



Absence of social recognition in laboratory-reared cuttlefish, *Sepia officinalis* L. (Mollusca: Cephalopoda)

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(Received 11 April 1995; initial acceptance 2 August 1995;
final acceptance 12 December 1995; MS. number: A7299R)

Abstract. Five experiments were performed to determine the level of social recognition in captive-reared adult cuttlefish, *Sepia officinalis* L. No evidence of discrimination of familiar from unfamiliar individuals was found in either females or males. Despite good evidence for mate guarding, no recognition of individual mates was found. Within sex classes, associations between freely moving animals were not different from random (f–f, f–m and m–m). Male dominance, measured by displacement success, was consistent from day to day, was related to size and was consistent with number of copulations obtained. Dominance ranks were not learned or recognized and did not result in energy savings through a reduction in agonistic encounters. Social interactions of these marine invertebrates depend upon relative size, internal motivation and the behaviour patterns of conspecifics, rather than upon any direct recognition of social partners.

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The striking physiological and behavioural convergences noted thus far between cephalopods and fishes (Packard 1972) have provided insights into the evolution of complex behaviour patterns in the marine environment and suggest that an understanding of the social behaviour of cephalopods could aid our understanding of the evolution of social behaviour in general. A key element of the social structure of any group is the degree to which individuals recognize one another. Archawaranon et al. (1991) outline three levels of social recognition. The simplest level of social recognition is binary discrimination; for example, familiar versus unfamiliar, mate versus non-mate or more dominant versus less dominant. A second level of complexity is the recognition of multiple classes of individuals; for example, own-group versus neighbouring-group versus unfamiliar group, or the recognition of multiple classes of kin based on degrees of relatedness. The most complex type of social recognition is the ability to discriminate between unique individuals. Degree of social recognition underlies a number of

important theories in sociobiology: the ability to make at least binary discriminations is essential for the formation of dominance hierarchies, the ability to recognize at least classes of individuals is essential to kin selection, and true individual recognition is essential to reciprocity (reviewed in Zayan 1992, 1994).

Complex social recognition occurs in many groups of vertebrates (reviewed in Halpin 1980; Breed & Bekoff 1981; Colgan 1983; Ydenberg et al. 1988; Zayan 1994). Individual recognition has been demonstrated in several species of teleost fishes (reviewed in Colgan 1983; also Myrberg & Riggio 1985; McGregor & Westby 1992). Among invertebrates, evidence for social recognition is more limited. Familiar–unfamiliar recognition has been demonstrated in ants (Jutsum et al. 1979), bees, cockroaches and numerous crustaceans (reviewed in Halpin 1980). Among molluscs, species recognition has been demonstrated in slugs, which preferentially follow mucus trails of conspecifics (e.g. Cook 1977). Little is known of the degree of social recognition shown by any of the cephalopod molluscs.

Cuttlefish are neither solitary, as are octopuses (Octopoda), nor schooling, as are squid (Teuthoidea), and provide an interesting

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opportunity for examining social recognition in cephalopods. Cuttlefish show complex intraspecific visual displays (Hanlon & Messenger 1988), form short-term female-male pair associations (Tinbergen 1939; Hanlon & Messenger, in press) and are individually recognizable by their unique zebra-like body patterns (personal observation). Although preliminary experiments (Tinbergen 1939) resulted in no evidence that cuttlefish recognize each other as individuals, recent experiments have provided evidence for male dominance hierarchies and a reduction in aggression between previously encountered opponents (Adamo & Hanlon 1996). To determine the level of social recognition displayed by this group of invertebrates, I examined the behaviour patterns of individual cuttlefish in both pre-arranged and unrestricted social encounters.

METHODS

Subjects were laboratory-reared *Sepia officinalis* L., cultured at the National Resource Center for Cephalopods at the Marine Biomedical Institute in Galveston, Texas. Techniques for rearing and maintaining this species have been described in Forsythe et al. (1991, 1994). I began experiments immediately after the subjects attained sexual maturity (approximately 5 months of age). At this point, cuttlefish become weakly sexually dimorphic in body patterning and postural displays; before this time, it is not possible to determine the sex of a particular animal from external features. I performed all experiments with the same generation of animals. Experiments began in August and finished in December 1994.

In each experiment, mantle length (ML) served as a measure of size. Before the start of experiment 1 and at the end of experiment 5, I lifted subjects briefly out of the water to measure their mantle lengths. At regular intervals during experiments, I obtained mantle lengths on freely swimming animals. Animals habituated to people would permit a flexible ruler to be slowly and gently placed above and just touching their mantles while they hovered in place. At death, I weighed, measured and autopsied all animals for verification of sex. Most died of senescence.

Thirteen of 45 animals had been tagged in a previous behavioural experiment; all other animals were experimentally naive. I identified

individual cuttlefish by stable, unique bands in their zebra body patterns. Scars and other marks healed rapidly and apparent size varied substantially depending on posture and patterning. Some of the animals used in earlier experiments were used again in later experiments.

Within each experiment, all of the tanks used were interconnected in a single system of recirculating seawater obtained from the Gulf of Mexico (Forsythe et al. 1991). Water temperature ranged from 18 to 22°C. Lighting was provided by a combination of natural light and artificial light on a 12:12 h light:dark cycle. Animals were fed frozen shrimp twice per day ad libitum.

During experiments 1-3, cuttlefish were housed in round tanks (1.52 m diam. × 46 cm deep) with white interiors, in small groups of either all females or all males. Animals remained in these groups for more than 3 months, starting 6 weeks prior to experiment 1.

In experiments 1 and 2, the test arena was a round tank identical to the home tanks and surrounded with an opaque curtain. An opaque partition isolated the animals for an initial habituating period before each trial. I was able to lift the partition by means of a pulley system without coming into the subjects' view.

I moved animals between tanks by herding an individual into a transparent plastic box (when subjects were small) or bag (when subjects became larger). I could then easily lift them and carry them in a small amount of water from tank to nearby tank. The cuttlefish quickly habituated to this process and normally remained calm.

A video-camera mounted above the test tank recorded all behavioural interactions in experiments 1 and 2 (CCE-TR81 video Hi 8 camera recorder). I captured and analysed individual frames with a video analysis system (NIH Image software on a Sony Computer Video Deck CVD-1000 and a Power PC Macintosh AV 8100). This software provided the coordinate system for distance and length measurements, all angle measurements, and regional grey-scale pixel counts for measuring mantle darkness. Grey-scale measures were based on an area of at least 100 pixels and were highly robust to variations in the exact outlines of the region to be measured (variability < 2% in repeated measures).

In experiments 4-5, I observed freely swimming cuttlefish housed in a single 1.83 × 3.65 m tray, with water 35 cm deep and a mottled dark grey

and brown interior. I provided egg-laying material consisting of lengths of air hose anchored with bricks.

To evaluate the significance of the results, I averaged each individual's responses for the particular test and time block. I used these averages as my individual measures. Unless otherwise specified, I used two-tailed, non-parametric statistics (Sokal & Rohlf 1969; Siegel & Castellan 1988) to test for significant differences between groups of individuals.

EXPERIMENT 1: FAMILIAR-UNFAMILIAR RECOGNITION BY FEMALES

Methods

Subjects in experiments 1 and 2 were 21 cuttlefish of an appropriate size. By chance, 16 were female and were used in experiment 1, and five were male and were used in experiment 2. Six weeks prior to the start of trials in experiment 1, I placed females in four groups of 4-6 animals each (some tanks contained females not used in experiments). Subjects remained in these groups throughout experiments 1-3.

In this experiment, I compared the behaviour patterns of each female when placed in a test arena with a familiar conspecific female and when placed with a size-matched, unfamiliar conspecific female (mantle length within 0.5 cm). I conducted tests of each subject on successive days and randomized the order of presentation.

I gave subjects 10 min to habituate to the new tank before raising the partition. By this time, all subjects had either settled quietly on the bottom or were swimming about looking for a way out. At the start of the trial, I hoisted the partition so animals could freely interact. After half an hour in the test tank, I returned subjects to their home tanks.

The variables I used to score the females' behaviour patterns were taken from video frames captured by computer (see above) once every 10 s for the first 5 min after the barrier had been raised. The values used in statistical analyses were averages over three time blocks: minute 1, minutes 2 and 3 together, and minutes 4 and 5 together.

During the 6 weeks prior to experimental trials, undisturbed females normally spent much of their time quietly resting on the bottom of the tank,

adjacent and touching another female. Their body patterns were usually pale and generally matched those of the other females in their home tank. Alarmed females either darkened or became extremely pale, occasionally with darkened mantle ocelli. Agitated animals swam actively about the tank. If one animal darkened, often the others also darkened; active swimming appeared less contagious. The variables I chose as indicators of social recognition therefore included mantle darkness, distance to the other female, distance moved (computed from the coordinates of each individual in each frame scored) and congruence (computed as the absolute value of the difference in mantle darkness of the two females within each frame). I used Wilcoxon signed-ranks tests to evaluate the significance of differences in subjects' behaviour patterns when placed with the familiar and with the unfamiliar conspecific.

Results

I found no significant differences between pairs of familiar and unfamiliar females: movement (minute 1, $z=0.26$; minutes 2-3, $z=1.24$; minutes 4-5, $z=0.88$; all $P>0.20$), mantle darkness (minute 1, $z=1.55$; minutes 2-3, $z=0.26$; minutes 4-5, $z=0.16$; all $P>0.10$), congruence in mantle darkness between females (minute 1, $z=0.16$; minutes 2-3, $z=1.03$; minutes 4-5, $z=1.14$; all $P>0.25$), and distance between females (minute 1, $z=1.14$; minutes 2-3, $z=1.36$; minutes 4-5, $z=1.24$; all $P>0.20$).

EXPERIMENT 2: FAMILIAR-UNFAMILIAR RECOGNITION BY MALES

Methods

Subjects were placed in two groups of two or three males each, 6 weeks prior to the start of trials. Procedures of experiment 2 were identical to those of experiment 1, unless otherwise noted.

Mature males perform agonistic displays (referred to as 'Intense Zebra Displays', Hanlon & Messenger 1988) that can include intensifying the brightness contrast in their zebra bands, circling or 'standing' close to one another in a parallel (head-to-head) or anti-parallel (head-to-tail) position, extending their fourth arms towards the

other and darkening their head and arms. No interaction escalated to shoving, grasping or biting during these experiments.

To measure displays, in addition to the variables recorded in experiment 1, I also measured maximum and minimum mantle darkness to evaluate contrast, overall body direction (towards, away or parallel to the other male) and the angle between the body axes of the two males. I also used the latter angle to compute an index ranging from 0, indicating parallel or anti-parallel, to 90, indicating perpendicular or not at all parallel. In experiment 2, I analysed one frame every 5 s for the first minute, and every 10 s for five additional minutes. For purposes of analysis, results were averaged by time blocks of minutes 1, 2-3, and 4-6. Because I had an odd number of subjects, I was unable to analyse the data using matched pairs, as I had in experiment 1. I instead used Wilcoxon-Mann-Whitney tests to evaluate the significance of differences in subjects' behaviour patterns when placed with the familiar or unfamiliar conspecifics.

Results

I found no significant differences between males in the company of familiar and unfamiliar males, for the following behaviours: movement (minute 1, $W_x=26$; minutes 2-3, $W_x=27$; minutes 4-6, $W_x=29$; all $P>0.15$), mantle darkness minimum (minute 1, $W_x=23$; minutes 2-3, $W_x=27$; minutes 4-6, $W_x=26$; all $P>0.35$), maximum (minute 1, $W_x=23$; minutes 2-3, $W_x=21$; minutes 4-6, $W_x=20$; all $P>0.75$) and average (minute 1, $W_x=23$; minutes 2-3, $W_x=20$; minutes 4-6, $W_x=22$; all $P>0.75$), and orientation of subjects (towards, parallel, or away from the other male) (minute 1, $W_x=25$; minutes 2-3, $W_x=19$; minutes 4-6, $W_x=23$; all $P>0.60$). Sample size was too small to evaluate differences in distance between males, angle between body axes of the two males in the test arena and angle away from either parallel or anti-parallel. There were no consistent patterns across time blocks for any of these variables.

EXPERIMENT 3: MATE RECOGNITION

Methods

Four males were housed individually in tanks similar to those of experiment 2. Females

remained in the same home tanks as in experiment 1. Each afternoon, I placed one female into each of two males' tanks. Copulations that ensued (usually within 5 min) were timed for duration. Males that did not copulate within 10 min did not copulate at all during that experimental session.

After copulation, or after 10 min, I estimated the distance between the female and male in body lengths from nearest point to nearest point. Distance was recorded at 5-s intervals for the first 3 min and then at 10-s intervals for 2 min further.

After this initial 5-min period, I removed the females and replaced them by either (1) a different female who had just copulated, (2) a different female who had not recently copulated (at least 24 hours but not more than 1 week since last copulation) or (3) the same, original female. I again recorded distances between the male and female for 5 min, as above.

Once this second 5-min period had elapsed, I again removed females and replaced them with the original female; I again recorded distances according to the same sampling procedure. Females were then returned to their home tanks and males were left isolated for at least 24 hours before another trial began.

Males received 2-6 trials; five females were used as partners. I used Friedman analyses of variance by ranks to compare distances between all three of the 5-min blocks, Wilcoxon signed-ranks tests to compare distances between time blocks 1 and 3, and Kruskal-Wallis one-way analysis of variance by ranks to examine differences between treatments during the second time block. Because I did not manipulate pairs to either encourage or discourage mating, sample sizes of groups are uneven.

By testing two female-male pairs simultaneously, I had two females to exchange, each of whom had mated at approximately the same time. This necessitated two different human observers. In a control trial, the difference in estimates between the two observers for average distance between subjects, measured in mantle lengths, was 3%. To balance for any differences between human observers, each male subject was observed by only one of the experimenters under all test conditions. Observers did know the conditions being tested; however, tapes from experiments 1 and 2 had not yet been viewed or analysed and the

human observers did not expect the results found in any of these three experiments.

Results

Copulations were always initiated by the male swimming to and grasping the female. Copulation occurred in a head-to-head position; the male's arms wrapped around and grasped the female's head. Copulations lasted 2.5–7 min, with an average of 4.4 min. The female sometimes resisted after being grasped. This situation caused the pair to barrel-roll irregularly around the tank. In a typical mating, after several minutes, the male's body moved with a rhythmic, pumping action while the female remained calm. Shortly thereafter, the female initiated the termination of mating by attempting to break free; the male resisted at first but released her within about a minute. Once released, the female jetted vigorously around the tank for about 10 s, with abrupt changes in direction. The male jetted after her. She then settled down quietly near or on the bottom; he hovered above and slightly to the side of her and often touched her with drooping arms.

Procedures of this experiment did not significantly disrupt this behaviour. Distances between pairs during the first time block were not significantly different from those during the third time block ($z=0.79$, $N=17$, $P>0.20$; Fig. 1). The mean distance maintained by pairs after copulation decreased markedly from pre-copulation distances, a result consistent with an interpretation of mate-guarding. Distances between pairs during the second time block (minutes 6–10) differed significantly with mating status (mated or unmated) ($H=11.31$, $df=3$; $P\approx 0.01$), with pairs including an unmated male maintaining the largest average distances and pairs with both animals mated maintaining the closest proximity. Multiple comparisons showed that distances differed significantly between the situations where both had recently mated and where the female had recently mated but the male had not ($d=10.58$, one-tailed $P<0.01$). If the male had mated, distances differed significantly with whether or not the female had also recently mated ($d=8.58$, one-tailed $P<0.05$).

I compared average distances between female-male pairs during the three time intervals: minutes 0–5, immediately following copulation;

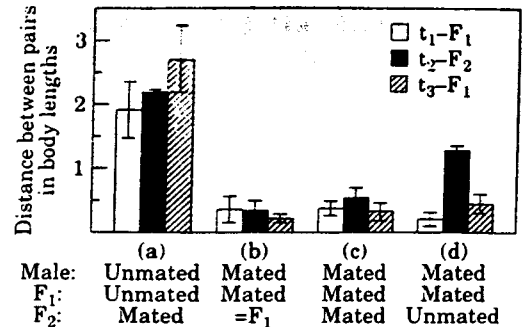


Figure 1. Mean \pm SE distances in body lengths between pairs within each time block, t_1 , t_2 , t_3 , for each type of pair ($N=2, 4, 6, 5$). Distances between pairs were not different between times 1 and 3. (a) Pairs with an unmated male remained the farthest apart throughout the three time periods. (b) Mated pairs remained in close proximity; removing and returning the same female (second female=first female; control) in t_2 had little effect. (c) Exchanging the original mated female with another recently mated female in t_2 did not have a significant effect on proximities of the females and males. (d) Exchanging the original female with an unmated female in t_2 did have a significant effect: distances maintained were intermediate between those when both had mated (b and c) and those when the male had not mated (a).

minutes 5–10 with an exchanged female; and minutes 10–15 with the original female (Fig. 1). I found no differences in distances when the original female was removed and replaced (control, $F_T=0$, $P>0.10$, $N=3, 4$), so that the experimental procedures were not overly disruptive. Likewise, I found no differences in distances when the original female was exchanged with another female who had been mated at the same time in an adjacent tank (second female mated: $F_T=0.78$, $P>0.10$, $N=3, 6$). This result was particularly striking because subjects were not matched by size; females varied from 18.7 to 22.6 cm ML, and males ranged from 18.3 to 23.0 cm. When the second females had not copulated recently, however, distances between the female and male were significantly greater than with the original female ($F_T=8.4$, $P=0.01$, $N=3, 5$). In summary, I found that the distance between females and males was influenced by the mating status (recently mated or not) of both the female and the male but was not influenced by the identity or sizes of the individuals.

EXPERIMENT 4: PREFERENCES DURING FREE-ASSOCIATION

Methods

Subjects were six mature females and nine mature males maintained together in a large tray (see above). Once each day, either in the morning (about 0900 hours) or in the evening (about 1700 hours) for 10 days (five mornings and five evenings in haphazard sequence), I estimated and recorded, in body lengths, the distance between every pair of two animals (105 possible pairs) according to a pre-determined sampling sequence. To obtain relative proximities, I ranked distances from each individual to every other individual, within sex, for each observation period. I compared median distances of pairs, by sex, with an analysis of variance (Sokal & Rohlf 1969); to test for all other non-random association patterns, I used Friedman analyses of variance by ranks.

Results

Distances between subjects differed between sexes, with both types of same-sex pairs maintaining closer proximity than mixed-sex pairs ($F_{2,102}=5.64$, $P<0.01$). This result reflected preferences for different areas within the test tank. Females tended to congregate in one or two of the corners of the tank or else by the materials supplied for the attachment of eggs. Males, in contrast, congregated in the centre of the tank. They spent most of the time engaging in agonistic displays; occasionally one would chase one or many females or swim over to inspect the eggs.

I found no evidence for preferential associations within sexes, as measured by ranked individual-to-individual distances. For each of the six females, associations with other females appeared random ($F_r=2.25-7.96$, $N=5, 10$; all $P>0.05$). For eight of the nine males, associations with the other males also appeared random ($F_r=1.64-11.56$, $N=8, 10$; all $P>0.10$). The ninth male's associations differed significantly from random, overall ($F_r=20.02$, $P<0.01$, $N=8, 10$), yet no associations with particular other males were significant (paired contrasts, all $P>0.05$).

Between-sex associations also appeared to be largely haphazard. For the six females, four were randomly associated with the males ($F_r=2.12-8.83$, $N=9, 10$; all $P>0.30$). One female was found

particularly close to one of the males, who had been particularly active in mating and attempting mating during the time of this experiment ($\chi^2=15.51$, $df=8$, $P<0.05$). The sixth female's associations, while non-random, revealed no associations with any particular male ($\chi^2=20.06$, $df=8$; $P<0.01$). For all of the nine males, associations with the females did not differ from random ($F_r=1.99-11.00$, $N=6, 10$; all $P>0.05$).

EXPERIMENT 5: MALE DOMINANCE HIERARCHIES

Methods

Five mature males and three mature females were maintained in the large tray as in experiment 4. I observed animals for 3-4 h each day for 6 days, during which time I recorded the outcomes of all male-male interactions that included an intensification of zebra bands. All interactions ended with either one or both males paling and/or retreating. I considered a male as displaced only when he actively swam away from the other male, who was not actively swimming anywhere other than perhaps after the retreating individual. Dominance hierarchies were constructed for the males based on success in displacements. I noted all the copulations observed during the course of the day, both during this experiment and during experiment 4, as a measure of mating success.

I measured size in several ways. I measured the mantle length of unrestrained individuals prior to the start of this experiment and on restrained live animals at the end of the experiment. Mantle length, cuttlebone length and wet weight were measured upon the death of the subject. Because different subjects lived for different periods of time (1-6 weeks after the end of this experiment), these measurements were biased in favour of longer-lived and perhaps healthier subjects. All five size measures resulted in identical final relative size rankings. I used Kendall's coefficient of concordance to test for consistency between rank measures.

Results

Male dominance ranks, determined by successes in displacing other males, were consistent across days ($W=0.50$, $N=5$, $P<0.01$). Reversals were common; the most dominant male (A)

Table I. Dominance matrix for five males

		Winners				
		A	B	C	D	E
Losers	A	—	7	3	2	1
	B	13	—	4	8	4
	C	10	5	—	3	1
	D	10	33	9	—	2
	E	9	18	3	8	—

Displacement frequencies for each pair of five males (A–E). For example, B displaced D 33 times, and was displaced by D only eight times.

Table II. Rank of five males

Male	Initial size*	Final size	Number of copulations*	Displacement success*
A	1	1	1	1
B	2	2	4.5	3
C	3	5	2.5	2
D	4	3	2.5	4
E	5	4	4.5	5

*Initial size, number of copulations and displacement success are significantly related.

won 76% of all interactions while the least dominant individual (E) won 17% of his interactions (Table I).

The rank orders of final size (26.5–29.0 cm), number of copulations (1–6), and dominance, as measured by displacements, were not significantly related ($W=0.66$, $N=5$, $P<0.05$; Table II). Rank orders of an earlier size ranking ('initial size' in Table II), number of copulations, and dominance were significantly related, however ($W=0.82$, $N=5$, $P<0.05$). As a young adult, male C developed several infected skin lesions. Although he recovered well, his growth was impaired and his relative size rank changed from third to fifth among the five males. For females, mantle length was not related to number of copulations.

DISCUSSION

Although not one of the experiments provides conclusive evidence that cuttlefish do not recognize their conspecifics, taken together, they cast doubt on the possibility of any complex social recognition in this species.

In experiments 1, 2 and 3, behaviour patterns did not differ between familiar and unfamiliar pairs. Interactions, particularly between mates and in male–male agonistic encounters, would reasonably be expected to vary if recognition had occurred. For example, a male's failure to distinguish between his mate and another recently mated female could result in his guarding a female as she lay eggs fertilized by a different male. For males, continually having to establish dominance rather than remembering who is dominant and who is subordinate could be costly in their natural habitat. Male–male contests involve highly conspicuous visual displays that could attract predators. In experiment 5, I did not see any reduction in the number of male–male contests across observation periods; indeed, during experiment 2 when males were housed in small groups for several months, they displayed to each other almost continuously. These experiments provided no evidence for discrimination of familiar from unfamiliar individuals.

Were the experimental arenas too stressful or artificial to allow recognition? This possibility seems unlikely. In experiments 1–3, test arenas were identical to home tanks. In experiment 1, females settled quietly on the bottom, the way they did in their home tanks, usually well within 10 min. In experiment 2, males appeared no more active than in their home tanks. Results from these experimental manipulations were supported by the absence of evidence for preferential associations between freely associating animals when I observed them in their home tank without disturbance (experiment 4). It is certainly possible that all laboratory behaviour is non-representative of natural behaviour; however, the conditions of these experiments did not appear to be unusually stressful for these laboratory-cultured cuttlefish.

That male cuttlefish form dominance hierarchies (experiment 5) provides evidence for the assertion that dominance hierarchies are not dependent upon individual or even class recognition (Archawaranon et al. 1991; Zayan 1992). Adamo & Hanlon (1996) found that males retested with a male that had recently defeated them were less likely to engage in a second contest. My results suggest that, for cuttlefish, the reduction in the subordinate males' aggression might not result from recognition of opponents but rather from a change in internal state as a

result of the defeat (see Karavanich & Atema 1993 for a carefully documented counter-example in lobsters). I predict that if a defeated male were presented with a different male of similar size, he would show the same reduction in aggression that he would when presented with his former opponent. Reduced aggression following defeat is insufficient evidence for opponent recognition. In cuttlefish, dominance hierarchies do not appear to be learned and do not result in energetic savings from reduced conflict.

The unique zebra bands on individual cuttlefish can be used by humans to identify individuals from the time the bands first appear, at sexually maturity (about 10 cm ML). Cuttlefish have adequate visual receptivity to distinguish each other's banding patterns (Budelmann 1994). Whether they are incapable of perceiving and remembering these distinctions or whether they are simply not motivated to discriminate is unknown.

An absence of social recognition is not inconsistent with what is known of cuttlefish in the field. *Sepia officinalis* has not been seen in aggregations; animals are usually seen alone or in pairs (R. T. Hanlon, personal communication). *Sepia latimanus* gathers for reproduction in small groups of up to six animals (Corner & Moore 1980). In such small groups, the cues from relative size, sexual receptivity and mating status could provide enough information for cuttlefish to focus their behaviour patterns on an appropriate conspecific. Male *S. latimanus* appeared to establish stations on the edge of the reef where they intercepted females arriving to lay eggs (Corner & Moore 1980). Males could avoid repeated contests with the same opponent by fleeing the place of their defeat.

In conclusion, I found no evidence that recognition of social partners plays a role in cuttlefish social interactions. Instead, the social interactions of these marine invertebrates appear to depend on relative size, internal motivation and the behaviour patterns of conspecifics. These results thus show no evidence for complex social knowledge. What cephalopods are doing with their large brains remains an open question.

ACKNOWLEDGMENTS

I thank R. T. Hanlon, R. H. Wiley and S. A. Adamo for their invaluable comments and discus-

sions relating to this project. This manuscript is much improved thanks to the helpful comments of B. G. Galef, Jr., R. H. Wiley, R. T. Hanlon, B. U. Budelmann and two anonymous referees. The work was supported by a National Institute of Health postdoctoral fellowship (NRSA # 5F32HD07686-02) and by the National Resource Center for Cephalopods (DHHS grant # RR01024) at the Marine Biomedical Institute, University of Texas Medical Branch, Galveston, Texas. Essential technical support was generously provided by D. Brining, J. Collins, P. DiMarco, J. Forsythe, P. Lee and J. Ni.

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