 1054 girls arbitrarily drawn from 4th- and 5th-grade classes, plus 1025 male and 1016 female students sampled from various departments in several prestigious universities. Taiwan has 9 years of public education; however, college entrance there requires passing very competitive entrance examinations. The acceptance rate is only about 3 percent of the applicants in the universities sampled. Thus the elementary school sample can be considered to be a fair representation of the general population, whereas the college sample is highly selected for academic intelligence.

The questionnaire is similar to the one used in Oldfield's Edinburgh study (*3*). It asks about the hand used in the following 12 activities: unscrewing a jar lid, opening a door, striking a match, hammering a nail, brushing teeth, erasing a blackboard, cutting with scissors, throwing a ball, raising the hand (before asking questions in class), reaching into a jar, eating (with chopsticks), and writing. For each activity, the subject was to put two crosses under either "Right" or "Left" if he habitually used the corresponding hand for it. He was to put one cross each under "Right" and "Left" if he used the two hands interchangeably. The same questionnaire also asked about birth order, twin birth, and whether or not the respondent had experienced frequent remindings or requests to change hand use from the left to the right during early childhood.

Our main analyses about social and neuropathological factors in handedness are given below. Results from the elementary school and the college samples are combined in our discussion except where a significant difference has been found between them. Results from the two sexes are similarly combined.

Of the 4143 subjects, 18 percent reported having experienced frequent requests to change hand use from the left to the right. A scanty 0.7 percent of the subjects still used the left hand for writing, and 1.5 percent still used the left hand for eating. Since only individuals who have a natural tendency for left-handedness or