MATING GAMES SQUID PLAY

ALSO ON WEB

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In the summer of 1998 I began a long-term field research project in Bonaire to evaluate the skin colours and patterns of *Sepioteuthis sepiodea* and understand their communication. Evaluating this system is going to take a lot of time. Along the way, I and my many volunteer assistants were able to watch squid mating strategies. This is a first report of what we saw.

Like most Cephalopods, *Sepioteuthis* squid leave the best to the last. For most of their lifespan they are not interested in sex. They hunt by themselves at night and gather in schools or shoals in the daytime. They swim in a kind of lineout, keeping together, watching for predators and staying in the same bay or shore area. During the last weeks of their lifespan, however, that all changes. Sex (and status) becomes the center of their days.

As they have permanent separate sexes and male sperm is cheaper than female eggs to produce, mating theory predicts that males should be more competitive and more managing in the business of pairing and mating than females, who should be more choosey about who they accept. This aspect of courtship seems to be true for squid. Moynihan & Rodaniche (1982) and other researchers have pointed out the variety and importance of visual signals on the skin of *Sepioteuthis*, so they should use these in courtship. What else shapes the system? The third important influence is the social group. Squid court and mate in groups of from four to fifty, so during interaction with the other sex they are susceptible to a lot of influences from each other. It's quite an open system.

The first visible sign of interest in sex is a subtle division of the group into male-female pairs. Males and females seem to prefer larger partners, and eventually they sort into same-size pairs. This sign of interest is often accompanied by an exchange of skin signals. The male does Stripe, a pair of wide black longitudinal stripes on either side of the mantle, with paler areas in between. The female does what we called Saddle, which is probably the same as what Moynihan & Rodaniche (1982) called Pied. We used this name because it's such a good description of the pattern. All the female's mantle goes white, except for a thin line of dark brown on the very anterior like a saddle over her body. Often the dark line extends a bit mid-dorsally towards the anterior end of the mantle. When they did the nearly 300 Saddle-Stripes we recorded, the pair were nearly always positioned with the female directly over the male.

These displays seem to signal interest but not more than that (like the exchange of a long kiss in humans). We saw Saddle-Stripe in smaller squid who showed no other sexual behavior, and we saw it in a pair after they had mated or attempted mating. More interesting, we saw it in a newly formed pair after a take-over and in a longer-term pair after the male had challenged another male. Sometimes a pair would match up for a minute, exchange a Saddle-Stripe and then go away or back to others. Maybe it's a kind of testing, of level-setting.

The next signal we saw indicated much more than passing interest in partnering. When a male went pale and started Flickering the intensity on and off, a VERY visible signal in the shallow water, it showed a serious intent to mate. Males pass spermatophores to the female by sticking them onto her skin just below the eyes. A willing female often turns pale herself and the pair swim fairly quickly side-by-side back and forth in a Rocking motion with him still Flickering for a minute or so. Then he darts around in front of her and puts the spermatophores in place; the probability of this transition is 0.3. The female can then take them and puts them in her mantle cavity, where the sperm are stored for later fertilization of her eggs.

All this depends on the female being willing. If she isn't, she has a bag of tricks up her sleeve. First, she may just jet away, and if this jet isn't too fast the male may Chase her. Sometimes the chase urns into Rocking and then they mate; it could be that females are testing males for fitness by doing this. If she's only mildly resistant, she may put an agonistic pattern of rough vertical Zebra tripes on her skin. If she's really serious she can dodge when the male chases, go down to the ottom near the sand or coral, and do a linear arms-up posture with dark skin that seems to really ean business. If she does these things, the probability of a mating attempt drops to near zero.

lore than this refusal can go wrong when a male tries to mate. As they are all in the group gether, other males see the signal and challenge him over half the time. Challenges tend to be ccompanied by a very obvious Zebra striped signal on the skin. As one male starts to Flicker, nother will put rough vertical stripes on the skin over a white or yellow background and come at m. This challenge can result in a takeover and formation of a new pair or just disrupt the mating. watched once for forty minutes as a male started Flicker, a juvenile swam at him in Zebra, and the ale replied in Zebra and chased him away. This happened over and over, eventually the male ave up and the pair never did mate.

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metimes this challenge escalated into the Formal Zebra challenge (James Wood coined the rase Full Assed Zebra for it). A pair of males take over-under position, put a Zebra on the skin, d often push each other at the posterior end of the mantle. The Zebra looked different depending position; it was on white and the arms were widely spread if the squid was Under, on dark brown d arms less spread if he was Over. There was some jockeying for position, because when we alyzed 21 displays the Under squid not only had brighter Zebra, it won the contest. This change took a full minute on average and the two males were oblivious to anything else ppening at the time, which puts an open-ocean animal in danger. It was one activity that was sy to film, and we could even reach out to touch squid during a Formal Zebra, impossible herwise. Still, understanding what squid 'mean' by these signals will take a lot of time. See wings et al, 1997, for a good detailed discussion of animal communication.

urtship and mating went on mostly in the early morning and late afternoon. Consortship could reasonably long-term; we watched one pair form about 7:30 a.m. and they mated throughout e next few hours. They mated quickly twice within an hour, then the male had a prolonged period Flickering and eventual mating later in the morning. Near noon he Flickered and tried to pass ermatophores, but was rejected--he was more eager than her. We recognized a few individuals scars on the body, and larger pairs were stable over a few days. On the other hand, I saw a ale in a consort pair go off to do a Zebra challenge with others. A smaller male came in to the

temporarily abandoned female, they did a Saddle-Stripe and he Flickered and they mated, all in about one minute. Pair stability and thus male access to females probably varies with maturity.

If males are motivated to protect their reproductive investment, we would predict that they would try to isolate a female with whom they had mated, and guard her from other males. While males mate guarded, it seemed relatively ineffective in the group. There were a lot of Zebra exchanges, there was a lot of jockeying for position. In the line-out of the group there was frequent interposition and shifting, active attempts at guarding and takeover of females by males. There was also subtle position changes and repulsion by females, much harder to document. Eventually, pairs left the group, though slowly and drifting away and back. When they were more than 2 meters from the other squid, a male would often show a Lateral Silver keep-away signal on his mantle. On the side AWAY from her and TOWARD the other squid, he would turn a bright silver-white. We used to enjoy watching how he held this pattern as they moved. If he ended up on the other side of her, e switched sides immediately. Sometimes they got closer to the others and he put a bit of Zebra ver top of the white. (We could argue he was being two-faced, but could also point out the ccomplishment of sending three signals at once, on different areas of the skin!).

's intriguing to think about why they separated and why they didn't separate sooner. It's in the ıale's best interest to isolate a female if he has mated with her. Maybe the group offers the rotection of many eyes to spot fish predators, and there's a tradeoff in benefits. Maybe he alances the advantage of the opportunity to fertilize other females possible only when they are in ıe group. Alternately, perhaps it's in the female's best interest to stay with the group and mate with everal males. Maybe she only allows herself to be herded into isolation when she has done so, hen she has enough sperm or her eggs are mature enough to be ready to lay. Maybe she has ettled on her best choice. This is an intriguing question but one that will be difficult to answer.

fter they drift apart from the group, the female will begin to spend time investigating the coral on e sea bottom. She searches for a protected niche, a crevice out of the way of the scavenging rasse that eat anything out in the open. Finding one, she will squeeze down and under, move ggs out past the spermatophoric gland to fertilize them, give them a gel coat and attach them, a w at a time. We only saw this once, and the female turned a deep dark brown while she was ›ing it. She probably lays a few each time and the male may leave her to go back to the group. s reproductive investment is over when she stops mating and begins to lay--though of course it ıys to make sure she survives to lay the eggs. Once in a while we saw a big solitary male come ' the group, Zebra at all the males and then just leave. Maybe this was one of the 'leftover' males ›m a pair.

ter this devotion to the business of reproduction, both male and female squid die. They probably ‹ eaten by predatory fish as they lose strength and vigilance. We saw yellowtail snapper, a small ember of the tuna family, constantly patrolling the area. Squid inevitably paled and jetted away their approach, often before we even saw the fish, and we also saw a couple of capture attempts. ›nstant vigilance and sudden speed would fail at the end of their lifespan, so that's probably how uid die in the wild. (But on the way to their demise, they certainly had a heck of an orgy).

ese mating games are not out of the way for the average snorkeler to see--you don't even need scuba dive. We watched *Sepioteuthis* in Bonaire but they are found all over the Caribbean. ey are an inshore species, swimming in about 2-3 meters of water. A group seems to be place- ecific so when you find one you can go back to it for days or even weeks. There are only two es to keep in mind. First, they were most active in early morning and a little less in late afternoon.

Go at noon and it's all over (they will most likely be taking a siesta). Second, squid spook very easily. To watch them you must float (or hover, if you are using scuba) nearly motionless until they habituate to your presence and go back to what they were doing. Wear a wet suit, because even in 28 degree water you get pretty cold when not moving. In return, you can watch great colour changes, chart intricate status moves and get a good view of squid mating games.

To read:

Hanlon, R.T. & Messenger, J.B. (1996). *Cephalopod Behaviour*. Cambridge, Cambridge University Press – this is a good overview.

Moynihan, M. & Rodaniche, A.F. (1982). The behavior and natural history of the Caribbean reef squid *Sepioteuthis sepiodea*. With a consideration of social, signal and defensive patterns for difficult and dangerous environments. *Advances in Ethology 25, 1-151.* – this reference has more detail on *Sepioteuthis* and their skin patterns, posture and behaviour than you may need.

Owings, D.H., Beecher, M.D. & Thompson, N.S. (1997). Perspectives in Ethology 12: Communication. New York, Plenum. – a very thorough discussion of the subject, nothing on cephalopods.

Mating Strategies

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Methods:

A school of approximately 8 squid, named Oceanside for the waterfront restaurant in front of which it swam, was located for intense observation. The location was sheltered from trade winds and surf, but there was some surge. Water depth where the school moved ranged from 1.5 to 3 m. The bottom was a mixture of sand, coral and coral rubble. The school was normally 10-20 m offshore, although it came within a few metres at times and pairs occasionally moved out to the drop-off to deep water 100 m from shore. During the observation time this school apparently broke up at the end of the lifespan of the squid, and another, designated Oceanside II and with up to 14 squid, drifted into the area. The school dispersed at sunset and the individuals spent the night hunting. It reformed at dawn, and school membership thus varied somewhat, but members were apparently fairly school faithful (several individuals were identified by scars on the mantle and fins and their presence noted). A full-day observation on June 6, 1998, revealed that the animals were crepuscular in activity, so intensive observations were carried out between 0700 and 1230, and between 1630 and 1830.

A pair of snorkellers floated for a shift of 60-90 minutes' observation, each following a pair of squid. If a new pair was formed, the female was followed, except on June 18th, when males were followed to make sure no special behaviour was missed in this procedure). Notes were taken on underwater slates and transcribed the same day into computer. Special attention was paid to the colours and patterns, the body and arm postures and relative positions of squid, with Moynihan & Rodaniche's (1982) description as a guide. Details were compared and discussed in the evenings. Since animals swam in loose pairs, the relative position of pairs and any takeovers of consortships were identified, as well as reproductive and agonistic behaviours. At the end of each 'shift' the new observer was informed which animals were being followed and the focal animal sampling continued if possible.

From May 30 to June 3rd, a pair of observers filmed the Oceanside school and the Junk school (which may have become Oceanside II) to record visual skin patterns and reproductive and maintenance behaviours. This film was analyzed for details of patterns and posture.

Results:

Because most of the squid were reproductively active, these behaviours became the focus of description. Squid were followed for a total of 65.6 animal-hours. Observations were divided for assessment of frequency of activities into In (47.4 hours), when the pair was within 1 m or less of the group and Away (18.2 hours), when they were 2 m or more away from it. Instances and context were recorded for pair stability behaviours, reproductive signals and mating, and agonistic behaviours.

Reproductive Signals:

Saddle (by the female) and Stripe (by the male) were short (5 s or less) signals, apparently the first and moderate signs of sexual interest. In Saddle the female paled all the mantle but a small strip along the anterior margin, sometimes with a strip extending mid-dorsally less than halfway to the posterior; the arms and head were also pale. This pattern was called Pied by Moynihan and Rodaniche (1982) and was renamed to reflect its exact appearance. While full Saddle left only a small area of the mantle in dark brown, the pattern apparently could be partially expressed. It was seen in slow expression to 'peel forward' as an area of paling from the posterior mantle, and might only be a circular area of paling as Part Saddle on the lateral posterior mantle. Stripe consisted of two wide longitudinal dark stripes on each lateral mantle. One was just below the mid-dorsal though separated by a pale line, and the other was just above the fin line. Sometimes a thin fin line Stripe was seen which could have been a partial Stripe.

Saddle and Stripe were recorded 2.9 times per hour when a male-female pair was in the group and 1.7 times per hour when the pair were away from it. Nearly always the female was positioned above the male. Of the approximately 300 Saddle-Stripes observed, 197 were so close to simultaneous that an initiator could not be designated. 27 were initiated by the female and 35 by the male. Interestingly, 40 were produced by the female and unanswered, only four by the male. Of these, half were in response to a male Flicker. While the pattern only occurred once when a pair was not discernable, it did not occur equally frequently over the duration of pairings. A Saddle-Stripe was produced 50 times < 30 seconds after a new pair had been formed and 43 times < 30 seconds after a male had challenged another male and returned to consortship with the female, 175 times simply during the consortship. Only once was it the precursor to a mating attempt, but it was common before and after the more intense Flicker signal and the parallel swim that often preceded mating.

Females expressed a partial rather than a full Saddle more frequently when the pair was away from the group than in it, 1.6 times per hour versus 1.2, and part Saddle might be held longer than full. It was also preceded by and followed by other reproductive signals.

Lateral Silver was a relatively long-term signal (up to a minute) emitted by males in which one side of the squid was paled to a shiny white, with a dark band sometimes produced for contrast along the dorsal mantle. The other side was generally brown, often with a Green Eyebrow signal and paling of the dorsal arms. It was always produced when he and a consort female were in relatively long-term consortship and usually when they were separated by over 1 m from the rest of the group. the lateral signal was away from the female, switching sides if he moved over to her other side. Sometimes Zebra stripes were put on top of the Lateral Silver, generally if the group drifted to less than 1.5 m away from the pair. It occurred 1.8 times per hour in pairs designated Away and 0.2 times per hour in those designated as In a group. It appeared to function as a 'keep away' signal, and was not shown during close contact or challenges between males.

Flicker was a male signal apparently of strong sexual interest and intent to attempt mating, duration from under 10 seconds to 2 minutes. A squid would pale, then increase and decrease the luminance of the body surface at a very high frequency. It was fairly common, 0.84/hour, when pairs were In the group and 0.7 per hour when they were Away from it. Often, 43 times, it followed a Saddle and Stripe signal and 33 times it was followed by this pair of signals. It also often stimulated an antagonistic Zebra challenge by another male, 36 times, and this resulted in a return of the Zebra display 17 times and a chase of the challenger 15 times. Such challenges could cut off the sequence and prevent a mating attempt, and several instances of a juvenile male repeatedly provoking a Zebra challenge were observed.

Female response to a Flicker varied widely. She gave an aggressive Zebra display to a male Flickering 29 times, an unanswered Saddle 20 times, she escaped from him and a chase ensued 28 times, and the pair began a parallel swim of anywhere between ½ m and 2 m for up to a minute 44 times. Females could combine these responses, and sometimes a male attempted mating even after receiving one of the apparently negative signals. A few times a female was observed making serious evasive actions including dodging when chased, diving to the ocean bottom and assuming a linear arms-up posture. These were apparently serious and successful refusals. If a couple swam parallel (often the female also became pale, though not with the intensity variation) the male would swim very quicky around to the anterior of the female and attempt to place spermatophores on a patch anterior of her eyes. Completion of mating would ensue if she moved these from the exterior and placed them near her spermatophoric gland to store the enclosed sperm.

Probabilities can be assessed for these sequential steps to mating. If a couple did Saddle-Stripe, there was $p=0.17$ that the male would Flicker. If he did so, there was $p=0.33$ that the pair would Parallel Swim. Given this, a mating attempt ensued with a $p=0.30$. Much of the lack of success resulted from interference by other males in the group.

When a couple were moving close to one another within the group, interference in the consortship was common. During In observations, an exchange of Zebra agonistic signals took place 1.75 times per hour and a Formal Zebra challenge once per hour. These frequencies are likely

underestimates, as Formal Zebras tended to lead to several exchanges and a mixing-up of group membership that made it difficult to follow individuals. Zebra exchanges were given 1.39 times per hour in Away, and Formal Zebra challenges 0.58 per hour.

There was a noticeable difference in position maintenance if the pair were outside the group. Inside there were 0.82 instance per hour where males obviously interposed between the female of their consortship and another male (and many more subtle ones). they were Displace in the consortship 0.6 times per hour, and yet were able to Replace themselves 0.33 times, nearly half. Sometimes it appeared that a male would take over a consortship and Saddle-Stripe, then 'lose interest' and move away, particularly if the female was smaller and apparently not reproductively 'interesting'. Nevertheless, pairing within the group was relatively fluid. Away from the group Interpositions occurred 0.16 times per hour, Displacements were 0.05 per hour and there were no Replacements. Movement away from the group correlated with a large increase in pair stability.

Agonistic Signals:

The common agonistic Zebra body pattern is very modifiable in Sepioteuthis. Its hallmark is uneven and irregular dark stripes, and its common though not exclusive use is in male-male agonistic signals. Of 340 Zebra signals recorded, 79% were sent by males and 21% by females. Twelve percent were sent to fish, most to the large (up to 1.5 m) but unaggressive coral-eating parrotfish. Females sent Zebra displays to males, but most, were male-male signals, in three types of situation.

In addition to categorizing by area, the Zebra can be quantified by apparent signal strength, in a score from 0.25 to 10. The signal increases in salience as it is expressed over a larger area, so a Zebra over ½ the mantle on the normal pale brown background is a standard 1. As background pales the contrast increases, so a Zebra on yellow background is 1.5 and on white is 2. The arms are approximately half the area of the mantle, so half the arms on brown would be designated as ½, and so on for more area and contrast. Females sometimes put Zebra stripes on the fins, adding a possible score of 1 on brown. The special case in the formal Zebra where the arms are spread widely allows for an additional score of 1 to 4 depending on how far widely they are spread (up to 360 degrees if the lateral arms are pressed back along the mantle). This quantification allows assessment of matching of Zebra signal strength to situations.

1: Male-Male Zebras:

a) Basic: Males who were simply swimming in consortship with a female often emitted a Zebra display without any accompanying action. Of 98 instances, most were on part or all of the mantle with brown or white; the mean display score was 2. When no cause could be seen it was 1.57; when a consort pair was beside the score was 1.66 and a juvenile 2.10. If courtship was visible next to the squid, the mean score was 2.75.

b) Interactive: If the Zebra displays are catalogued when there was at least one movement of two males relative to each other, they are different, but need more division into different situations:

1) Juveniles: they often approached larger males (juveniles were defined as both visibly smaller than the adults and as not holding consortships). When they did so, there was a discrepancy in the amount of Zebra, 4.3 for the juvenile and 2.1 for the consort adult male. Yet the juveniles always withdrew from the challenge (note that this action often disrupted mating).

2) Side-by side challenges: these involved at least one Zebra and at least one approach. Fourteen involved a size discrepancy and twelve did not. The approaching squid averaged a higher Zebra display score than the consorting male, 2.8 versus 1.0. Yet this did not assure a win as the animal with more Zebra won in only eight instances. When there was a visible size discrepancy, the larger animal win in 10 of 12 instances and when there was none the consort win in 11 of 14.

3) Approach Zebras: these were produced as large males who had not previously been part of a group came into it with Zebra displays on their skin. Nine instances were recorded, and the Zebra scores from the approaching animals averaged 5.0. This was in strong contrast with the average of 0.7 for resident males, who often did not respond at all. Nevertheless, the outside challengers simply passed on and left the group with no other behaviour.

c) Formal Zebra Challenge: Sometimes two males would take a particular set of positions and patterns that differed from the normal Zebras to one another. They would go one over the other, spread arms, rise in the water column and push against one another. these challenges lasted commonly for one minute but could go to 2 minutes, and the challengers became oblivious to anything else going on. Rarely they would grapple with arms or jockey for position during this display. There was some variation. Of 21 Formal Zebras, the squid underneath scored 8.9 in Zebra intensity and the one above 5.6. the one displaying below won in the sense of regaining or taking over consortship in 15 of the 21 displays. Twice the display was equal and there was no clear winner. Once a larger male was over and had a lesser score, yet 'won' a new consort. Twice a small male consort displayed Over and less yet returned to the female, this may be related to the reluctance of large males to assume consortship with smaller females. In general the contest was a ritualized test of status.

2: Female Zebras

Females were observed to produce Zebras to males over somewhat different areas of the body surface than the males to each other. The used arms only or mantle and arms and fin surface for Zebra displays. Their mean Zebra score was 2 for 23 instances, but these also differed by situation. When females signalled males during a mating situation (n=11) the average score was 3.0 and when it was outside the possibility of mating their score was 1.1. Thus the female Zebra signals were also graded by situation.

What is noticeable here?

First, the exchange of visual signals is basic to courtship. And as the squid are colour blind, it is not surprising that their transmission is not colour-dependent. Saddle, Stripe, Flicker Zebra and Lateral Silver are all very visible in black and white. Nevertheless, the signals are all accompanied by position or motion components. Saddle and Stripe are in Over, Flicker leads to mating when the male and female rock back and forth in parallel. A female who flees, dodges or takes an arms-up posture discourages mating. Lateral Silver is a clearly lateralized signal--the male only displays it to the side away from his consort and towards rival males. And the Formal Zebra challenge by two males is again in over-under, accompanied by much fin beating, some posterior mantle contact and probably pushing. Position signals status and the lower male usually 'wins'.

Second, despite the large number of signals and the sometimes obsessive mate-guarding, this is a fairly open mating system. The group reassembles each morning and short consortships are opportunities for males who might not otherwise reproduce. Consortships within the group are vulnerable to formal Zebra challenges, takeovers and temporary lapses. Small males can forma a temporary consortship of even one minute and mate. thy can challenge a flickering male and prevent his mating. Thus although males hold consortships, there can be a reproductive cost to even lapsing for a minute. this is particularly true with for Formal Zebra challenges. A formal challenge an last two minutes and during this time males or oblivious, vulnerable not just to mate takeovers but to an array of predators.

Females use subtle actions to move away from non-preferred males and towards preferred larger ones. Males cannot mate with an unwilling female; the array of responses to Flicker ranges from compliance to testing to outright refusal. Females also have the choice of whether to accept and transfer spermatophore, although it is not known whether they make a choice here.

Given this, and given the lack of challenges and takeovers when a pair does leave the group, why do not males separate the females sooner? Juvenile squid are quite group-dependent. There may be a predator-avoidance cost to leaving, as many eyes watch for Jacks in particular. Alternately, females may resist leaving the group. It is the best interest of a male to make sure a chosen female is not inseminated by other males, but the female may gain by accepting sperm from

several potential fathers. As mating continued in both situations, they do not separate just when the female is ready to lay eggs and no longer sexually attractive.

Third, the Zebra is a complex graded visual signal. Despite the variety of situations is which it is found, it is apparently an agonistic signal. Obviously a squid signalling to a fish does not expect a response, this must be a signal of 'annoyance'. this seems similar to the Basic zebras given by males in consortship when no action of reply is seen. Still, it might prevent action. Both these signals score low quantitatively.

It is different when actions accompany Zebras. but then something becomes clear. Zebras may be a clear signal of underlying motivation, but the approaching animal gives more Zebra than the one in consort and thus in possession. And when winning is calculated, the high scorer in Zebra numbers doesn't win. When size differs the larger wins. When size is apparently equal (and often when it is not) the consort wins. Then there is the strange Zebra challenges by newcomers to an established group. It's almost as if they weren't 'in earnes', making Zebras without even pausing to back up their challenges.

The most intense Zebras result from Formal Zebra challenges, and these are serious ritualized contests. At first glance it looks as if the outcome is set before the challenge is made, but that's not true. Under displays more Zebra and wins, but there is sufficient jockeying for position that Under is actively established at times. The pushing must add to the challenge and may be part of the formal assessment (do they exchange positions if the Over male is stronger?). This formalized signal exchange seldom, though sometimes, leads to a grasp of arms in what might be viewed as actual fighting.

And what about female Zebras? It will take a lot of time to accumulate enough to see the gradations, yet they are there. Not only that, they involve the fins, as male Zebras never do. thus they are probably 'saying' something different yet related with this skin pattern.

SEPIOTEITHIS REPRODUCTIVE STRATEGIES

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Sepioteithis sepioidea squid bring five things to their reproductive strategies:

1) Life History: the individuals live about a year, and within this lifespan follow a semelparous reproductive pattern. Thus all individuals probably devote the last month of this lifespan predominantly to courtship, mating and female egg laying, after which they die.

2) Social Organization: squid gather in schools, ranging in size from five to fifty (although twelve may be an average). These schools likely coalesce as the individuals settle near shore out of the plankton and school members are probably not related. School loyalty is probably a general but not absolute rule; thus an individual squid coming to maturity is normally surrounded by individuals he or she has known for up to nine months of the lifespan.

3) Daily Rhythm: Each night the squid in a school disperse, possibly for safety from predatory fish and definitely during which time they do most of their foraging (which is never cooperative). Each morning the school re-forms gradually over the course of the first half hour to hour of daylight. This re-forming may produce structural flexibility and doubtless gives reproductive opportunities that would not be possible in a fixed organization of a group.

4) Neural Capacity: The Cephalopods are known as the most intelligent of the invertebrates, and their behaviour is marked by flexibility. As they have lived with potential mates and rivals much of their lifespan, we can expect that they will bring this capacity to reproduction. A special aspect of the neural capacity is the control of colour and pattern on the skin. Each yellow, red or brown chromatophore has a separate nervous supply, and the result is a visual pattern production and changeability that is unmatched. Note that nevertheless signals amongst individuals must be relatively stereotyped to be understood.

5) Physical Structure: Cephalopods have lifelong separate sexes. The sperm are contained in packets called spermatophores, which are produced and stored by males. These are taken by the males out of their mantle cavity, passed in the act of mating and adhere to a patch on the female just above the arm bases and below the eyes. From there she takes the spermatophores and places then near her oviducal gland in her mantle cavity. There they burst and release sperm into the oviducal gland and are stored inactive until she lays her eggs. By necessity this arrangement requires close contact, male initiation and close cooperation by the female.

Individuals in a given group are close but not identical in age and size (aging of Cephalopods has so far not been possible; size is the best indicator). Courtship begins among them and the presence of sexual behviour may stimulate its expression by others, as well as rivalry and takeover attempts by other males. As the animals come to full maturity, consortships develop between a particular male and female, although these are not the only opportunity for mating. Gradually the linear spatial arrangement and the group cohesion

break up as consort pairs replace them, although it appears that this re-forms each day until the animals split away and/or die. Females who have laid eggs are probably not attractive to males, and they may return to the group and produce a temporary skew in the sex ratio, with ensuing conflict.

Steps in the mating sequence are indicated by exchange of visual signals, generally described by Moynihan & Rodaniche (1982). However, each is accompanied by a specific spatial position or movement pattern which they did not necessarily link.

a) Saddle (by the female) and Stripe (by the male) are the signs of sexual interest. The Saddle is renamed from Moynihan's Pied as it is a better descriptor of the visual pattern. Nearly all the dorsal surface of the mantle is blanched by chromatophore contraction. All that is left brown is a strip at the very anterior of the mantle, extending all the way down the sides of the animal (and even onto the ventral surface, though this is difficult for a snorkeler to record). Often a brown line extends mid-dorsally halfway back along the mantle surface. The dorsal head region is brown but the arms are pale, though the arm tips may be pale brown. In full Saddle there may be yellow laterally along the fin bases and laterally on the head. Saddle may come on full or be expressed in part. It can be seen to 'peel forward' from the posterior end of the mantle, though in full intensity it comes on simultaneously. Part Saddle involves blanching of only some of the dorsal mantle surface, the posterior area. There is often a small blanched area in the posterior mantle, this may be a very partial Saddle. It is typically seen during maintenance of a consortship.

The Stripe was also named by Moynihan and is descriptive. The center dorsal mantle is a shining silver reflective surface, which stands between two wide longitudinal dark brown stripes. In addition, a paler area separates these from thinner brown stripes laid along the mantle surface just above the fin bases. Intensity of Stripe is not indicated by spatial area but by contrast intensity, as full intensity is maximal darkening and contrast. In addition, Stripe may involve only the two wide dorsal lines. The two lines at the fin bases may be put on separately as a male swims in consortship with a female, and these last not seconds but up to a couple of minutes.

Saddle and Stripe are the first visual signals of sexual interest in a group. In addition, they appear to be the first signals indicating an interest in a new pairing, and they may appear again after full courtship and mating, ending off the sequence. Squid give them when a new pairing is initiated, when another courting pair has stimulated sexual interest, even when they are simply swimming in consortship. They never lead directly to mating. They are generally but not constantly together. Either a female or a male may initiate the display and it remain unanswered.

Saddle and Stripe are produced in Over, with the female swimming above the male and less than a body length separating them. They do not have to be exactly above one another but they are close to that, possibly a little lateral separation. They may be swimming together or separate, the male may swing under the female or she may position herself over him.

b) Zebra is a signal of aggression, generally but not always expressed by a male. It can vary tremendously over area, background colour and amount that the arms are spread laterally. Within a sexual context it can be expressed by a male that is in consortship with a female, by a male approaching either a pair or another male or by a pair of males each maintaining a consortship side by side. A female expresses Zebra when she

is being approached for mating by a male she does not intend to mate with. This pattern is on all the dorsal surface with yellow-brown background, and the stripes are also expressed on the fins, unlike in males.

While all the gradations are doubtless important, only the Full Zebra shows signs of the ritualization that passes a clear signal. A pair of males in rivalry for a female, or a consort and intruder, or a male attempting to mate with a female and an intruder will express full Zebra pairing. This pattern is clearly shown in Moynihan and Rodaniche, and the Zebra is also present although much clearer in striping in Sepia and Loligo (see Messenger (19XX); Adamo & Hanlon (1996); Hanlon & Messenger(1996)). The essence of Zebra is dark irregular stripes extending downward along the dorsal and lateral mantle surfaces, dark elongate spots along the arms.

In Full Zebra a pair of males move together and upward in the water column for a period of a few seconds to nearly a minute. One takes position Under the other. Although there may be some jockeying for position and the relative position may switch, the Under male is the 'winner' in terms of maintaining or gaining access to the consort (see Hanlon & Messenger, note difference from Moyniham & Rodaniche). The two are less than a body length apart, and it may be common for the posterior mantle ends to touch. It is rare but can happen that they two males actually grapple with their arms, they are no doubt sending tactile signals to each other but actual contact is minimal.

The top male has less overt Zebra signals. He has a base colour of brown on the dorsal surface (although of course that is less visible to his rival). His ventral mantle surface is white and may have dark spots on it; this would be visible to his rival. There are probably a dark stripe at the edge of the fins, maybe accompanied by pale brown at the outside edge of the fins, a pale stripe thus between. The arms are minimally spread, less than 60 degrees from straight forward.

The lower male is very overt. All the dorsal body surface is white and the Zebra stripes and elongate dots stand out on the pale background. He also has a dark stripe at the fin bases but they are pale except for that. The arms and tentacles are conspicuously spread, all the way back so the tentacles may lie along the lateral mantle surface for a spread of up to 280 degrees.

c) Half and Half: this pattern is expressed by a male when he is swimming in consortship with a female, generally a little separated from the group (perhaps 2 meters or more). He is always beside her and less than a body length away, and he is always between her and the group. At maximum half the body and arms, the half away from the female he is with, is silvery white, hence Moynihan and Rodaniche have called it Lateral Silver. It has been named Half and Half to indicate the active division of colours that is also seen in the octopuses (see Packard & Sanders)--it is not just an expression on one side of the body. The other half of this pattern is pale to dark brown on the side of mantle and arms towards the female, accompanied by a wide shiny reflective green over the eyes called Green Eyebrows. If the male shifts to the other side of the female, he smoothly replaces the two halves of the pattern on the appropriate sides in milliseconds. It is apparently a 'keep away' signal, though it does not always prevent displacement.

The partial expression of this pattern seems to be a combination of Green Eyebrows with a pale spot on the posterior end of the mantle called Rear Light by Moynihan & Rodaniche. A consorting male may alternate periods of these with periods of Half and Half; these are maintained for up to minutes. In addition, when the

light level or perhaps the motivational level is low, the pale may be less apparent and the dark less extensive; the pattern may be paling of one side with shiny dorsal silver stripe and a brown line lateral to the female.

There appears to be no response to this by the female, and it is likely a male-male signal expressed when a consortship is established. A consortship can be maintained without it, including the spatial separation from the group and tight couple swimming. It is thus not clear exactly when it is used in this situation.

d) Flicker: This is an unmistakable sign of a male's intention to mate with a female. It will not happen at least until they have exchanged Saddle and Stripe and at the most they have been carrying on a consortship for hours. He is chalky white, not the shimmery white with reflective surfaces that other colours produce. The colouration flickers on and off--the pattern, time and extent of on-off have yet to be documented and he may do it differently in different situations (Moynihan & Rodaniche noted the paling but missed the flickering (Hanlon & Messenger note it as pulsing); as there are lots of other palings, this is an appropriate name). The on-off is clear to all around including the human observer.

The movement patterns accompanying Flicker vary with time and the receptivity of the female. The male in flicker will attempt to swim parallel with the female he will attempt mating with. If she presumably is receptive, thy will swim slowly and in parallel, if she is not there will be a Chase of up to tens of meters and at quite high speeds. A Chase may turn into a parallel swim or may be broken off by female avoidance strategies. If the female consents, the two will begin to do rocking, which Moynihan & Rodaniche described. And Hanlon & Messenger suggest initiates courtship It is a fairly fast back-and-forth parallel swim with a slight movement at the end of each 1-2 m arc. After a period in Rocking the male will dart around and deposit spermatophores on the female's skin surface; Hanlon & Messenger note this is not always successful. Following this he will continue Flicker and parallel swim. This may result in another mating but probably more normally subsides into parallel swim, a set of Saddle and Stripes and then consortship with Basic Brown.

Flicker is so unmistakable that it seems to come on suddenly, but there may be indications that a male is about to 'break out' in it. A pair may swim together, each doing colour changes in no obvious pattern. They may do Rear Light, he in particular may do Pale Arms, she may do Cheap Industrial Carpet. This last is a pebbling of dots of white (and quite silvery), green and blue on the mantle that gives a textured appearance to the mantle. It appears to be a sign of sexual interest. If a male is acceptable to a female when he gives Flicker, the female may go Pale, but there is no Flickering component.

Because of the underlying social situation, males and females express different reproductive strategies. There are many opportunities for mating and each must behave so as to continue their line. However, the male's actions to pass the spermatophore place his strategies in the Active category and the female's to maximize quality may put hers in the Controlling one. For both sexes the indicator of mate quality appears to be size, which would indicate more eggs in a female. Presumably it would demonstrate a better ability to feed and put on weight, as well as reproductive maturity, in both sexes. Size based dominance within an artificial group was also found for *Octopus joubini* by Mather.

a) Females: they must have a strategy to attract and accept the 'best quality' males, as indicated by size. This is probably indicated first by who the female does Saddle to and whom she replies to when he does

Stripe, but these may also be limited by the opportunities presented by different males and by the likelihood that she will want to accept sperm from not one but several individuals. In additions, she may try to avoid or break consortship, to reject a mating attempt and not to take sperm into her oviducal gland is she chooses not to (this last step is difficult for the observer to follow).

Females do not control the consortship but they may manipulate it to some extent. A female in consortship with a male may drift over close to another male, and he may replace the consortship. She may drift close to another pair and induce a Zebra conflict and possible takeover. She may be 'taken over' by a male but move closer to the original and cause a return to the first paring. Females seem more willing to maintain consortship with bigger males.

Within the consortship, females have a very large role in acceptance of mating attempts. When a male does Flicker and attempts a parallel swim, the female can attempt to assure it doesn't lead to mating. If she simply flees, he will Chase, for several tens of meters, and a Chase can break off and terminate mating opportunity. If she is unreceptive she will do Zebra displays at him, in part or all through his approach with Flicker. She can also avoid in several ways. One is to go down towards the bottom, as the Chase usually results in rising in the water column. Another is to assume a linear arms-up posture with upward tilt of 60 degrees, and this may be accompanied by a Basic Brown resting colour. This is perhaps particularly effective because the female will encourage a courting male by putting on Pale. A most serious avoidance strategy is to dodge, as he begins the chase she abruptly changes direction and may do it again and again. All of these avoidance strategies may also serve to test for the male's motivational strength and 'quality', as the effort of extended fast swimming involves much energy expenditure in squid (see O'Dor).

Of course the female can simply choose not to store a male's sperm in her oviducal gland and all the male's efforts will have been for nothing. It is not clear what controls this last step.

b) Males: the males have a much more active part to play in the mating strategies. Presumably they will approach, court and try to mate with the best quality females and then to keep others from access to them. Males will approach and initiate Stripe with females, presumably seeing the answered Saddle as a sign of 'interest'. In the morning a small male may be able to initiate a pairing and mating with a female who will later be unavailable. The Saddle-Stripe combination can but usually does not lead to a Flicker and mating (I once saw the whole sequence in less than a minute). The male will be more 'eager' for mating than the female. We saw a paired male and female over a morning. They mated twice early, once a bit later consensually. Then they mated after a chase in mid-morning and she refused a mating by late morning. This could be either exhaustion by the female or the decline in activity with daytime that we see; they mate in late afternoon also. Males continue Flicker and Chase after a mating but seldom if ever manage to mate soon after.

Access to females may be by the 'luck' of gathering with her in the early morning and courting and mating before other larger individuals come by. This may be the only sure access strategy for small males. The second and much more common access strategy is displacement of other males from a consortship. An extremely common procedure is for one male to approach a pair, usually at early courtship, and Zebra. With great size asymmetry, the larger male may simply move in next to the female, in extreme cases not even doing a Zebra of any extent. A big male may Zebra, take over and then move on, as if assessing the female and finding her 'not worthwhile'. Or he may be in a line of four, win a Zebra and go over to the other female

do a Saddle-Stripe and then go back to his own. Once a small male went through a quick Saddle-Stripe, Flicker and mating with a female. He tried twice more and was stopped by a Zebra from a larger male. There is a sense in all this of proving dominance and not just doing displacement, also a sense in which Zebra usually signals aggression but the males 'know their place'.

An answering Zebra depends on the situation and the particular males, on their relative size, stability of pairing and sexual motivation. A challenge may be low-level and the consort win, pairing continue. It may be low-level and the new male take over. It may be answered by a 'lesser' Zebra by a larger male, or even no Zebra at all, and the situation remain stable. A male who is doing Flicker will be particularly likely to respond at a high level. Males in longer consortships may not even receive Zebras, having possibly been big enough and had the pairing stable enough that they only make Half & Half, which repels even Zebra attempts. This was violated by one male, who did a piece of lateral Zebra right over the white part of Half & Half at an approaching male. He can be argued t have sent three signals at once.

A small male who may not otherwise be able to pair with a female may use a Zebra as a challenge and test of other males, who are in consortships. He may approach, Zebra and get a Zebra response, back off a bit and soon try again. One male I watched did this again and again and again to a Flickering male, who finally turned and Chased him arms-first. Or a male may intrude with Zebra, be Zebraed in return and the consort chase him mantle-first for meters distance. This is a risky strategy as other males may 'move in' on the female if he's gone for long, or there are lots around; he may just move back in and displace them, however.

While males and females are usually members of a stable group, there are relatively often 'intruder' males who have not been with them, at least that day and perhaps longer. Stability is disrupted by an intruder; he may test the largest male in his consortship, or he may displace him and the displacement extend, or he may lose challenges but stimulate several Zebras and some Saddle-Stripes. Once a big male came in, displaced the male from the largest female (but she eluded him and returned to the male she had been with). He then swam with low speed down the line of late juveniles, low Zebra on, and left the group swimming with high velocity towards the Junk group.

Low intensity Zebra can escalate to a high intensity one, producing a really spectacular, long and highly distracting display. High intensity Zebras come when a pair of males are in consortship or when one is in Flicker, possibly also with an intruder. They are highly ritualized; the displays differ by position and the lower male is more intense and 'wins'. They may be entered into by males who are physically relatively 'equal' though high sexual motivation may influence this too. The lower animal wins (see Hanlon & Messenger also). There may be some jockeying for the lower position and squid may switch positions, though in general the positions are maintained. Does that mean that this is just a 'formality'? Probably this is often true.

Males try to set up a consortship with a large, desirable female. This is clearly not a matter of minutes, as within the group there's a lot of switching and displaying and testing. As the consortship is set up, the pair will be on the edge of the group--this can be after mating, but mating can occur after this partnership is spatially obvious and mate guarding has set in. Males will put on fin spots, insert themselves between the female and the rest of the group and do Zebras at other males. This continues long term. As consortship contiues (and as maturity gets nearer and the pairing more serious) they drift from the group. What was a line-out now seems to be sets of pairs, less than a body length apart with a few meters between them.

Within this kind of grouping is probably a couple of smaller, less mature, 'leftovers'. If a female has laid eggs and there are more males than females, there may be a skewed male/female sex ratio leading to Moyniham & Rodaniche's and Hanlon & Messenger's comments on 'courting parties'. As the consortship continues in displacement from the group, males use Half and Half to serve as 'keep-away' signals. Eventually the female lays eggs, possibly with a male still in consortship. The pairing may be disrupted by dark and dispersion of the group, it is not known if the pair resumes in the morning.

In Phase I of the study, a squid school that could be easily watched was located near the Oceanside restaurant which was part of the scuba diving resort complex on Bonaire. Squid were observed by snorkelers, concentrating on the early morning and late afternoon times that a whole-day observation found was their peak times of activity (see the enclosed Self-Funded Research Grant Report: 1998). Since the squid were reproductively active, much attention was focused on their agonistic and reproductive skin displays as well as mating behaviour. General information about other displays allowed us to begin to construct a repertoire of these patterns from video analysis carried out in the early part of 1999.

Research in this phase of the study is being reported in several ways. Invited talks have been given at the Biology Department of Dalhousie University and the Psychology Department of Memorial University, entitled "Mating Games Squid Play"; a similar talk will be given at Humbolt State University at the end of March. An informal description of the work has been placed on the Cephalopod Page at http://is.dal.ca/~ceph/TCP/Mather.html to give general information to the public. An oral presentation entitled Mating Games Squid Play is scheduled for the Animal Behaviour Society annual meting in June and another on The Sepioteuthis Formal Zebra for the American Malacological Socity in July.

Phase II of the study will be 6 weeks long, from May 1st to June 12th, and is part of my 6-month Study Leave in Spring of 1999 (as reported in the Study Leave Proposal). Volunteers will be assisting me again for two-week periods. So far there are four (the maximum possible for the same rented house) for the first two weeks, three for the second and four for the third. They come from Seattle, Portland, Vienna, Southampton, Bellingham, Baltimore, Kearney, NJ, Vancouver and Lethbridge. Five are graduate students.

Phase II of the study will concentrate on gaining more depth and specificity on the reproductive and agonistic displays (see Appendix I for the detailed instructions for prospective volunteers). Provided the squid are mature, we hope to follow individuals longer than in Phase I. I plan to document the steps in the critical mating sequence, from the male Flicker display to the passage and storage of spermatophores, more thoroughly. The Zebra display appears to have a great potential for the complexity of display ncessary to describe it as a language or a pre-linguisitic communication, and we will chart its many quantitative manifestations. In addition, and depending on time available, we hope to expand our understanding of the repertoire, chart the spatial relations of the squid schools and find out how squid give

different displays to different fish species. If the squid are not reproductively active we will be able to fill in our understanding of their repertoire with details on the wide range of camouflage patterns (see Moynihan, 1985) and parallel Hanlon et al's (1999) study on camouflage by foraging Octopus cyanea.