

FEMALE CHOICE OF MALES IN CUTTLEFISH (MOLLUSCA: CEPHALOPODA)

by

JEAN GEARY BOAL^{1,2)}

(Marine Biomedical Institute, University of Texas Medical Branch,
301 University Boulevard, Galveston, TX 77555-1163, USA)

(Acc. 17-III-1997)

Summary

In captivity, male cuttlefish use visual displays to establish size-based dominance hierarchies and larger males obtain most of the copulations. This experiment was performed to determine if females prefer the larger, more dominant males and whether females use male visual displays to evaluate males. Twenty sexually mature, virgin female cuttlefish were given up to six opportunities to approach one of two males out of a pool of ten adult males, or to approach neither. Females did have significant preferences between males, but they were not related to male dominance. Females showed a consistent and significant preference for the more recently mated male. These preferred males were also more likely to mate again, when given the opportunity, than were less-preferred, less-recently mated males. Females also preferred males that showed fewer zebra displays. Viewing male-male interactions did not affect their choices. Results suggest that female preference could be based on chemical cues, while visual displays may function primarily as agonistic signals. Females who mated did so repeatedly before laying eggs, providing opportunity for sperm competition.

¹⁾ E-mail: boal@mbian.utmb.edu

²⁾ I thank R.T. Hanlon and P.G. Lee for helpful discussions regarding this project. L. Wollerman, S.A. Adamo, and an anonymous reviewer provided excellent critiques of earlier drafts of this manuscript. This work was supported by a National Institute of Health postdoctoral fellowship (NRSA# 5F32HD07686) 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 J.M. Collins, P.E. Turk, and L.S. Walsh. I thank R. Hylton, S.A. Gonzalez and A.C. Roberts for help with animal care.

Introduction

Little is known about the reproductive strategies of cephalopods. Evidence for assessments of rivals by males (Tinbergen, 1939; Adamo & Hanlon, 1996; DiMarco & Hanlon, 1997), possible sperm competition (Cigliano, 1995) and alternate male strategies such as 'sneaking' (Hanlon *et al.*, 1994) indicate that the complex dynamics found in many insect and vertebrate groups may also exist among this group of mollusks.

In the cuttlefish, *Sepia officinalis* L., males use the Intense Zebra Display to assess rivals (Tinbergen, 1939; Adamo & Hanlon, 1996). In this display, the contrast between the light and dark bands on contestants' mantles and arms are intensified so that their normal, cryptic body patterns come to resemble the bold patterns of zebras (Hanlon & Messenger, 1988, 1996). The facial area darkens, the pupil facing the opponent dilates, and the strongly striped fourth arm is extended towards the opponent. Contest winners have darker faces than do losers (Adamo & Hanlon, 1996), and dominant males are generally larger than subordinate males (Boal, 1996).

Among captive cuttlefish, dominant males obtain more copulations than subordinate males (Boal, 1996). Copulations are initiated by the male grasping the female, and in smaller tanks, males almost always succeed in mating despite occasional vigorous resistance by females. In larger tanks, however, where females have the ability to flee or hide, resistant females normally remain unmated (Boal, 1996). It is reasonable to suspect that copulations in the open ocean are usually consensual.

If female choice occurs, preferences are not likely to be based on males' potential resource contributions because no parental care is provided to eggs or offspring by either parent. Females could prefer healthier males, however, such as those with fewer parasites (Hamilton & Zuk, 1982; *e.g.* Kavaliers & Colwell, 1995) or those with 'good genes' (Zahavi, 1975, 1977). Sick males show less contrast in their banding patterns than do healthy individuals (*pers. obs.*; see also Adamo & Hanlon, 1996). We know nothing about mate choice in cephalopods, but female preference for bright males has been demonstrated in several freshwater fishes (reviewed in Turner, 1993).

The Intense Zebra Display has been described as, "the most spectacular part ... [of] the elaborate courtship behaviour of male *Sepia*" (Boletzky, 1983, p. 47, *emphasis mine*). Could these bold displays indeed serve to

attract females, as well as serve in male-male dominance assessments? Do females use male-male displays to assess potential mates? Do females prefer larger, more dominant males? And, do females desire multiple matings, or are such events aberrations of captivity or results of male desires for multiple matings? To address these questions, I provided female cuttlefish with repeated opportunities to choose to approach either of two males. Female behavior was examined for evidence of consistent preferences and for evidence of an effect of male visual displays on preferences.

Methods

The animals used in this experiment were *Sepia officinalis* L. that had been reared in the laboratory from eggs harvested from the English Channel. Rearing and maintenance techniques have been described elsewhere (Forsythe *et al.*, 1991, 1994) and will not be reproduced here.

Experimental subjects were 20 adult females, ranging in size from 18-26.5 cm mantle length (\bar{x} = 22.25, SD = 2.45). Ten males were also used, ranging in size from 18-26.5 cm mantle length (\bar{x} = 21.35, SD = 2.36). It was not necessary to tag individuals because cuttlefish are recognizable by their unique zebra bands (pers. obs.). All females and one of the males were experimentally naive. The other nine males had been videotaped for one day each in a study of visual display behavior, one month prior to this experiment.

Female and male cuttlefish were separated as soon as they became sexually dimorphic, at sexual maturity. No copulations had been observed before that point. Isolated females laid some eggs before the experiment began; however, because none of these eggs were viable and unmated females are known to lay infertile eggs (Forsythe, pers. comm.), I presumed that all animals were virgins when the experiment began.

Both test tanks (described below) and the much larger holding tanks (2.4 × 5.5 × 0.9 m deep) were interconnected in a system of recirculating seawater obtained from the Gulf of Mexico (see Forsythe *et al.*, 1991, 1994). The experiment was conducted indoors, in June and July of 1995. Water temperature ranged from 21-23°C. Animals were fed frozen shrimp twice per day *ad libitum*.

Trials were conducted in four fiberglass rectangular test tanks, 1.2 × 1.8 m. In each tank, two water inflow sources were located at the west end and a stand pipe for water outflow was located in the center (Fig. 1). Partitions (A) could be slid into tracks attached vertically along the side walls of the tank, 60 cm from the west end. Further partitions (B) bisected the west end into two equal compartments. Partitions were made from either clear, non-polarizing plexiglass or opaque fiberglass. Partitions (A) did not fit tightly against the floor of the tank so that water passed from the sub-compartments to the main compartment. Partitions (B) fit snugly against the bottom.

Females were assigned to groups of four females each. Each female of a group was placed into a test tank (usually on a Friday afternoon) and allowed to habituate for at least 48 hours before experimental trials began (usually on Monday morning). Experimental trials were run between 9:00 and 18:00; most trials occurred between 10:00 and 12:00.

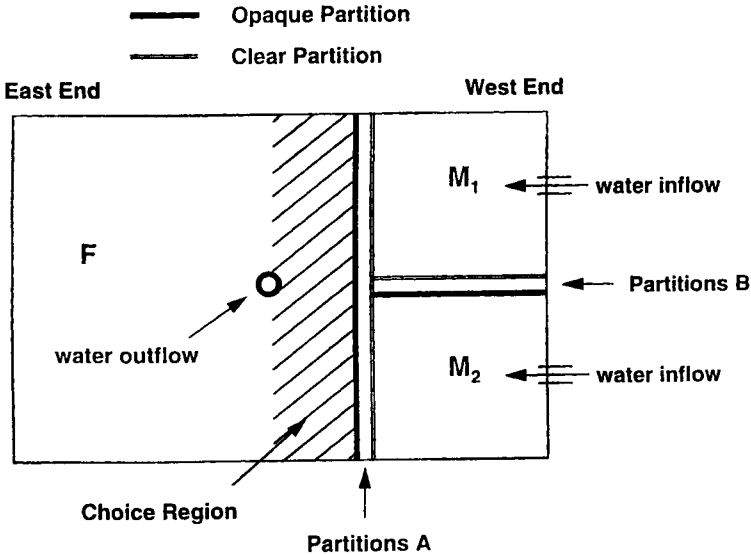


Fig. 1. Schematic of the test tanks. A single female was housed in the main compartment. One male was placed in each of the two small compartments for each trial. Water passed from each male's compartment under partition (A) to the outflow stand-pipe on the female's side. Opaque partitions could be lifted so that animals could see each other.

At the start of the day, both opaque and clear partitions (A) were placed into a female's tank, with the opaque panel on the side closer to the female. Either a clear or an opaque partition (B) was inserted to create two smaller compartments. Females were tested multiple times for preferences. Half of the females in each group received the first half of the trials with an opaque partition (B) and the second half of the trials with a clear partition (B); for the other half of the females, the order was reversed.

In preparation for a trial, a single male was placed into each of the two sub-compartments of the test tank and allowed to habituate for 20 minutes, with the location of the individual males alternated between trials. The opaque partition (A) was then raised so that the female could view both males and the males could see her. If the partition (B) between the males was clear, the males could also see each other.

Trials began once the female had inspected both males. Usually the female immediately swam up to the clear partition (A) and inspected both of the males within five minutes of raising the opaque partition (A). If the female stayed on one side for the first four minutes, I moved her gently to the other side with a net, to ensure she had seen both males. In this case, the trial started after six minutes. If the female had not moved from where I had herded her with the net after six minutes had elapsed, I moved her to the center at the far end of the tank before starting the trial. This rarely occurred.

I defined the region within the female's compartment between the partition (A) and the stand-pipe as the choice region (see Fig. 1). This area was about as wide as the total length of the females, including arms. If the female (or the mid-point between her eyes) was within the choice region directly in front of a particular male, I counted her as 'choosing'

that male. If she was in the area of the tank not included in the region of choice, I counted her response as 'no choice', or not interested.

Using a video camera mounted on a track above the test tanks (CCE-TR81 video Hi-8 camera recorder connected to a remote, portable JVC video monitor), I was able to view trials while remaining out of sight. During trials, I recorded the female's location every five seconds for five minutes (60 observations). This interval was frequent enough to capture virtually all the female's movements. I recorded a subset of trials for analysis of male display characteristics (trials for females 5-8 and 17-20). Natural lighting was supplemented with artificial lights during all trials.

After each trial, if the female had spent at least two-thirds of the trial time within the choice region of one of the males, I returned the less preferred male to the holding tank, removed all partitions, and left the more preferred male with the female for approximately half an hour. Usually, the pair usually mated; I timed copulations for duration. Sometimes the male never initiated a copulation; thus, no copulation occurred. Occasionally the female would actively resist the male's approaches by swimming vigorously away from him whenever he approached. In this case, I promptly removed the male; resistant females will sometimes dash themselves into the sides of the tank and ink if unable to avoid an unwanted suitor.

If the female had not spent at least two-thirds of the trial time within the choice region of one of the males, I returned both males to their holding tank.

Each female was tested once each morning for up to four mornings. If she spent at least two-thirds of her time in the choice region during the morning trial, she was tested again that afternoon. Trials for each female ended when she had received six trials or had shown no interest on four consecutive days. Twelve females were presented with the same pair of males (AB) in each trial. For seven of the females, one of the males had to be replaced (AB; AC) because of health concerns. For one female, one of the males had to be replaced a second time (AB; AC; AD).

Once trials for all four females in a group were completed, I moved them to a holding tank where they were housed as a single group. I counted the number of eggs laid on each day for 30 days. Meanwhile, I tested the next group of four females. At the end of the experiment, I placed all of the females and all of the males in a single, large holding tank and allowed them to interact freely. I observed all behavior and noted which animals copulated over the next four hours, and intermittently thereafter for the remainder of the animals' life spans (two months).

I measured choice of males in two different ways. (i) Magnitude of choice. I calculated the total number of counts the female spent directly adjacent to each male in each trial. To obtain a female's overall response, I averaged her scores across trials. In either case, these scores could be converted to a percentage of choices expressed (excluding 'no choice' counts) that reflected degree of preference. (ii) Dichotomous choice. Whichever male a female chose more often than the other was considered the preferred male, regardless of the margin of difference. This computation was performed either for each trial or for each set of trials run with a particular female and pair of males. Ranked male attractiveness to females was computed from dichotomous choices using a preference matrix adapted from dominance matrices (Martin & Bateson, 1993).

I analyzed the data three different ways: (i) all trials in which a female was in the choice region at least two-thirds of the time; (ii) all trials in which a female ever entered the choice

region; and (iii) all trials run. Results were similar, regardless of which data set I used. In initial analyses, I used all trials in which a female ever entered the choice region, unless otherwise indicated.

In *post-hoc* analyses, I used only those trials in which the female was in the choice region at least two-thirds of the time. Post-hoc analyses were verified using two subsets of the data: females that mated during the course of the experiment ($N = 14$), and females that never mated during the experiment ($N = 6$). Results for these subgroups did not differ from those of the whole group.

Unless otherwise specified, responses with the two types of partition (B) between males were similar and so were pooled.

Male behavior was scored from videotapes. For each trial, I scored the males' behavior once each 20 s for a total of 10 scores. I noted which male, if either, was displaying zebra banding or a dark face. I noted the orientation of each male, either towards or away from the female. I also noted which of the two males was swimming more actively during the five second interval immediately preceding the sampling instant. For each behavior, only intervals in which there was a clear difference between the two males were included in the analysis.

Results

1. Choice behavior

In total, 92 trials were completed using 20 females. In 27 of these trials, females spent the entire time within the choice region, swimming vigorously against the clear partition (A). In 37 of the trials, females swam actively around the entire tank, but spent much of their time in the choice region. In the remaining 28 trials, females settled on the bottom of the tank at the end farthest from the males and never entered the choice region.

By female, the average amount of time spent in the choice region was 51%: six females were found in the choice region more than 75% of the time, 13 females were found in the choice region between 20 and 50% of the time, and one female was found in the choice region less than 10% of the time.

Males also swam against the clear partition (A). When the partition (B) between the two males was opaque, all their activity was directed towards the female. When the partition (B) was clear, the orientation of their activity was divided between the female and the other male. Males displayed actively any time they could see another cuttlefish.

Females presented with the same pair of males multiple times were consistent in their choice of males, repeating their previous (dichotomous)

choice significantly more often than they changed their choice (a total of 31 repeats and 12 changes; Wilcoxon signed ranks test, $T+ = 55$, $N = 10$, $p = 0.001$). Choices were not exclusive; in repeated choices, females (dichotomously) chose their preferred male, calculated from total combined counts, 70% of the time and their non-preferred male 30% of the time.

II. Female preferences and male dominance

Results did not support the hypothesis that females choose dominant males.

First, (dichotomous) choice outcomes between particular pairs of males were not consistent between females. Females disagreed with each other as often as they agreed (Wilcoxon signed ranks test, $T+ = 23.5$, $N = 8$, $p > 0.25$).

Second, female (dichotomous) preference for males was not related to known indices of male dominance. Females did not prefer the larger of the two males presented (larger chosen in 34 out of 67 trials; 11 out of 20 females). Ranked female preference of males was not related to ranked male size (Spearman rank-order correlation coefficient $r_s = -0.20$, $N = 8$, $p > 0.50$). Female choices were also not related to the relative darkness of the two males' facial region (Wilcoxon signed ranks test, $z = 0.54$, $N = 19$ trials, $p > 0.29$), a good predictor of the male's success in male-male agonistic bouts (Adamo & Hanlon, 1996).

Third, female behavior was not influenced by viewing male-male interactions. When males could see and display to each other (partition (B) was clear), females were no more likely to enter the choice region (by trial: Student's $t = 1.30$, $df = 65$, $p > 0.90$; by female: paired comparisons $t = 0.18$, $df = 13$, $p > 0.50$), did not show stronger preferences between the two males (by trial: $t = 0.34$, $df = 65$, $p > 0.90$; by female: paired comparisons, $t = 1.93$, $df = 13$, $p > 0.05$, trend in opposite direction), and were not more likely to choose the larger of the two males (by trial: Student's $t = 0.29$, $df = 65$, $p > 0.90$; by female: $\chi^2 = 2.0$, $N = 18$ females, $df = 1$, $p > 0.10$) than when the males could not see each other (partition (B) was opaque).

III. Female preference and male displays

Male zebra patterning appeared to repel rather than attract females. In all videotaped trials, whether or not pairs of males could see each other,

preferred males were significantly less likely to be exhibiting zebra banding than non-preferred males (Wilcoxon signed ranks, $z = 2.005$, $N = 23$ trials, $p < 0.05$).

To verify this unexpected finding, I recorded the location of the last four females (17 to 20) for five minutes immediately prior to raising the opaque partition (A) at the start of a trials, and again for five minutes after I returned the opaque partition (A) at the end of the trial. In these trials, females usually remained near the same male after the partition (A) was raised that she had preferred before it was raised (same choice *vs* different choice, Wilcoxon signed ranks test, $T+ = 10$ (maximum possible), $N = 4$ females, $p = 0.06$), a further indication that females were not choosing males based upon visual inspection. Furthermore, females were found within the choice region significantly more often when the opaque partition was in place than after it was lifted (sum of choice responses, Wilcoxon signed ranks test, $T+ = 20$, $N = 6$ unique M-F pairings, $p = 0.03$), providing further evidence that male visual displays repel rather than attract females. This effect was not a result of test order: females were found within the choice region 72% of the time before the opaque partition was initially lifted, 51% of the time after it was lifted, and 86% of the time after it was returned.

Female preference was also not related to the males' activity level or their body orientation (towards *vs* away from the female).

IV. Female preference and male reproductive history

A *post-hoc* analysis revealed that female choices coincided with male reproductive history; preferred males had mated more recently than non-preferred males (Wilcoxon signed ranks test, $z = 2.004$, $N = 34$ trials, $p < 0.05$; trials extended over 42 days, virgin males were arbitrarily assigned a value of 45 days since last copulation).

General level of interest of females, on the other hand, was not related to male reproductive history. Females were equally likely to enter the choice region, regardless of whether the choice was between two virgin, two non-virgin, or a virgin and a non-virgin male (analysis of variance by trial, $F_{2,43} = 1.34$, $p > 0.25$).

Females' preference for recently-mated males probably explains consistent preferences within individual females (see I. above). Females tended

to repeat their previous choice if choosing between virgin and non-virgin males (6 changes vs 12 repeats) but did not show such a tendency if they were choosing between males of similar history (both virgin or both non-virgin, 9 changes vs 7 repeats). Among choices between males with similar mating history (virgin or non-virgin), females were still no more likely to choose the larger male than the smaller male (12 vs 10).

The likelihood that males would mate, if given an opportunity, varied with the male's mating history. Recently-mated males (within 48 hours) were most likely to mate again (12 of 16 trials), non-recently mated males were equally likely to mate or not mate (five of nine mated again), and virgin males were least likely to mate (five of 17 trials resulted in a copulation). The difference between recently-mated and virgin males is statistically significant (Fisher's exact p , one-tailed, $p = 0.01$).

V. Reproductive behavior

Females who chose males during experiments mated repeatedly: the six females most interested in the males mated, on average, three times each (maximum possible = 6). All four of these six females still alive at the end of the experiment mated again within 24 hours of being housed with males. Females that never mated during choice experiments ($N = 6$) generally did not mate for several weeks after being placed with males at the end of the experiment; however, once they did begin mating, usually about one month later, I observed that they also mated repeatedly.

Five males mated at the first opportunity, one mated the second opportunity, and four males never mated, despite many (2, 3, 17, and 34) opportunities. Larger males were no more likely to mate than smaller males, when given the opportunity ($\chi^2 = 2.165$, $df = 2$, $p > 0.30$).

Copulations occurred in a head-to-head position. Usually the male initiated mating by pursuing the female around the tank. Sometimes the females initiated courtship by approaching the male, swimming side-by-side, and even putting her head near or in front of his. In one case I observed a female face a male and spread her arms in anticipation of a copulation. Males always initiated the actual copulatory event by grasping the female either directly on the head or elsewhere; in response, a receptive female would squirm around to face him. During the initial period of mating, females often showed active swimming movements; later, the female's swimming

movements become minimal. Copulations were terminated by the female. First the female began to wave individual arms and show stronger fin-swimming; this was followed by attempts to jet backwards away from the male. Although he often maintained his grasp initially, the copulation ended soon thereafter.

Copulation times did not vary with the overall mating experience of the participants (mean copulation times: virgin males, 2 min 50 s; experienced males, 2 min 53 s; virgin females, 2 min 44 s; experienced females, 2 min 59 s; differences not significant). However, for experienced females, copulations that occurred more than 24 hours after a previous copulation took significantly longer than those that occurred sooner ($\bar{x} = 3 \text{ min } 25 \text{ s}$ vs $\bar{x} = 2 \text{ min } 21 \text{ s}$; Student's $t = 2.27$, $df = 10$, $p < 0.05$). For males, recency of last mating did not influence copulation time (2 min 59 s vs 2 min 56 s; Student's $t = 0.12$, $df = 15$, $p > 0.90$). Observed copulation times ranged from 1 min 49 s to 4 min 42 s. One outlying copulation time of 10 min 24 s was excluded from the above analyses because the male died within 24 hours of this mating.

Peak egg-laying occurred 4 days after peak mating frequency.

Discussion

Females demonstrated consistent preferences for some males over others. They did not base their choices on characteristics known to correlate with male dominance such as body size or patterning. I also found no evidence that females were evaluating males on the basis of male-male interactions since female choices were not affected by the type of partition (B) in place between the two males (clear or opaque). Male-male visual displays are probably not used by females to assess mate quality.

The only display characteristic that correlated with female preference was absence of zebra banding. Females were less likely to approach males when they could see them (clear partition (A)) than when they could not (opaque partition (A)). Both females and males intensify their zebra banding patterns in conflict situations (personal observation), and, contrary to published reports (Tinbergen, 1939; Mather, 1986), I have occasionally seen females, as well as males, exhibit an intense zebra display. It appears, therefore, that these visual signals are agonistic in nature and may actually repel females.

A similar repellent effect of male aggressive signals to females has been found in treefrogs, in which aggressive calls by males appeared to reduce male attractiveness to females (Wells & Bard, 1987).

An advantage of this experimental design over forced-choice designs was that the preferences of sexually receptive females were not masked by those uninterested in mating. Cuttlefish are not gregarious; uninterested females stayed far from the 'choice regions' adjacent to males. Although no difference was found between choices of very interested females (responded at least two thirds of the time) and less interested females, preferences could easily have been masked in a forced-choice design by uninterested females who generally spent long periods of time sitting in one place on the bottom of the tank.

Females chose males that were more likely to mate. Females were able to detect which males had previously mated and how recently they had mated, and they preferred to approach more recently mated males. These recently-mated males were, in turn, more likely to mate again than were other males. These results are consistent with those of Boal (1996), who found that individual cuttlefish did not appear to recognize their own mate from another recently-mated animal of the opposite sex, yet did discriminate between individuals based on mating status (whether or not they had mated recently). Females were never placed with the male they did not choose, however, so that our understanding of difference between preferred and non-preferred males remains incomplete.

Chemical cues (pheromones) provide a plausible explanation for female behavior since female choice regions were directly downstream from males. We know little about chemical communication in cephalopods, but we do know that cephalopods have chemoreceptive abilities (Gilly & Lucero, 1992; Lucero *et al.*, 1992). In nautilus and octopuses, chemotaxis is important in the location of food (Budelmann, 1994; Basil & Hanlon, unpubl. data) and in squid, ink appears to elicit alarm responses in conspecifics (Lucero *et al.*, 1994). Female cuttlefish can detect the sex of other cuttlefish using chemical cues alone (Boal & Marsh, unpubl. data) and both squids and cuttlefishes show great interest in egg masses in the laboratory, inspecting, handling, and blowing water at them (pers. obs.). This egg-handling behavior appears to release mating behaviors in *Loligo pealei* (Hanlon, pers. comm.), suggesting that the eggs contain a pheromone important to

sexual behavior. Chemoreception has not been thought previously to be of great significance to cephalopods (Budelmann, 1994), but across taxa, olfaction is usually important in reproductive behavior, including to the choice of mates (Bateson, 1983). The use of pheromones by cephalopods, suggested by Woodhams & Messenger (1974) and Hanlon & Messenger (1996), clearly merits further investigation.

The distance that signals must travel to the intended receiver could have influenced the sensory modalities cuttlefish use: for short-distance agonistic communication, brief, highly controllable visual signals; for long-distance reproductive advertisement, highly specific, non-degrading chemical signals. In support for this hypothesis, visual displays appear to function as agonistic signals among nearby conspecifics and do not attract females. Similarly, chemical signals may function for reproductive signaling; water from a displaying male does not cause other males to display (Adamo & Hanlon, 1996).

My hypotheses about possible chemical communication in cuttlefish are tentative. Because I did not anticipate the possible importance of chemical cues to cuttlefish behavior, this experiment did not explicitly test whether chemical cues can explain females' choice of mates. The partition (B) between the two males was not sealed, nor were water currents measured. It remains for future experiments to determine conclusively what role chemical cues play in cuttlefish social behavior. For now, chemical cues remain the best hypothesis for female preferences.

Female behavior provided opportunity for sperm competition, and offers a possible explanation for observed post-copulatory mate-guarding by males (Boal, 1996). Sexually receptive females mated repeatedly. Their mate preferences were not exclusive; they chose the less-preferred male 30% of the time. Egg-laying occurred days after copulation. The possibility for sperm competition has also been noted in octopuses (Cigliano, 1995); however, unlike in octopuses, copulation times with cuttlefish were shorter with recently-mated females, rather than longer. Male cuttlefish are unlikely to be engaging in some behaviors associated with sperm competition, therefore, such as transferring more sperm, or mechanically displacing or removing a previous male's sperm (Birkhead & Hunter, 1990). Male octopuses do not guard mates; it appears that males of the two species have evolved different strategies for protecting their sperm investment.

This experiment demonstrates that females could play quite an active role in cuttlefish reproductive behavior by locating and perhaps choosing between potential mates. Do females have such an opportunity under natural conditions? Cuttlefish are probably not social; instead, they probably live widely spaced along the continental shelves (Boletzky, 1983; Boal, 1996; Hanlon & Messenger, 1996). Corner & Moore (1980) observed that in *Sepia latimanus*, a related species, males were stationed along the reef in places where they could intercept females coming to lay eggs. If dominant males chase other males away from potential spawning sites, female preference for recently mated males could result in their indirect selection of socially dominant males. This scenario cannot account for large, socially dominant males that are not yet sexually ready, however. In this study, for example, the largest male obviously dominated all other males in the all-male holding tank. Nevertheless, he never mated during these experiments, even though he was chosen on seven different trials by females who mated readily with other males. His lack of mating persisted for nearly a month after experiments had ended. Once he did become interested, however, he mated up to several times a day. Perhaps uninterested males do not station themselves along the reef in this way. Alternatively, females could lay eggs near males that they find or choose by following chemical cues. It will require future field observations of known individuals to determine the relationship between male social dominance and reproductive success under natural conditions.

References

- Adamo, S. & Hanlon, R.T. (1996). Do cuttlefish (Cephalopoda) signal their intentions to conspecifics during agonistic encounters? — *Anim. Behav.* 52, p. 73-81.
- Bateson, P. (1983). *Mate choice*. — Cambridge University Press, Cambridge.
- Birkhead, T.R. & Hunter, F.M. (1990). Mechanisms of sperm competition. — *Trends Ecol. Evol.* 5, p. 48-52.
- Boal, J.G. (1996). Absence of social recognition in laboratory-reared cuttlefish, *Sepia officinalis* L. (Mollusca: Cephalopoda). — *Anim. Behav.* 52, p. 529-537.
- Boletzky, S.V. (1983). *Sepia officinalis*. — In: *Cephalopod life cycles*, Vol. I: Species accounts (P.R. Boyle, ed.). Academic Press, New York, p. 31-52.
- Budelmann, B.U. (1994). Cephalopod sense organs, nerves and the brain: adaptations for high performance and life style. — *Mar. Fresh. Behav. Physiol.* 25, p. 13-33.
- Cigliano, J.A. (1995). Assessment of the mating history of female pygmy octopuses and a possible sperm competition mechanism. — *Anim. Behav.* 49, p. 849-851.

- Corner, B.D. & Moore, H.T. (1980). Field observations on the reproductive behavior of *Sepia latimanus*. — *Micronesica* 16, p. 235-260.
- DiMarco, P.F. & Hanlon, R.T. (1997). Agonistic behavior in the squid *Loligo plei*: fighting tactics and the effects of size and resource value. — *Ethology* 103, p. 89-108.
- Forsythe, J.W., DeRusha, R.H. & Hanlon, R.T. (1994). Growth, reproduction and life span of *Sepia officinalis* (Cephalopoda: Mollusca) cultured through seven consecutive generations. — *J. Zool. (Lond.)*, 233, p. 175-192.
- —, Hanlon, R.T. & DeRusha, R. (1991). Pilot large-scale culture of *Sepia* in biomedical research. — In: *The cuttlefish: Acta I. Int. Symp. Cuttlefish Sepia* (E. Boucaud-Camou, ed.). Centre de Publications de l'Université de Caen, France, p. 313-323.
- Gilly, W.F. & Lucero, M.T. (1992). Behavioural responses to chemical stimulation of the olfactory organ in the squid, *Loligo opalescens*. — *J. Exp. Biol.* 162, p. 209-229.
- Hamilton, W.D. & Zuk, M. (1982). Heritable true fitness and bright birds. A role for parasites? — *Science* 218, p. 384-387.
- Hanlon, R.T. & Messenger, J.B. (1988). Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): the morphology and development of body patterns and their relation to behaviour. — *Phil. Trans. R. Soc. Lond. B* 320, p. 437-487.
- — & — — (1996). *Cephalopod behaviour*. — Cambridge University Press, Cambridge.
- —, Smale, M.J., & Sauer, W.H.H. (1994). An ethogram of body patterning behavior in the squid *Loligo vulgaris reynaudii* on spawning grounds in South Africa. — *Biol. Bull.* 187, p. 363-372.
- Kavaliers, M. & Colwell, D.D. (1995). Discrimination by female mice between the odours of parasitized and non-parasitized males. — *Proc. R. Soc. Lond. B* 261 (1360), p. 31-35.
- Lucero, M.T., Farrington, H. & Gilly, W.F. (1994). Quantification of L-Dopa and dopamine in squid ink: implications for chemoreception. — *Biol. Bull.* 187, p. 55-63.
- —, Horrigan, F.T. & Gilly, W.F. (1992). Electrical responses to chemical stimulation of squid olfactory receptor cells. — *J. Exp. Biol.* 162, p. 231-249.
- Martin, P. & Bateson, P. (1993). *Measuring behaviour*, 2nd edn. — Cambridge University Press, Cambridge.
- Mather, J.A. (1986). A female dominated feeding hierarchy in juvenile *Sepia officinalis* in the laboratory. — *Mar. Behav. Physiol.* 12, p. 233-244.
- Tinbergen, L. (1939). Zur Fortpflanzungsethologie von *Sepia officinalis* L. — *Archs. neerl. Zool.* 3, p. 323-364.
- Turner, G.F. (1993). Teleost mating behaviour. — In: *Behaviour of teleost fishes*, 2nd edn (T.J. Pitcher, ed.). Chapman & Hall, London, p. 307-332.
- Wells, K.D. & Bard, K.M. (1987). Vocal communication in a neotropical treefrog, *Hyla ebraccata*: responses of females to advertisement and aggressive calls. — *Behaviour* 101, p. 200-210.
- Woodhams, P.L. & Messenger, J.B. (1974). A note on the ultrastructure of the octopus olfactory organ. — *Cell and Tissue Research* 152, p. 253-258.
- Zahavi, A. (1975). Mate selection — a selection for a handicap. — *J. theor. Biol.* 53, p. 205-214.
- — (1977). The cost of honesty. (Further remarks on the handicap principle). — *J. theor. Biol.* 67, p. 603-605.
-