Effects of Crowding on the Social Behavior of Cuttlefish (*Sepia officinalis*)

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Abstract | To evaluate the effect of crowding on cuttlefish (*Sepia officinalis*), a benthic cephalopod, the behavior of captive-reared cuttlefish was monitored for a period of 1 month. One group of 6 cuttlefish was housed in a tank 6.1 m in diameter (4.87 m^2 per cuttlefish); another group of 6 was housed in a tank 1.5 m in diameter (0.29 m^2 per cuttlefish). Cuttlefish spaced themselves within each tank so as to avoid other cuttlefish. Those in the small tank hovered more and sat on the bottom less, showed more zebra patterns and Intense Zebra Displays (associated with aggression), ate less food, and were displaced by other cuttlefish 3 times as often as those in the large tank. Most aggression resulting in displacement was directed at females by males and sometimes resulted in physical injury to the females. Subjects' body patterns were highly predictable, using the following variables: activity, sex, tank, and number of nearby cuttlefish. Analysis of results indicated that behavior was strongly affected by housing conditions and suggested that this species is probably semi-solitary in natural conditions.

Laboratory-cultured cuttlefish (*Sepia officinalis*) have been the subjects of a growing body of behavioral research (1–7); however, the effect of captivity on the behavior of cuttlefish is unknown. Cuttlefish have been cultured in our laboratory to supply researchers and public aquaria more or less continuously since 1983, yet the effect of tank size and animal density on growth, overall health, and reproduction are unknown. There is increasing interest in rearing cuttlefish for human consumption (8–9); information about the ways in which housing conditions affect the behavior of cuttlefish would be useful for basic behavioral research and mariculture.

Although much is known about the biology of *S. officinalis* (10), the only field study of this species focused entirely on body patterns (2). The social behavior of this particular cuttlefish in its natural habitat is unknown. In the only field study of any cuttlefish's social behavior (11), groups of approximately 5 *S. latimanus*, a closely related species, were recorded off the coast of Guam. The authors hypothesized that male *S. latimanus* may aggregate solely during reproductive season to compete for females; at other times, these cuttlefish could be solitary. From these paltry field data, it is difficult to evaluate normal behavior of captive *S. officinalis*.

Cuttlefish show a variety of body patterns for crypsis (blending into the background) and communication, and these behaviors have been described qualitatively in great detail (2). Quantitative data do not exist for the frequencies and contexts of these patterns, however, making it difficult to infer function.

It is well documented that crowding can have a major impact on growth and behavior in a wide range of taxa. In aquaculture, the effects of crowding can be serious (12–15); nevertheless, optimum density has often been determined by the capacity of the filtering system used to maintain proper water quality rather than from any but the most extreme behavioral criteria. Behavioral indications of stress could be helpful in monitoring conditions for captive cuttlefish.

To better understand the social behavior of cuttlefish and the effect of housing conditions on their behavior, we monitored cuttlefish housed in small groups at the common stocking density of approximately 3 adults per m^2 (16–19) or at a 16-fold lower stocking density. Few laboratories are equipped with tanks that are sufficiently large to permit a study of this kind; we were fortunate to have access to a 6.1-m diameter tank for 8 weeks during the summer of 1995. Although 8 weeks was not sufficient time to allow for replication of the study, even one short study had the potential to provide new information about cuttlefish social behavior.

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Materials and Methods

Apparatus: This study was conducted at the National Resource Center for Cephalopods at the University of Texas Medical Branch in Galveston, Texas. Two circular fiberglass tanks were used: a small tank (diameter, 1.5 m; depth, 0.6 m), and a large tank (diameter, 6.1 m; depth, 1.5 m). Density in the small tank was 0.29 m^2 per cuttlefish, whereas density in the large tank was 4.87 m^2 per cuttlefish. Both tanks had side water inflow pipes, center water drains, and matte-black interiors, and soft substrate was not provided. The tanks contained recirculating seawater collected from the Gulf of Mexico. Water characteristics were kept as similar as possible between the 2 tanks, and temperature was maintained at approximately 21°C. Details of the aquatic system are described elsewhere (17–18). Ambient lighting from east-facing windows was supplemented during daylight hours with overhead fluorescent lights.

We devised a coordinate system for describing the position of each cuttlefish by using weighted strings spaced equally around the inner tank wall with marks designating the lower, middle, and upper sections of the water column. Location coordinates consisted of string number and depth section. In the small tank, we arranged 6 strings around the perimeter with the lower section from 0 to 0.15 m, the middle from 0.15 to 0.38 m, and the upper from 0.38 to 0.61 m above the floor of the tank. During the study, a single observer viewed the small tank from above. In the large tank, we placed 21 strings around the perimeter with the lower section extending from 0 to 0.30 m, the middle from 0.30 to 0.91 m, and the upper from 0.91 to 1.5 m above the floor of the tank. Four large windows in the sides of the large tank allowed us to observe the cuttlefish during the study without disturbing them. Two investigators observed the large tank simultaneously so that we could determine the exact location of each cuttlefish by triangulation.

Animals: Subjects were laboratory-reared cuttlefish. We were able to identify each cuttlefish on the basis of its relative size and unique zebra bands (5). We measured the mantle length of each

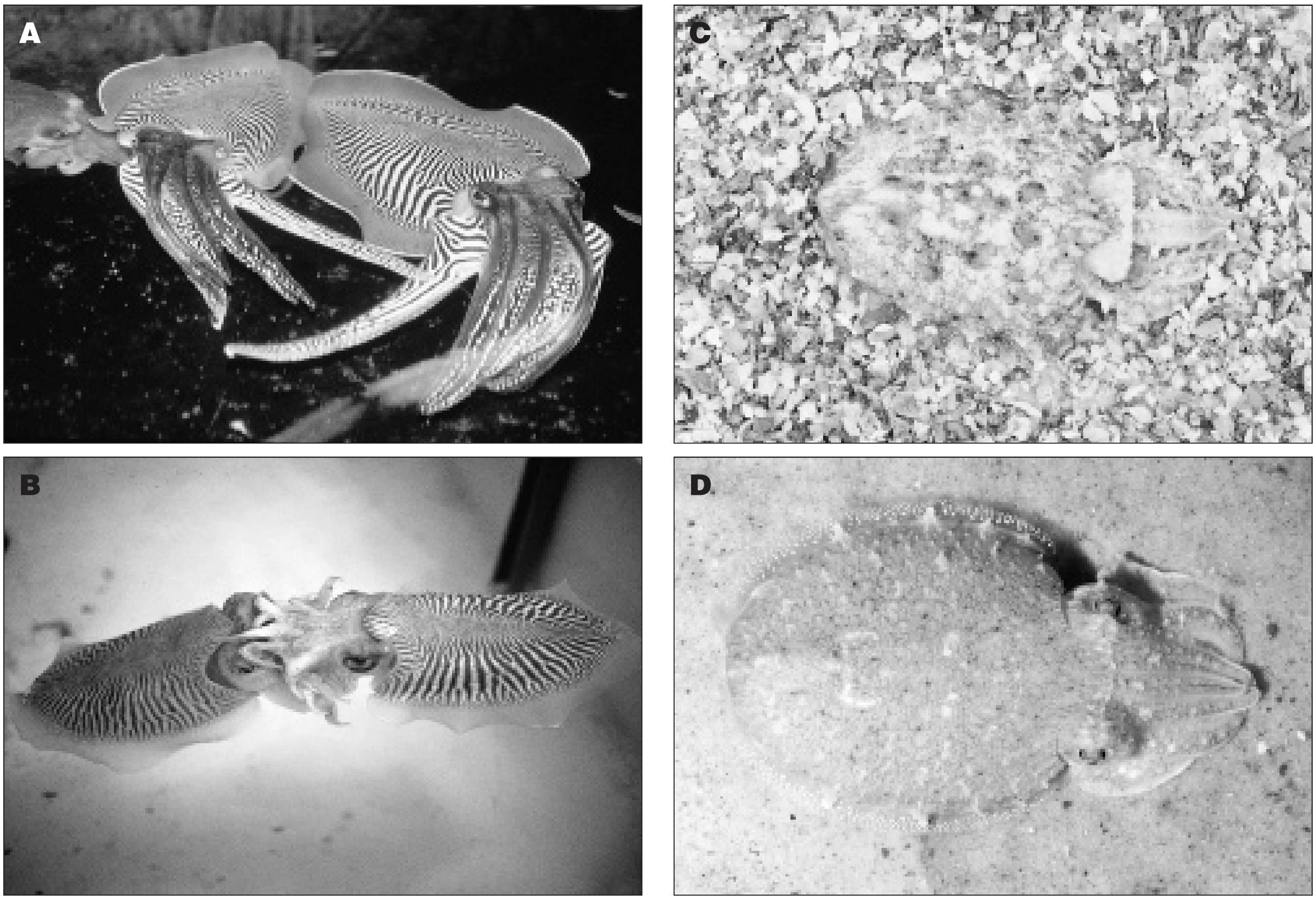

FIG.1. Cuttlefish can change their body patterns in fractions of a second. In this figure, some of the most common body patterns are shown. The Intense Zebra Display (A) is used primarily by males in agonistic situations. Zebra patterns (B) can be shown by both females abd males; in this mating pair, only the male (right) is showing a dark eye ring and striping on the fourth arm. Mottle (C) and uniform (D) patterns are cryptic patterns often shown by cuttlefish resting on the bottom.

subject at the beginning and the end of the study, and cuttlefish were assigned to groups so that the groups were balanced for body size. Mantle length ranged from 10 to 19 cm at the beginning and from 14 to 21 cm at the end of the study (approximately 4 to 6 months after hatching).

The intent was to place 3 females and 3 males in each tank. We used body patterns to determine the sex of the cuttlefish. During an Intense Zebra Display, adult cuttlefish exhibit a conspicuous zebra pattern consisting of sharply contrasting light and dark bands and dark eye rings; they also extend their fourth arm toward their opponent (2,4,20) (Figure 1A). Cuttlefish usually exhibit the Intense Zebra Display during agonistic encounters with a conspecific (20). Although females are capable of showing Intense Zebra Displays (20), most are performed by males, and only males are reported to have leucophores emboldening the white bands of their fourth arms (2). Our subjects were subadults at the start of the study, making it difficult to determine their sex with confidence. The sex of each cuttlefish was verified during necropsy. We discovered at the study's conclusion that the large tank had contained 3 females and 3 males, and the small tank had contained 4 females and 2 males. During the study, 1 female in the small tank and 1 male in the large tank died; leaving 3 females and 2 males in each tank. Most analyses are for these 2 groups of 5 sex-matched cuttlefish.

Procedures: Subjects were given a minimum of 2 days to habituate to the new surroundings before behavioral observations began. Observation periods took place twice daily, once in the morning and once in the afternoon. The order for observation of the 2 tanks within morning and afternoon sessions was randomized. During observation periods, cuttlefish were fed frozen shrimp *ad libitum* by scattering a sufficient quantity of food throughout the tank such that there was always some food that remained uneaten.

Focal animal studies: We observed each cuttlefish for two 5-min segments during each observation period. At 1-min intervals during these 5-min segments, we recorded location, activity, body pattern, and number of near and far neighbors. Recorded activity included swimming, hovering, sitting on the bottom, floating, or jetting.

Principal body patterns and chromatic components were recorded on the basis of descriptions of juvenile patterns (2) with minor changes as specified. Recorded patterns included 10 whole-body patterns: light zebra (zebra bands on an overall light body pattern), dark zebra (zebra bands on an overall dark body pattern), zebra (bold zebra bands only), strong zebra (bold zebra bands, dark rings around the eyes), mottle, light mottle, dark mottle, uniform light, uniform dark, and the dynamic pattern passing cloud (Figure 1). Three particularly visible chromatic components were also recorded: white square, paired mantle spots, and white mantle bar. For example, in our notations, what Hanlon and Messenger (2) term diematic was coded as uniform light pattern with paired mantle spots as additional chromatic components to distinguish overall body brightness from particular component features.

As an indication of social tolerance, we defined the number of near neighbors to be the number of other cuttlefish within 1 body length in the small tank and within 2 body lengths in the large tank. The number of far neighbors was defined to be the number within 2.5 body lengths in the small tank and 5 body lengths in the large tank. Preliminary observations indicated that these distances, although not metrically equivalent between the 2 tanks, appeared to be functionally analogous. There was insufficient room in the small tank for cuttlefish to be 5 body lengths from each other; cuttlefish in the large tank were never within 1 body length of each other.

Scan sampling: In addition to observing a specific cuttlefish for 5-min segments, we recorded 2 types of social interactions throughout the observation period: displacements and Intense Zebra Displays. For each interaction, we recorded which cuttlefish were involved and which cuttlefish was displaced. We defined displacement as a social interaction between 2 cuttlefish in which one retreated at the approach of another, with or without overt aggression. For Intense Zebra Displays, we recorded which cuttlefish withdrew. Note that in our terminology, strong zebra pattern was used to describe body coloration, whereas Intense Zebra Display referred to a social interaction.

For each observation period, we computed the number of shrimp that had been eaten by subtracting the number of shrimp remaining in the tank at the end of the observation period from the number of shrimp that had been added at the start of the period.

Data analysis: Total observation time was 122 h during 32 days and divided evenly between the 2 tanks. Data for 2 sick cuttlefish that died before completion of the study were not included in statistical analyses. Sex ratios of the 2 tanks were the same (3 females: 2 males) for the second half of the study.

For analyses of body patterns, we calculated the mean frequency of each pattern for each cuttlefish in each category (e. g., sex, tank). Because it was unlikely that the behavior of one cuttlefish in a tank was completely independent of others in the same tank, we used analyses of variance to evaluate significant differences (21). Computations were performed, using commercially available software (Statistica for Windows, StatSoft, Inc., Tulsa, Okla.).

Results

Location: Female cuttlefish usually sat on the bottom at the periphery of the tank. Males generally swam in the middle of the tank or sat on the bottom at the periphery. Each cuttlefish was located at all (small tank) or nearly all (large tank) locations in the tank during at least some of the study.

In the small tank, the 6 cuttlefish spent, on average, 26% of their time in the sixth of the tank in which they were found most frequently. The 2 males in this tank clearly avoided each other; the 3 of the 6 sectors of the tank most frequented by one of the males were the 3 least frequented by the other male, and vice versa. Females avoided other females. The sixth of the tank most frequented by each of the 4 females was a sixth of the tank not often frequented by other females. Sectors frequented by males and females overlapped.

In the large tank, the cuttlefish spent their time in a much larger area; nevertheless, a similar pattern to that in the small tank prevailed. Approximately 10 body lengths separated the areas most frequented by the 3 males, and approximately 20 body lengths separated the areas most frequented by the 3 females. As in the small tank, males and females did not avoid each other; areas frequented by males were also frequented by females.

Further evidence that the cuttlefish avoided each other was found in distances to other cuttlefish. In the small tank (approximately 23 body lengths in circumference), males and females spent more than 89% of the time without another cuttlefish within 1 body length (approximately 22 cm) and 43% of the time without another cuttlefish within 2.5 body lengths. In the large tank (approximately 96 body lengths in circumference), the cuttlefish spent 93% of the time without another cuttlefish within 2 body lengths and 87% of the time without another cuttlefish within 5 body lengths.

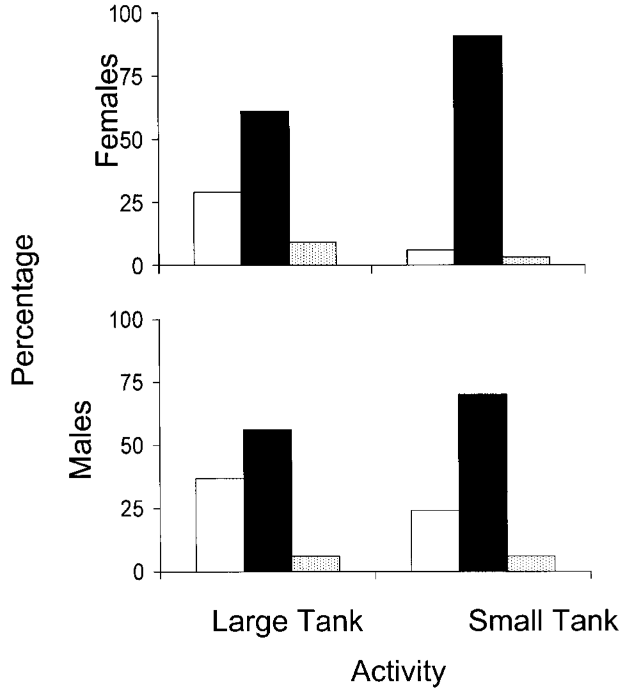

FIG. 2. Relative frequencies of various activities, by sex and tank size. Open bars = sitting on the bottom; solid bars = hovering; hatched bars = swimming. Females hovered more and sat less than males, and cuttlefish in the small tank hovered more and sat less than those in the large tank.

In the large tank, the amount of time spent at the periphery also varied by sex. The females and the most stationary male spent two thirds or more of their time next to the wall of the tank. The percentage of time the other 2 males were found at the periphery was 50 and 5%, respectively. These data were not collected for the small tank, because there was little open area available.

Feeding and growth: As a group, cuttlefish in the large tank consistently ate more food per day than cuttlefish in the small tank (14 of 18 days in which there was a difference in consumption between the groups; Sign test, $P < 0.02$). Mean ± SD number of shrimp eaten per cuttlefish per day was 10.9 ± 2.38 in the large tank and 8.8 ± 1.4 in the small tank, a 24% difference.

Cuttlefish grew an average of 2.55 cm in mantle length during the month of the study. The sample size was too small to detect significant differences in growth by sex or tank. The least-active male in the large tank grew the least (1.0 cm). An intermediate amount of growth was evident for the 3 females in the small tank (2.0, 2.0, and 2.5 cm). More growth was evident for the 2 males in the small tank (2.5 and 3.5 cm), the 3 females in the large tank (2.0, 3.0, and 3.5 cm) and the most-active male in the large tank (3.5 cm).

Activity: On average, subjects hovered 70% of the time, sat on the bottom 23% of the time, and swam 6% of the time. Other activity, such as jetting and floating at the surface accounted for only 0.4% of the observations. We did not detect an effect of time of day (morning or afternoon) on activity. Males were more sedentary than females, spending significantly more time sitting on the bottom ($F_{1,6} = 12.24$, $P < 0.05$) and significantly less time hovering ($F_{1,6} = 9.65$, $P < 0.05$). Cuttlefish in the large tank were more sedentary than those in the small tank (Figure 2), spending significantly more time sitting on the bottom ($F_{1,6} = 14.73$, $P < 0.01$) and less time hovering ($F_{1,6} = 13.30$, $P < 0.05$). Amount of time spent swimming and interaction terms between sex and tank were not significantly different.

Activity, as measured by change in location during a single

Table 1.Frequency of body patterns, expressed as a percentage of all patterns observed in the specified situation.

Variable	Strong zebra	Light zebra	zebra	Dark zebra	Light mottle	mottle	Dark mottle	Uniform light	Uniform dark	Passing cloud
Small tank	2	10	65	9	2	5	4	1	2	0
Large tank	1	22	42	10	5	9	7	1	3	1
Female	0	20	40	11	5	11	8	1	3	0
Male	3	10	74	7	1	2	2	0	0	0
Morning	1	10	58	10	3	8	7	1	2	0
Afternoon	1	22	50	9	4	7	3	0	2	0
Sit	0	23	59	5	3	5	2	1	1	0
Hover	1	14	54	10	4	8	6	1	2	0
Swim	7	9	39	19	0	9	12	0	2	3
Jet	0	23	23	31	0	8	0	0	15	0
Others not nearby	1	16	53	9	4	8	6	1	2	0
One cuttlefish nearby	10	8	54	12	1	3	6	4	2	0

observation period, differed by sex and tank. Activity among females was fairly consistent within each tank. Females in the large tank were stationary nearly half the time (40 to 54%); those in the small tank were stationary less than a third of the time (15 to 31%). Activity among males differed within tanks. In the large tank, one of the males remained stationary about half the time (49%), similar to the value for females, whereas the other 2 males were stationary less than a fourth of the time (14 and 24%). In the small tank, 1 male was stationary less than a fourth of the time (20%), similar to the value for females, whereas the other remained stationary about half the time (52%). In each tank, the male with the most atypical pattern (most stationary in the small tank, least stationary in the large tank) also showed the most Intense Zebra Displays during the course of the study.

Body patterns (focal animal studies): Cuttlefish most often had zebra patterns, followed by light zebra and then dark zebra patterns. The association between body patterns and single variables was determined (Table 1). Only males showed strong zebra patterns, usually when they were swimming. Zebra pattern was more frequent in the small tank than the large tank and more frequent in males than females. All other body patterns were more frequent in the large tank than the small tank and more frequent in females than in males.

We examined the relative frequencies of the 10 body patterns on the basis of 4 categorical variables: subject, tank, sex, and activity when displaying (sitting, hovering or swimming). Number of near neighbors appeared to be important to body patterns (Figure 3); however, we were unable to include this factor in statistical analyses because of the relative rarity of observations when there were one or more nearby cuttlefish. Cases in which a cuttlefish was jetting or floating were excluded from the analysis because of insufficient data.

Because it was probable that our categories of body patterns were not independent of each other, we performed a principal component analysis, using relative frequency of body patterns for each cuttlefish, tank, sex, and activity. Two biologically meaningful factors were identified.

The first factor explained 32% of the variability in the data and was characterized primarily by zebra (+) and mottle (-). Regression analysis of this factor, using the 4 independent variables, was significant for sex and activity (adjusted $r^2 = 0.76$, $F_{4,25} = 23.81$, $P < 0.001$). Males and all sitting cuttlefish had the most positive values (most zebra, least mottle), and females and all swimming cuttlefish had the lowest negative values (least zebra, most mottle).

The second factor explained 24% of the variability in the data and appeared to describe an overall light-dark quality of patterns (light zebra, light mottle, and uniform light (+) versus dark zebra, dark mottle, strong zebra, and passing cloud (-). Regression analysis of this second factor, using the 4 independent variables was significant for activity, sex, and each cuttlefish (adjusted $r^2 = 0.64$, $F_{4,25} = 14.06$, $P < 0.001$), with the highest positive values (lightest patterns) associated with males and all swimming cuttlefish and the lowest values (darkest patterns) associated with females and all sitting cuttlefish.

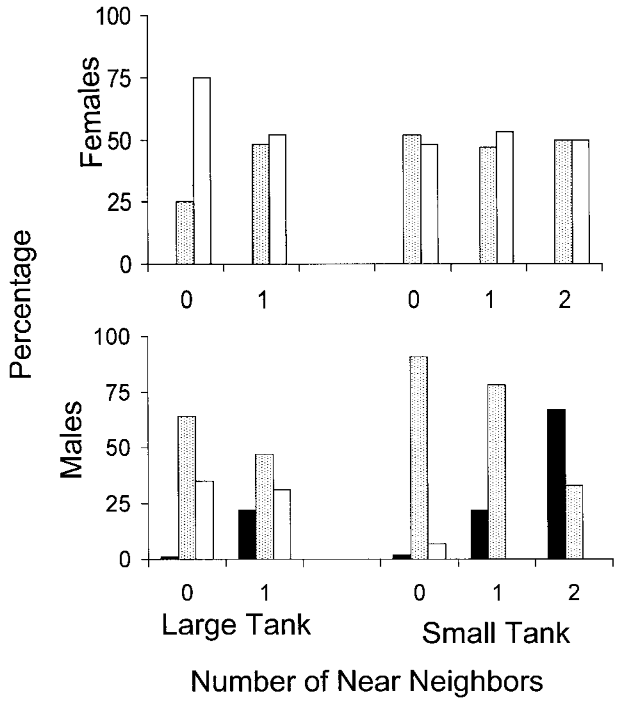

FIG. 3. Body patterns for female and male cuttlefish in the large and small tanks, on the basis of number of near neighbors. Solid bars = strong zebra; hatched bars = zebra; open bars = all other patterns. Notice that females in the large tank had zebra patterns twice as frequently when another cuttlefish was nearby as when other cuttlefish were not nearby, whereas females in the small tank had zebra patterns about half the time, regardless of number of nearby cuttlefish. These results suggest that zebra patterns could be a social signal. Males in both tanks were more likely to have a strong zebra when another cuttlefish was nearby, confirming that strong zebra is a social display. In the small tank, the almost total lack of other patterns for males and the consistently high frequency of zebra for females suggests that other patterns are not social signals. It is apparent that crowding affected behavior in the small tank, even when other cuttlefish were not nearby.

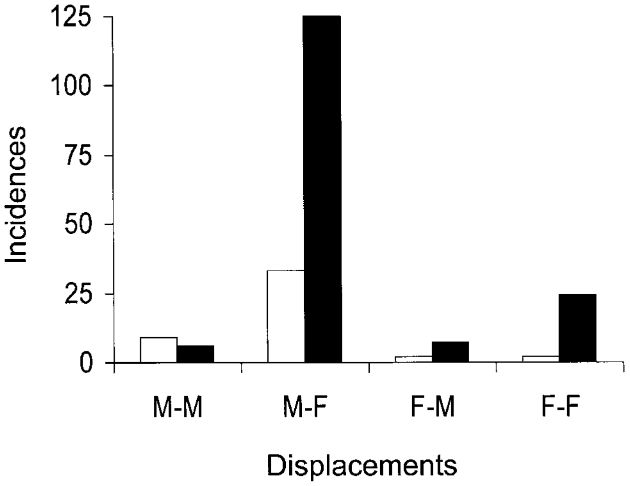

FIG. 4. Frequency of displacements observed in the large, less-crowded tank (open bars) and the small, more-crowded tank (solid bars). The first letter indicates sex of the cuttlefish initiating the displacement; the second letter indicates sex of the cuttlefish displaced (e. g., M-F indicates males displacing females). Females were significantly more likely to be displaced than would be expected strictly by chance.

Because males exhibited the zebra pattern more than females, and only males exhibited the strong zebra pattern, we looked for evidence that the 2 types of patterns were linked. There was only a slight difference in the frequency at which the males within tanks exhibited the zebra pattern. In the large tank, the male that showed the zebra pattern the most (56%) also showed most of the Intense Zebra Displays (84%); however, in the small tank, the male that showed the zebra pattern the most (53%) showed fewer of the Intense Zebra Displays (39%), refuting any simple hypothesis for the association between these 2 behaviors.

The 3 chromatic components (mantle bar, spots, and square) were recorded in 10% of observations; these components help achieve disruptive coloration in cryptic body patterns (2). All patterns other than strong zebra were sometimes accompanied by 1 of these 3 chromatic components. The overall body patterns most commonly associated with a chromatic component were uniform dark (38%), passing cloud (25%), uniform light (21%), and mottle (19%). The distribution of mantle square with body patterns was not different from what would be expected from chance ($\chi^2 = 6.45$, df = 6, $P > 0.30$; strong zebra, uniform light, and passing cloud were too infrequent to be included). Mantle bar was non-randomly distributed ($\chi^2 = 26.55$, df = 6, $P < 0.001$) and was associated primarily with zebra (25%) and light zebra (21%) and secondarily with dark zebra (16%) and uniform dark (15%) patterns. Mantle spots was also non-randomly distributed ($\chi^2 = 34.84$, df = 6, $P < 0.001$) and was associated primarily with mottle (36%) and secondarily with zebra (21%) and light zebra (15%) patterns.

Social interactions (scan sampling): Considering only the 5 healthy cuttlefish in each tank that completed the study, more than 3 times as many displacements were observed in the small tank (162) as in the large tank (46). In both tanks, most displacements consisted of a male displacing a female (small tank, 77%; large tank, 72%; Figure 4); this bias differed significantly from what would be expected on the basis of strictly chance encounters (large tank: $\chi^2 = 24.39$, df = 3, $P < 0.001$; small tank: $\chi^2 = 174.58$, df = 3, $P < 0.001$).

More than 3 times as many Intense Zebra Displays were detected in the small tank (134), compared with the large tank (37). In the small tank, more Intense Zebra Displays were directed at females (80) than at males (54); nevertheless, Intense Zebra Displays by males in both tanks were significantly more likely to be directed at other males than would be expected on the basis of strictly chance encounters (large tank: $\chi^2 = 26.75$, df = 1, $P < 0.001$; small tank: $\chi^2 = 16.73$, df = 1, $P < 0.001$). During scan sampling, females showed Intense Zebra Displays twice (one each by 2 female initiators), both of which were in the large tank and were directed at another female.

Discussion

Not all portions of the tanks were used with equal frequency. In the large tank, a fourth of the tank featured several inflow pipes. None of the cuttlefish used this portion of the tank with great frequency, perhaps because of water currents or turbulence. In the small tank, the water was supplied from a spray bar positioned over the tank; it is not clear why one section of this tank was less preferred overall.

Cuttlefish avoided each other. In laboratory conditions without soft substrate provided, juvenile cuttlefish clump such that most of them are in direct physical contact with several others. In our experience, in even large tanks, only a small portion of the tank is used. Boal (5) observed that adult female cuttlefish stayed at the periphery of the tank while adult males congregated in the center, displaying to one another. In contrast, the subadults in our studies stayed far from each other. Cuttlefish in the large tank used the extra area to space themselves much more widely than was possible in the small tank. Males and females divided space independently; the cuttlefish avoided areas frequented by other cuttlefish of the same sex, but did not avoid areas frequented by cuttlefish of the opposite sex. Aggregations of large *S. officinalis* have not been reported in the field. It is plausible that this species prefers to maintain inter-animal distances larger than is feasible in captivity.

During the course of the study, cuttlefish in the large tank ate 24% more shrimp than those in the small tank. Cuttlefish in the large tank swam twice as much as those in the small tank, so it was possible that this activity resulted in higher food consumption. We believed this explanation unlikely, because neither group swam a great deal, and those in the small tank also rested on the bottom less that those in the large tank. We considered a more plausible explanation to be that the cuttlefish in the small tank were more stressed, resulting in lower food consumption.

In contrast to our results, Warnke (3) found that hatchling and young juvenile cuttlefish (up to 7 months old and a maximum mantle length of 6.4 cm) reared in groups of 4 ate more food than those reared in isolation. Our study differs from that study in that we varied density of cuttlefish rather than number of cuttlefish; thus, effects of social facilitation probably did not differ between our 2 groups.

In the small tank, cuttlefish spent more time hovering and less time sitting on the bottom or actively swimming than cuttlefish in the large tank. Cuttlefish are believed to be benthic (bottom-dwelling) animals that spend most of their time resting on the bottom with cryptic (camouflaged) patterns (10). In laboratory culture, soft substrate is not provided to simplify care and cleaning. Lack of soft substrate probably influences settling behavior. The increase in hovering and decrease in amount of time spent resting on the bottom for cuttlefish in the small tank, relative to those in the large tank, could also have been a sign of distress from overcrowded conditions.

Females spent less time resting on the bottom and more time hovering than did males. This finding was consistent with evidence that females were the primary targets of displacements.

It was possible that even the large tank was crowded, at least by cuttlefish standards. It would be interesting to compare the observations for the cuttlefish in this study with those of solitary cuttlefish of similar age.

In the interpretation of our data on body patterns, it must be borne in mind that subjects were not provided soft substrate. This was an unnatural situation; however, it did provide a standard environment for all subjects and is a typical laboratory arrangement. Body patterns were remarkably predictable and responsive to social (effects of sex, tank-density) and non-social (effects of activity, tank-physical environment) variables. This supported the long-standing hypotheses that body patterns function for communication and crypsis (7).

The only pattern with a definitively social function was strong zebra, which distinguished males from females. In each tank, one male showed more Intense Zebra Displays than the other male, indicative of a dominance relationship. This finding is consistent with results of previous studies (1,3,4,20). Males and females also differed in their use of other body patterns, with males showing more zebra and females showing more mottles. These chronic (long-lasting) body patterns appear to function for crypsis in calm cuttlefish. It is not clear why chronic male and female body patterns differed so substantially.

In both tanks, most displacements were males displacing females. The reduced total area of the small tank would have been expected to result in more encounters and, therefore, an increased number of displacements for both sexes. The frequency of displacements with crowding was not independent of sex, however, because almost all of the increase was attributable to displacements of females by males.

Displacements are not neutral to participants. Displaced cuttlefish are not able to settle calmly on the bottom. Sometimes they injure themselves as they jet into the side of the tank in an attempt to move quickly out of the way. In a previous study (3), it was reported that interactions during feeding included inking, chases, and injuries when cuttlefish jetted into the tank wall, and most of the observed aggression was by males. In the study reported here, we had difficulty initiating the study because of injuries sustained as the groups were being established. During a period of 3.5 weeks before the onset of the study, we found it necessary to replace 3 cuttlefish in the large tank and 6 cuttlefish in the small tank (sexes unknown) so that we could begin the study with 6 healthy cuttlefish in each tank. Injuries, primarily consisting of scraped mantles and cut or bruised posterior portions of the mantle tips, were not specifically recorded during the study, but were common. Analysis of our results clearly indicated that females in a mixed-sex group received a disproportionate share of the injuries associated with being housed in a small tank.

Evidence for dominance among juvenile cuttlefish is conflicting. Mather (1) reported that, among 10 juvenile cuttlefish (mantle length of 4.8 to 7.7 cm, estimated age was 2 to 4 months after hatching), females appeared to dominate males during feeding interactions; however, dominance was poorly predicted on the basis of sex or size. Warnke (3) found that, among 2 groups of 4 juvenile cuttlefish (mantle length of 4.9 to 6.5 cm, age of up to 5 months after hatching), large males dominated small females during feeding interactions. Our results, which were based on direct interactions between cuttlefish rather than on competitive interactions over food, indicated that males dominated females. It is difficult to reconcile results for these 3 studies. All have small sample sizes and are not directly comparable because of differences in behaviors measured. An additional problem is that in only 1 report (3) did the investigator know the exact age of most of the cuttlefish. Consequently, there could be important differences in the sexual maturity of the cuttlefish involved. Warnke (3) reported the lack of social interactions among the study population that was less than 4 months old. In our study, copulation was observed twice during the establishment of the 2 groups (before data were formally collected), indicating our cuttlefish may have been more mature than would have been expected strictly on the basis of their size. It is also possible that inconsistencies between these 3 studies indicate that observed interactions between cuttlefish are artifacts of captivity. Field observations are sorely needed to rule out experimentally-induced artifact in interpretations of dominance.

Intense Zebra Displays were predominantly, but not universally, exhibited by males and were more often directed at the other male in the tank than at one of the females. Males usually responded by also exhibiting a strong zebra pattern and sometimes extended their fourth arm for a full Intense Zebra Display. In this case, the display clearly appeared to serve in opponent assessment (4,20). Female recipients almost always swam away when Intense Zebra Displays were directed toward them. It would be helpful to look more closely at male-female interactions, because displacements of females by males and female avoidance of males' Intense Zebra Displays are related phenomena. In this study, we did not record the entire behavioral sequences of social interactions.

It is clear from this study that housing conditions have a substantial impact on cuttlefish behavior. In this study, we took advantage of a rare opportunity to use a large tank that became available for a limited time. To distinguish the effects of physical space from those of social density, this study would need to be expanded to include, at the minimum, different stocking densities in identical tanks. It would be particularly interesting to include cuttlefish housed alone to better assess the effect of social variables apart from physical factors. Nevertheless, this study provides good evidence implicating the importance of housing conditions on cuttlefish behavior. Future behavioral research will need to take careful account of housing conditions when attempting to make inferences about normal behavior, and behavioral comparisons for differing housing conditions will have to be made with great caution.

The effect of the differences in aggression on health that we found in this study should not be underestimated. Females in both tanks appeared to be continually harassed by males and clearly exerted considerable energy trying to get away. Females in the small tank especially were quite battered by impacts with the sides of the tank, a problem also reported by Forsythe and colleagues (17); however, the density of cuttlefish in our more-crowded tank was not unusual for standard mariculture conditions of this species (17,18). The Intense Zebra Display appears to be a good indicator of heightened aggression by males; separating males from females as soon as the males begin exhibiting Intense Zebra Displays could reduce the incidence of injury to females in captive situations.

Analysis of our data indicated that this species is probably semi-solitary. The heightened aggression (Intense Zebra Displays, displacements) seen in the small tank suggested that cuttlefish do not normally live in close proximity. Even in our large tank, cuttlefish spaced themselves apart and spent a preponderance of time without another cuttlefish within 5 body lengths. We suspect that cuttlefish are normally spread more widely apart than captivity permits. Because an Intense Zebra Display is clearly an elaborate, ritualized social display (4,20), it is not likely that this species is completely solitary. Corner and Moore (11) suggested that cuttlefish may be solitary most of the year, aggregating solely during reproductive season. Their hypothesis is consistent with patterns inferred from field sampling of *S. officinalis* (10) and seems a plausible working hypothesis until better data are available.

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