

THE MATING SYSTEM OF THE SQUID *LOLIGO VULGARIS REYNAUDII* (CEPHALOPODA, MOLLUSCA) OFF SOUTH AFRICA: FIGHTING, GUARDING, SNEAKING, MATING AND EGG LAYING BEHAVIOR

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ABSTRACT

The chokka squid migrates to coastal waters to spawn, and its behavior on shallow spawning aggregations was analyzed by video sequences taken during SCUBA diving. Most squids were paired (M/F) on the spawning sites, yet mate pairing duration was brief. Near to egg masses, a few lone large males were always present and would fight consort males to obtain access to paired females. Paired 'consort' males won 16 agonistic contests while unpaired 'intruder' males won 9; thus there was a considerable turnover rate for consortships. The larger male won in 14 of the 25 contests. Fighting involved mainly visual signalling but escalated to moderate physical contact (Fin beating) but not injury. Both sexes had multiple mates even within several hours. Two methods of mating were observed, each with different placement of spermatophores, and a third method possibly exists. Large paired males mated in the 'male-parallel' position and inserted spermatophores near the oviduct; egg laying usually occurred shortly thereafter. Small sneaker males were often successful in mating a paired female; they copulated in a modified 'head-head' position in which they attempted to place spermatophores amidst the female's arms. Remarkably, sneakers seemed to recognize when females were holding an egg capsule and then timed their copulation attempt at that time. Sneakers did not engage large male consorts in contests, and consorts seldom chased them away when they mated a female. The 'cuckolded' consorts did not attempt to mate females again before they laid the egg capsule. Males guarded females as they descended periodically to lay individual egg capsules. All of these features indicate a high level of sperm competition. There were no lone females on spawning sites, and all arrived there with stored sperm in the seminal receptacle, having presumably mated in the typical 'head-head' position previously. Females rarely rejected males (consorts or sneakers) and it is possible that they exerted some choice of male sperm. There was no form of parental care of the eggs or paralarvae. Reproductive tactics are discussed in relation to the life cycle of this valuable fishery species.

Most cephalopods live for only 1–2 yrs but they have large brains and diverse behavior (Packard, 1972; Wells, 1978; Moynihan and Rodaniche, 1982; Boyle, 1983; Fiorito and Scotto, 1992; Hanlon and Messenger, 1996). Unfortunately, there are few behavioral studies conducted in the natural habitat to help explain how their complex behavior is used to carry out important functions such as reproduction. Most squids are schooling cephalopods that have ample time for social interactions, and since they are often mature for a large portion of their brief lives, they spend much of their time in reproductive behavior (cf. Hanlon and Messenger, 1996). For example, it is common to find small female *Loligo* with stored sperm in the seminal receptacle, and female *Loligo pealeii* and *Loligo opalescens* arrive on spawning grounds already with stored sperm (e.g., Drew, 1911; Fields, 1965; Hanlon et al., 1999), which indicates mating activity earlier in the life cycle.

Within a population, the term mating system refers to the general behavioral strategy used in obtaining mates. It includes such features as (1) the number of mates acquired, (2)

the manner of mate acquisition, (3) the presence and characteristics of any pair bonds, and (4) the patterns of parental care provided by each sex (Emlen and Oring, 1977). Mating systems can be viewed as outcomes of the behavior of individuals competing to maximize their reproductive success (Davies, 1991). The conceptual beginning point of mating systems is promiscuity (i.e., all pairings are random and multiple), while monogamy represents the other end of the spectrum (Lott, 1991). To our current knowledge, there are no monogamous cephalopods. What little is known about cephalopod mating systems was reviewed most recently by Hanlon and Messenger (1996).

Mating systems in cephalopods have not been examined in much detail because direct underwater observations are difficult. The pioneering studies of Moynihan and Rodaniche (1982) and Moynihan (1985) have provided a glimpse of the complexity of reproductive behavior in the tropical coral reef squid *Sepioteuthis sepioidea*. Large aggregations of spawning squids are not well studied and diving conditions are not usually easy. McGowan (1954) and Hurley (1977) made some preliminary field observations of *L. opalescens*. Hanlon and colleagues (Hanlon et al., 1997; Hanlon et al., 1999; Buresch et al., 2001) have recently begun to study *L. pealeii* in its natural habitat. We had the opportunity in South Africa to conduct diving observations nearshore to complement previous work by Sauer and colleagues on this valuable South Africa fisheries species (Sauer et al., 1992; Sauer and Smale, 1993; Augustyn et al., 1994). In this paper we delineate the general features of the mating system of *Loligo vulgaris reynaudii* (Loliginidae) on nearshore spawning grounds, bearing in mind that reproductive behavior certainly occurs at some level during other times (and at other locations) of the brief life cycle.

MATERIALS AND METHODS

Nearly 11 h of squid behaviors were observed from 11 November to 1 December 1993 on spawning grounds in depths of 17–40 m during 33 SCUBA dives, all during the day. The diving sites were along the southeastern Cape coastline between Port Alfred in the east (33°36'87S, 26°55'51E) and the Tsitsikamma Coastal National Park in the west (34°01'81S, 23°56'43E), spanning ca 350 km of coastline that represent the prime spawning grounds of this squid (Sauer et al., 1992). Behavior was observed directly and in close proximity to squids because they habituated to divers immediately.

Video was mandatory because diving duration was limited to 20–40 min due to diving depths, thus time had to be maximized for data acquisition. More than 4 h of the behavior were recorded with a Sony TR81, Hi-band 8 mm video camera in an underwater housing. In addition, 1.3 h of video tape from another hand-held video camera during previous years were also reviewed.

Sequences of behavior of (1) male-female pairs, (2) male-female pair and lone male intruder, or (3) lone large males were videotaped most frequently because emphasis was placed on the events leading to egg laying, which had already been filmed in previous field studies (Sauer et al., 1992; Sauer and Smale, 1993). For standardization, we use the word 'paired' only for a male/female pair; no other pairings were observed. Playback and analyses were performed meticulously by first splicing together segments of similar types of behavior; for example, all matings, all agonistic bouts, etc. Video tapes were analyzed for specific behaviors; i.e., all tapes were viewed by looking specifically only for agonistic bouts. The same segments were reviewed again looking specifically for body patterns, then locomotor/postural components, then the behavior of the female during the male bouts, and so forth. The names of behaviors and skin patterns follow Hanlon et al. (1994). Multimotion video playback machines enabled detailed descriptions.

RESULTS

GENERAL STRUCTURE OF THE MATING ARENA.—Spawning aggregations vary greatly in size (Sauer et al., 1992) but, except for one dive, we worked on small mating arenas in which there were 3–10 small egg mops (each ca 1–3 m diameter) and between 10–100 mating pairs of squids in the field of visibility. Figure 1 depicts the general 3-dimensional layout and zones of activity on a typical mating arena. Immediately around the egg mop is the ‘egg-laying zone’ in which there are concentrated groups of male/female pairs that descend in a somewhat orderly fashion to deposit individual egg capsules in the mop. Integrated with this is the ‘agonistic zone’ in which lone large males intercept pairs and engage consort males in agonistic contests. Beyond this is the ‘mating/sneaker zone’ in which squid density is low by comparison, and in which large males are accompanying and mating females, and also in which sneaker males are cruising the area seeking opportunities for extra-pair copulations (EPC). We define the mating arena as the general area encompassed by the egg-laying zone through to the periphery of the mating/sneaker zone. The mating arena can vary greatly in size and was not measured. Finally there is a ‘transitory zone’ in which there is immigration and emigration to the mating arena. The defining aspects of the arena are the egg beds. Although there is nothing hard and fast about these ‘zones’—and they may be different at different times of year—they are the primary areas in which one can observe those behaviors they are named for. Occasionally, for

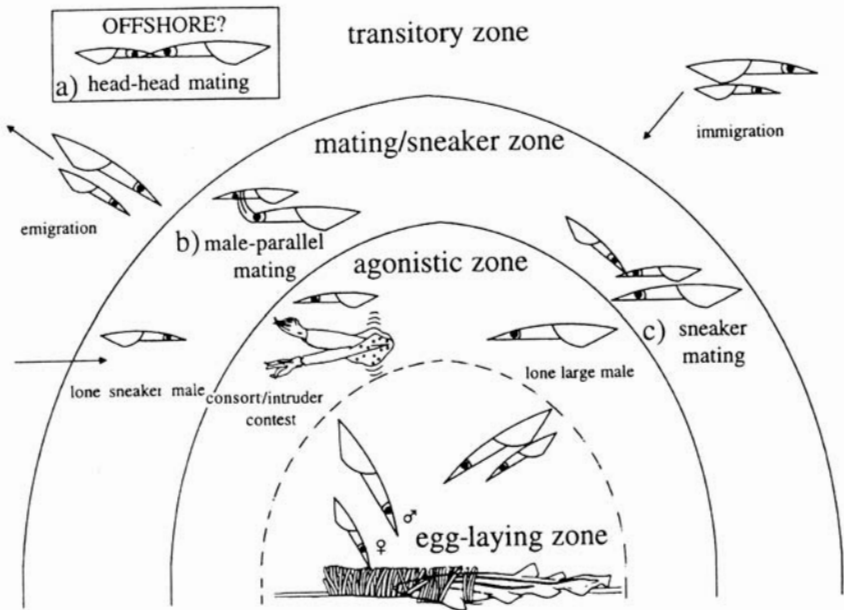


Figure 1. General schema of behavioral zones in a typical mating arena of the squid *Loligo vulgaris reynaudii* off South Africa. (a) Upon arriving on the spawning grounds, most females already have stored sperm in the seminal receptacle, indicating ‘head-head’ mating, which was not seen in the mating arenas. (b) Temporary pairings of large consort males result in ‘male-parallel’ matings. (c) Small lone ‘sneaker’ males occasionally succeed in obtaining extra-pair copulations in a slightly different position. As pairs move to/from the egg mops, they are intercepted by lone large male ‘intruders’ that engage the paired consorts in agonistic contests that often result in successful takeovers. Females are rarely susceptible to predation by benthic sharks when they oviposit. (Modified from Hanlon and Messenger, 1996: 116)

example, there are agonistic bouts and competition for females in the egg-laying zone, but most of that fighting behavior takes place within ca 3 m of the eggs.

Movement among these zones is variable but after egg laying the pair usually jets vigorously out of the egg-laying zone through the agonistic zone and then the pair moves gradually into the mating zone where they may circle like airplanes awaiting their turn to land at a busy airport. During this time the large consort male mates the female. Time spent within the agonistic zone seems most variable because it is dependent upon interference from agonistic encounters with the few lone large males that are always present. 'Winners' of those bouts usually move with the female outward to the mating zone, provided that she does not have an egg capsule in her arm, in which case she would descend to oviposit.

The operational sex ratio was skewed towards more males. We were not able to measure the exact numbers, but preliminary counts from some of the wide angle pans of the video camera indicated a ratio in the order of ca 1.4M:1F. The extra males were either lone large males (similar in size to the large consort males) or—more rarely in our observations—small males approximately the size of females (note the size dimorphism in the figures). Lone females were not observed in these mating arenas. Thus in a small mating arena, we might see 10 pairs plus two lone large males and two small sneaker males (i.e., 14 males and 10 females). This skewed operational sex ratio on the mating arena set up the gradient for sexual selection.

AGONISTIC CONTESTS BETWEEN MALES.—The majority of squids in the mating arena were male-female pairs. Lone large males competed for paired females on the spawning grounds; thus the most common interaction was to see a large lone male 'intruding' on the pair and engaging the paired consort male in an agonistic contest.

In total, 33 agonistic contests were filmed: 16 were won by the paired consort and 9 by the unpaired intruder. In the other 8 contests the original consort could not be deduced because the film started after the contest was underway.

Figure 2 shows the nature of the contest. Males assumed parallel positioning relative to one another and used visual body patterns followed by escalation to physical Fin beating. A major maneuver was the attempt by the intruder to position himself nearest the female, usually by jockeying and swimming under the consort male. Sometimes the intruder would jockey directly under the consort and swim forcibly upwards attempting to lift or displace the consort; both this maneuver and Fin beating were actual tests of strength and swimming ability. The paired consort male would parry the advances of the jockeying intruder and try to maintain his position immediately adjacent to the female. The winner of the contest was the male that was paired with the female after the contest.

The larger male in each contest won 14 of the 25 graded bouts (56%), regardless of whether he was consort or intruder. The smaller male won eight of the 25 contests (32%), and in three contests the males were the same approximate size. Mean duration of the contests was 7.5 s (range 1–21), Fin beating occurred in 19 of the 25 graded contests; mean duration was 2.4 s (range 1–11). We were unable to determine any simple relationships between the duration of the contest, the size of the contestants or the occurrence or duration of Fin beating.

Several components of body patterning were used exclusively by males during agonistic contests (Fig. 2; see other details in Hanlon et al., 1994). The predominant body pattern was Lateral Display (Figs. 2C,E), which began with Parallel positioning and then the chromatic components Arm spots, Fin spots, Lateral mantle streaks, Infraocular spot and

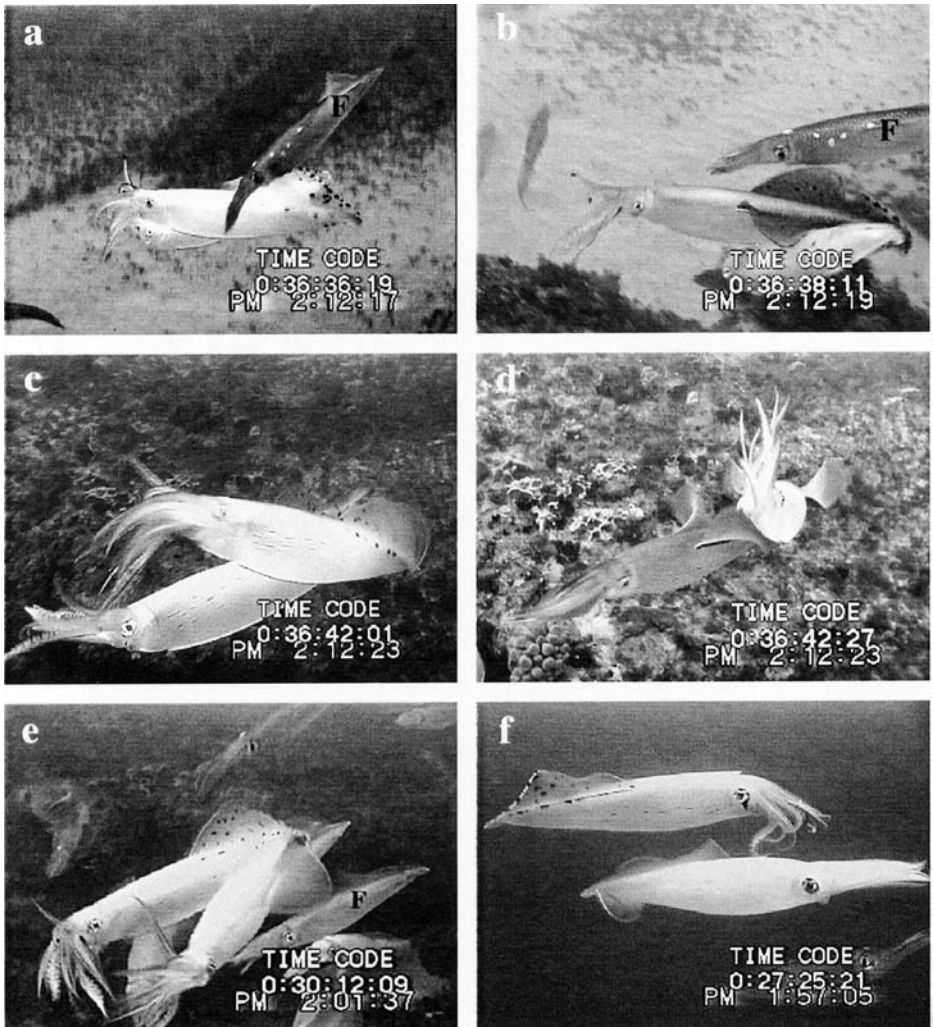


Figure 2. Agonistic contests. Frames a–d are a sequence of the same males. (a) Two large males White flashing to each other. The consort male (nearest the female, F) shows Fin spots, Raised arms, Dark first arms and ventral mantle stripe as he wards off the advances of the large lone male intruder below him. (b) Two seconds later, the intruder jockeys under the consort attempting to get near the female; the consort parries with Dark fins and Fin beating. Note the Splayed arms by the consort in a and b. (c) Four seconds later, the pair Fin beat strongly. Note the Lateral mantle streaks and the ventral mantle stripe. (d) The consort (right) continues White Flashing and Fin beating while the intruder goes slightly dark with Mantle margin stripe and begins to retreat. (e) A different agonistic contest in which the two males are engaged in a full Lateral Display (see text for fuller description). The female is just to the right of them. Note the Arm spots as well as Fin spots on the intruder male. (f) A low-grade agonistic encounter in which an intruder (top) shows Infraocular spot, Drooping arms and Fin spots to a consort.

Mantle margin stripe. This display also included the postural components Raised arms or Splayed arms, which was highly conspicuous even at a distance. There were then dynamic interactions that included White Flashing and Dark Flashing, both of which were

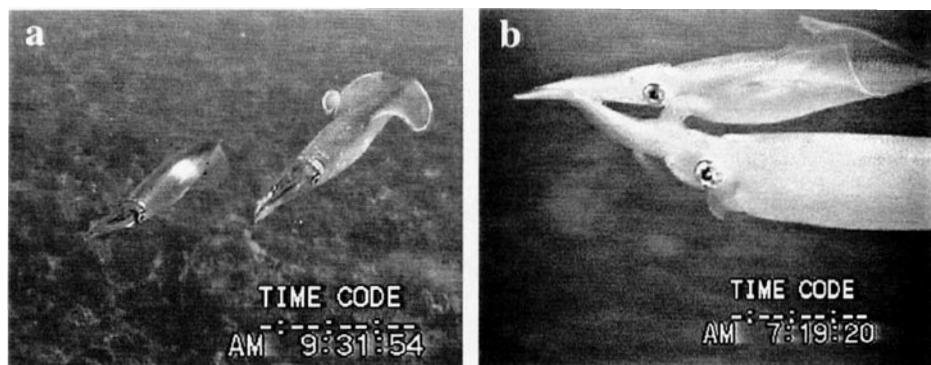


Figure 3. (a) Visual signalling between the consort male and female. Note the Accentuated oviducal gland of the female. (b) Male-parallel mating between a large consort male (below) and his female mate. Note how only the male's fourth arms are contacting the female.

highly conspicuous. Finally, in some cases, Lateral Display would escalate to Fin beating.

PAIR FORMATION.—Pairing was already accomplished when we conducted our SCUBA dives. However, Sauer et al. (1997) provided telemetry evidence that pairing may occur early as squids aggregate each day after a night of feeding while dispersed. It is clear from our observations that pairs are temporary because they change frequently during the day. Preliminary ROV footage from 1990 indicated that pair formation broke down at about dark; mostly females were present just before all the squids dispersed. The telemetry data (Sauer et al., 1997) also showed that squids moved to deeper water each evening.

There is a fair amount of visual signalling between the male and female, mainly the Accentuated oviducal gland (Fig. 3A). Males also often show the Accentuated testis component and it is possible that these signals help maintain the temporary pairing in some manner. No specific postures were noted, but it is noteworthy that in one instance when a female had been preyed upon by a shark, and then escaped (Smale et al., 1995), she attracted a sneaker male and a large male almost immediately. It is possible that her altered swimming or the pattern of her badly denuded skin may have served as a releasing signal for mating receptivity.

MATING BY LARGE CONSORT MALES.—The 'male-parallel' mating (Fig. 3B) was observed and filmed nine times. Large consort males grasped females from below, usually parallel to them but sometimes up to 20 degrees from parallel. The female was receptive and was held gently by the male's fourth arms, which were inserted into the female's funnel. Males then reached into their own mantle with the hectocotylied fourth left arm to grasp spermatophores and transfer them to the female's mantle; no other details such as spermatophore placement could be seen. In two sequences, the male transferred spermatophores twice during a single mating: once at 5 and 15 s during a mating of 23+ s, and once at 4 and 18 s during a mating of 39+ s. Since first transfer usually occurred so swiftly, it is unlikely that males were engaging in any sort of sperm flushing or spermatophore removal against previous males that had mated the female.

Mean duration of 'male-parallel' mating was 16 s and ranged from 2–39 s in our observations; however, nearly all mating durations were timed from when the mating was

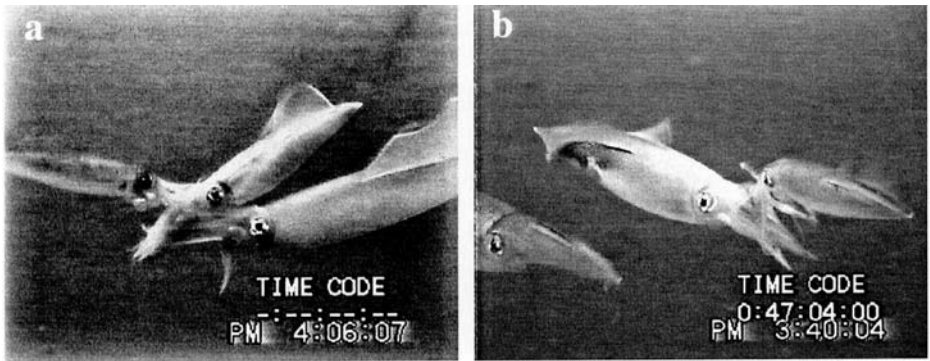


Figure 4. Extra-pair copulations by sneaker males. (a) Male-parallel mating by a consort male (bottom right) while simultaneously a sneaker male (left) mates the female in a different position. (b) Small sneaker male (right) mates a large female while she is holding an egg capsule in her arms. Note that the large consort male (left) is not fighting off the sneaker male.

already in progress. While mating, the male swam forward, slowly drifting downward on a slight angle.

Initiation of mating by the consort male was filmed once. An intruder male succeeded in winning an agonistic contest with a paired male, and they immediately swam upwards into the mating/sneaker zone and within a matter of seconds of the agonistic contest he gently 'reached' towards her twice in succession while swimming slowly up under her. The pair swam out of sight (water was murky) and actual mating was not observed. Termination of mating was gentle in all nine observations and occurred as the male released his hold on the female. During one termination, the female ejected three white particles from the funnel; they looked like spermatophores, but were not collected nor were they distinguishable on film. We once observed a female ink at the moment of the conclusion of mating; other times we saw females ink in response to small fishes (*Spondyllosoma emarginatum*; Sparidae) that closely approached a mating pair. It was not uncommon to see inking in the mating/sneaking zone.

The 'head-head' position of mating—with arms entwined—that is characteristic of *Loligo* spp. was not observed (Drew, 1911; reviewed in Hanlon and Messenger, 1996), but a modification of it was discovered (next section).

SNEAKER MALES AND EXTRA-PAIR COPULATIONS.—Nine sneaker males were filmed. These males were small, about the same or 2/3 of the females' mantle lengths (e.g., ca 90 mm ML) and about half the mantle length of other males on the spawning grounds. These sneakers were very swift swimmers and were difficult to see in the aggregations because there were few of them and they were highly mobile, possibly moving from aggregation to aggregation. They did not engage large males in agonistic contests.

Extra-pair copulations (EPCs) by sneakers were filmed 6 times. Mean duration was 6 s (range 2–11). Sneakers would swim in from any angle in the water column and position themselves facing the female and holding her near the base of her first arms (Fig. 4). The sneaker's hectocotylized fourth arm was placed into the arms of the females but no details were visible; it is possible that they were placing spermatophores directly onto the egg capsule that the female was holding because the egg capsule would be blocking access to the seminal receptacle. In most of the sequences, the sneaker performed a pecu-

liar 'lurch' forward onto the female as he mated her, but no arm movements of spermatophore transfer could be seen with this movement.

A noteworthy observation was that the large consort males did not chase or fight the sneakers in five out of nine encounters. In one encounter, the sneaker grasped and copulated with the female while she was already mating with the consort in the 'male-parallel' position (Fig. 4A). Both males continued to mate for 4 s and then both swam off. In another case, two sneakers copulated with the female independently within 27 s, and she then drifted downward to the egg mop and deposited an egg capsule while the large male guarded—but did not mate—her (see below).

In the three cases the consort male interceded only by making one short forward rush towards the sneaker; there was no pursuit or physical contact. In the fourth case, the sneaker tried to copulate with the female of a pair that was swimming swiftly away, and in this case the male consort swam very hard to stay between the sneaker and the female over a distance of 10–15 m until the sneaker swam off.

Identification of sneakers as males was not confirmed by collecting an animal, but on two occasions they showed the Accentuated testis component that has different placement than the Accentuated oviducal gland component of females (Hanlon et al., 1994). Sneakers had conspicuously narrower mantles than females, and this is characteristic of males in this species.

FEMALE CHOICE, EGG LAYING AND MATE GUARDING BY MALES.—Both sexes readily accepted copulations from multiple mates, even within the course of an hour. At first glance, it appeared that females were not exerting choice of mates because we did not observe lone females swimming about and investigating potential males as mates. However, analysis of the tapes showed that females rejected one of seven attempts by small males to obtain EPCs; consort males rejected sneakers two times.

In essence, the large male that was positioned next to the female at the end of an agonistic contest became, de facto, the mate of that female. We did not observe females rejecting the winners of bouts or actually choosing them. However, we emphasize that we did not dive at dawn to observe the daily process of initial pair formation each day (but see Sauer et al., 1997).

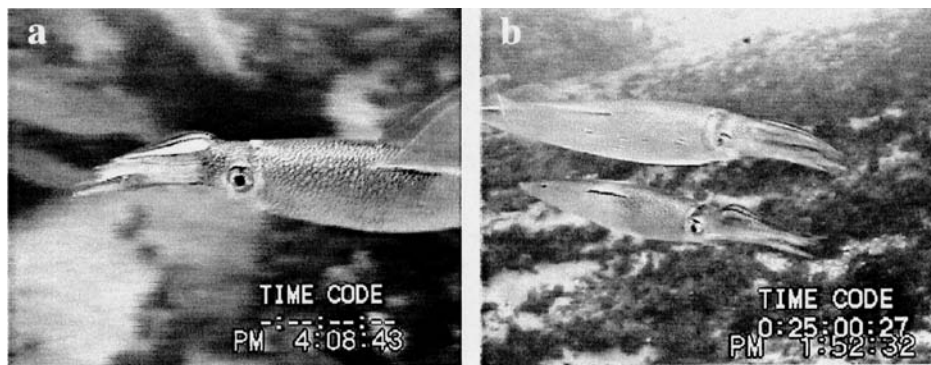


Figure 5. Paired females that are holding an egg capsule in their arms after mating with a consort male. Females can release stored sperm from the seminal receptacle onto the egg capsule in this position. The bulge created by the egg capsule (a) is not always this conspicuous, yet the sneaker males appear to be able to distinguish this subtle posture and thus time their EPCs with this female behavior. In (b) the female is below the male.

In general the mating pair would copulate in the mating/sneaker zone then slowly descend to the egg-laying zone where the female would deposit an egg capsule; the times varied considerably.

When does the female extrude the egg from her oviduct, and when does fertilization occur? Our observations indicate that she extrudes the egg capsule quite far from the egg beds. We think she was extruding and then holding an egg capsule in her arms when still in the mating/sneaker zone. We did not capture females at this time to verify the presence of an egg capsule in her arms. However, the bulge in the arms was noticeable (Fig. 5). Two events occurred at this time: first, the female had another element of potential choice in whether or not she exposed the egg capsule to stored sperm in the seminal receptacle, located below the mouth. Second, at this time the sneakers could deposit spermatophores or sperm directly on an egg capsule held in the female's arms, since this was exactly where the sneakers held the female. The time lag between mating and egg laying was only observed five times. After male-parallel mating with consorts, females laid eggs 2:30, 2:40 and 3:00 min later. After sneaker matings, females laid eggs 2:35 and 0:44 min later (note: these sneaker matings were in succession before a single egg capsule was laid).

DISCUSSION

The mating system of this squid provided the first record of sneaker male behavior among cephalopods; partial accounts were published in Hanlon and Messenger (1996), Sauer et al. (1997) and Hanlon (1998). The present paper complements the ethogram of behaviors published by Hanlon et al. (1994).

INTRASEXUAL COMPETITION: AGONISTIC BOUTS AND SNEAKER MALE TACTICS.—Fighting between large males was a conspicuous behavior on all mating arenas. One characteristic stood out: the bright white coloration that males used in these contests. White Flashing was common in all fights and could be seen many meters away even in these somewhat murky waters (visibility ranged 0.12–12 m). Such visually conspicuous signalling might be expected to incur a cost since predators could detect squids at a greater range. However, the only predation we observed on spawning grounds was that by a benthic shark that hid amidst egg mops and once seized a female as she deposited an egg capsule (Smale et al., 1995).

The details of agonistic contests are reminiscent of those we have witnessed in other loliginids such as *Loligo plei* (DiMarco and Hanlon, 1997), *L. pealeii* (Hanlon et al., 1999), and *L. forbesi* (Porteiro et al., 1990). Jockeying by lone intruder males and retaliatory parrying by paired consort males during agonistic contests represent sophisticated swimming ability. The female was often swimming or jetting away during bouts, and only the swift and agile male could watch and react to her movements while simultaneously engaging the contest. The latter aspect probably entails some sort of sequential assessment of the fighting ability of the male competitor (as in several other taxa; e.g., Leimar and Enquist, 1984).

Male size influenced the outcome of the contests: 56% of contests were won by the larger male, 32% by the smaller male, and in 12% the males were of similar size. Throughout the animal kingdom, larger males are usually the winners of agonistic contests, yet a substantial number of smaller males are motivated sufficiently to fight successfully for a mate. For example in cephalopods, Adamo and Hanlon (1996) found that male cuttlefish

that had lost an agonistic contest to a larger male were successful in fighting that same large male if the smaller male was given the opportunity to mate with a female cuttlefish in the brief interim between the fights. There is still much to learn about agonistic behavior in cephalopods (Moynihan, 1985; Hanlon and Messenger, 1996; DiMarco and Hanlon, 1997).

One interesting feature of these fights was the rate of successful takeovers by lone large males (36%). Although our sample size is very low, it indicates that large loners win one of three fights, which would lead to mate switching quite often (e.g., several times per day). In the future it would be beneficial to conduct focal samples on large males for several hours per day; unfortunately, depths and diving conditions will probably prevent this. By comparison, field studies of *L. pealeii* show that lone large males in that mating system achieve only a 10% takeover success rate (Hanlon, Shashar and Maxwell, pers. comm., 1998).

Small males competed for females by sneaking behavior. They did not engage any large male in agonistic contests, and they exhibited stealth by swimming mostly at the periphery of the mating arena, then darting in rapidly to mate with the female. Their swimming speed and agility were impressive because they would use their jet propulsion to catch up with swimming pairs, then rush in forward or backward and leap upon the female. Sometimes they would 'dive' in from above and grasp the female, then have to instantly twirl around to face her. These athletic locomotor maneuvers—jetting from aggressive conspecifics and jetting towards mates for EPCs—are not only signs of fitness, but they are functions of the giant axon that have not received the attention they deserve by neuroethologists.

INTERSEXUAL INTERACTIONS: MATE CHOICE.—We usually saw other squids in the water column during our dives, hence not all squids present in the area were actively engaged in sexual selection. How, for example, are mating pairs formed initially each day, and how is the operational sex ratio determined? We have indications from previous telemetry work (Sauer et al., 1997) that males seem to arrive first in the morning and circle above the substrate (or perhaps some existing egg beds), and then females appear and the mating arena becomes fully engaged in reproductive activity. Mechanisms of initial mate choice could not be deduced from our current set of observations but they should be addressed in the future.

A recent report by King, Adamo and Hanlon (1999) may throw light on this process. They showed that male *L. pealeii* are influenced by a sensory cue in egg capsules (even in the absence of females) that initiate high levels of agonistic behavior immediately. This highly robust reaction to a sensory stimulus may be a mechanism by which the cascade of sexual selection processes could be 'jump started' each morning, at least in mating arenas in which egg mops are already present (of course, this begs the question of who laid the first squid egg, and why!). For example, if the first males to arrive in early morning descended to the substrate and touched the eggs, this would lead to immediate agonistic behavior and possibly allow the largest or most dominant males to position themselves best for the arrival of females if indeed females actually do arrive later. This is speculation but could provide a working hypothesis for video behavioral sampling routines in future ROV or diving work on spawning grounds for many loliginid species.

Because females are the limiting resource, large males appear to be 'choosing' every and any female in the mating arena, and it appears that females are accepting (or possibly choosing) every large male that demonstrates that he can pair with her and maintain his

positioning next to her through agonistic contests against lone large males. In that regard, lone large males that win agonistic contests gain the opportunity to pair temporarily with the female, who accepts them when they attempt to mate her.

Small sneaker males appear to be more choosy, apparently restricting their efforts to EPCs with females that have just mated with consorts and are holding an egg capsule in their arms. Conversely, females accept almost all sneakers, who certainly exhibit stealth, health and superb swimming ability.

Another possibility is that females are exerting what Wiley and Poston (1996) termed indirect choice of mates. That is, by their distribution in the population, females could account for the skewed operational sex ratio that sets up a gradient of sexual selection in which males must compete vigorously for female mates. In such a ratio, females should be predicted to be choosy. Furthermore, by simply having a 'surplus' of males, the relative scarcity of females requires males to compete amongst one another, which is itself a mechanism of filtering healthy and strong males (i.e., only fit males can compete and win agonistic contests, etc.). While it is beyond the scope of this paper to delve into this subject, it may help explain why females seen in mating arenas engage in sexual selection processes even though they arrived on the spawning grounds with stored sperm already in the seminal receptacle.

SPERM COMPETITION AND THE MATING SYSTEM.—When this study was carried out (1993) it became the first cephalopod mating system in which underwater observations clearly demonstrated the high degree of sperm competition that is probably common among *Loligo*. Nearly all of the major criteria that encompass the varied behavioral, physiological and anatomical features of sperm competition (see Birkhead and Parker, 1997) exist in the mating system of *L. vulgaris reynaudii*.

All of the *Loligo* that have been studied show two 'typical' mating positions: male-parallel and head-head (reviewed most recently in Hanlon and Messenger, 1996). In this study, we noted what appears to be a third mating position (Fig. 4) in which we speculate that the small male sneaker is depositing spermatophores directly onto the egg capsule. No one has actually observed the typical head-head mating position in this species, but it is likely to occur because sperm can be seen in the seminal receptacle of freshly captured females (it appears as a bright white mass amidst the translucent skin below the mouth in the buccal region). It is possible, but not likely, that the squids in Figure 4 are placing sperm into the seminal receptacle (i.e., typical head-head mating) but this does not seem plausible because the female is holding a large egg capsule in her arms at the time of these matings. Perhaps future observations in the field or laboratory will clarify the mating dynamics that are occurring in *L. vulgaris reynaudii*.

One particular feature of the mating system of *Loligo* spp. that stands out among other animal taxa is the dual (perhaps triple in *L. vulgaris reynaudii*) nature of mating and sperm placement (Hanlon and Messenger, 1996; Hanlon, 1998). Clearly, females have ample sources of sperm to use for fertilizations because they all appear to have stored sperm (probably from multiple males) in addition to the spermatophores placed by consorts into the mantle cavity. Thus, every egg capsule extruded from the oviduct can be exposed to multiple sperm sources: (1) first from one or more consorts that recently mated her (male-parallel position) and placed multiple spermatophores on or around the oviduct, (2) second from stored sperm that she can access while holding the egg capsule in her arms, and (3) third from the possibility of sneakers placing sperm (or spermatophores) directly on the egg capsule. Since other loliginids have been demonstrated to lay tens of

egg capsules in a day (each with 100–300 eggs) (*L. pealeii*; Maxwell and Hanlon, 2000), and behavioral dynamics are complex (Hanlon et al., 1997), the probability of multiple paternity would seem to be very high. Indeed, recent results with *L. forbesi* (Shaw and Boyle, 1997), *L. pealeii* (Hanlon et al., 1997; Buresch et al., 2001) and preliminary results with *L. vulgaris reynaudii* (Shaw and Sauer, unpubl., 2000) indicate a high level of multiple paternity in many egg capsules.

The nature of sperm competition between *L. vulgaris reynaudii* consorts and sneakers is unclear and will only be resolved when DNA fingerprinting techniques are applied to laboratory mating trials or possibly field-collected samples on the mating arena. Large consort males mated for 16 s compared to 6 s for sneakers; in a few cases the consorts passed two sets of spermatophores. It is unknown whether consorts get more fertilizations (or all) when they mate parallel, but they pass many large spermatophores whose sperm have the first opportunity to enter the egg capsule jelly matrix and swim towards an egg. Nor is it known what the mechanisms of sperm precedence might be. For example, is last male precedence common when different large males mate a female sequentially in the male-parallel position? The placement of spermatophores by sneakers appeared different, and we suggest that sneakers are mating females that already have an egg capsule amidst their arms. If this is verified to be the norm, then sneakers may gain some advantage by using the tactic of placing spermatophores directly onto the egg capsule. It is curious that consorts seldom chased sneakers away (Fig. 5B). Perhaps sneakers only get a small percentage of the 100–300 possible fertilizations per egg capsule, and that it is not worthwhile for consorts to expend energy to chase away such small and fast males.

Features of this mating system share commonalities with *L. plei*, *L. pealeii*, *L. opalescens* and *L. forbesi* as partially reviewed in Mangold (1989), Hanlon and Messenger (1996) and Hanlon (1998). The mating systems of *Loligo* show some striking differences with another loliginid, the Caribbean reef squid *S. sepioidea* (Moynihan, 1985; Hanlon and Messenger, 1996), thus care must be invoked before generalizations are made about loliginid squid mating systems.

FISHING ACTIVITY COULD AFFECT SEXUAL SELECTION.—Fishing on a spawning aggregation may alter either the operational sex ratio or the proportion of individuals within the population using any given reproductive tactic (e.g., small sneaker males vs large consort males). The impact of targeted fishing on spawning grounds is central to the management of commercially valuable loliginid squids for at least three reasons: (1) the very short life cycle of about 1 yr; (2) squids form dense spawning aggregations, which are easily targeted by fisheries; and (3) the fishing techniques could remove certain sexes or sizes of squids, thus leading to 'unnatural' sexual selection processes that affect recruitment (see brief review in Hanlon, 1998). Recent field and laboratory studies on *L. pealeii* in the NW Atlantic (e.g., Hanlon et al., 1997; Hanlon et al., 1999; Buresch et al., 2001), *L. forbesi* in the NE Atlantic (e.g., Boyle et al., 1995; Shaw and Boyle, 1997), *L. vulgaris reynaudii* and others indicate that *Loligo* mating systems are complex, that sperm competition is a major feature of the systems, and that alternative reproductive tactics may be sufficiently flexible to withstand targeted fishing pressure, provided that the fishing pressure is not so great that it removes all or most of the spawning squids, or that it suppresses reproductive behavior. For example, the two (sometimes three) mating positions, each with different spermatophore placement, are quite unusual in animal mating systems but they enable female squids to acquire and store sperm at different times. Recent evidence also shows

that some female loliginids oviposit over many weeks (e.g., Moltschaniwskyj, 1995; Maxwell and Hanlon, 2000), often with no males present, and such alternative tactics enable females to lay fertile eggs despite population fluctuations induced by fishing. Continued collaboration and cooperation between commercial fishing interests in South Africa and the government and private research enterprises will help ensure that this valuable marine resource is managed properly.

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