RESEARCH REPORTS: 1998, 1999, 2000

DOES SEPIOTEUTHIS MAKE A VISUAL LANGUAGE ON ITS SKIN?

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The topic of this study is a large one, and the answer will take years to construct. However, four weeks of research in Bonaire, Netherlands Antilles, from May 25, 1998 to June 21, 1998 began to find pieces of the puzzle.

Research consisted of both ethological observation and still and video filming of the squid in the shallow waters (2-3 m) off the lee side of this small island. My husband Lynn Mather acted as base manger, organizing the volunteer team and the rented house and truck. Volunteers each assisted for approximately two weeks. They were Roland Anderson of the Seattle Aquarium, Jason Chinn, a student in the Biology Department of the University of Lethbridge taking an Applied Studies 2000 course on the basis of the experience, Alison King of Calgary, a beginning graduate student at Dalhousie University, Ulrike Greibel, a post-doctoral researcher at the Konrad Lorenz Institute of Ethology in Vienna, Domenica Smid-Provost, an undergraduate student in the Department of Psychology and Neuroscience at the University of Lethbridge and James Wood, a graduate student at Dalhousie University.

The first part of the research consisted of finding a good location at which to study the squid in their schools; they are found all across the Caribbean in shallow reef and eel grass areas. All near-shore areas around the island of Bonaire are marine park and snorkeling and dive sites abound. We searched the No Name Beach area near the airport, the Big Blue dive site at the north of the island, the Salt Loading Dock piers at the south end of the island and the Kralendijk city waterfront. We settled on an area in front of one of several dive resorts, following one school and then another which we designated Oceanfront 1 and 2 for the restaurant in front of which we first found them. Habitat dive resort kindly offered us access and minimal use of their facilities so that we could enter the water and rest near the squid.

During the city waterfront search, James Wood called our attention to the many shrimp species sheltering in the sea anemones which were common in the 1-2 m deep rocky zone. We took a day to conduct a survey of the commensal occupants of the anemones found along a 700-m stretch of the seafront. James is preparing a note for publication on the results.

Our initial approach to assessing the visual signals on the squid skin was to take still and video footage of the squid for later analysis of the patterns and construction of a repertoire. These patterns have been very generally described by Moynihan & Rodaniche (1982) but their appearance is not documented, and subsequent assessments by Forsythe & Hanlon (in Hanlon & Messenger, 1987) have also been piecemeal. Since Moynihan suggests that the components of skin displays might constitute a visual language, such documentation is a necessary first step. The videotapes are being analyzed in Lethbridge by Jason Chinn as part of his Applied Studies course.

It quickly became apparent that the skin colours and patterns were variable across contexts and also were imbedded in situation and actions. As this also needed documentation, the second half of the study was devoted to ethological observation of the signals, actions and situations in which the squid found themselves, by snorkelers. During the one day when both teams of volunteers overlapped, we conducted an all-day (0700-1900) survey of one school to catalogue activity. Although *Sepioteuthis* is reported to form schools in the day and swim singly at night, we found that the peak of interactive activity was crepuscular (early morning and late afternoon) and confined later observation to those times.

Both Oceafront 1 and Oceanfront 2 schools consisted of 10-12 sexually mature squid, who were courting and mating and exchanging visual signals in the process. This allowed us to observe many instances of skin patterns exchanged between conspecifics and concentrate on this aspect of their communication; signals to potential predators and prey will be observed in greater detail in the subsequent years to complete the repertoire. This focus also allowed me to evaluate the mating system and male and female mating strategies of this species. This is significant because essentially no work has been done on the mating strategies of any of the Cephalopods; octopuses tend to be solitary and their strategies simple and yet hard to read, squid live in open ocean locations where they are observed with difficulty, yet laboratory observations are artificial.

Sepioteuthis squid live about one year, growing up in groups of 5 to 40, likely mostly the same individuals and in the loosely organized social grouping of schools. As they mature, males and females exchange visual signals indicating sexual interest and begin to form temporary pairs. Both males and females select partners that are large (aging squid is a difficult task; large squid would nvertheless be older or better 'quality'). Males attempt to maintain pairing with a female and during this time to deliver a spermatophore sperm packet to a sticky patch on the front of her head. Gradually pairing becomes more stable and the pair drift away from the group, leading to the eventual dissolution of the school. Females lay eggs under coral heads or bottom trash (we saw one egg-laying); they may be attended by a male or not. As they become less attractive to him, the male may move near other pairs (hence Moynihan & Rodaniche (1982) described 'courting parties' of several males and one female, which we seldom saw). Both sexes die after reproduction.

The first visual signal of sexual readiness/interest is the female Saddle and the male longditudinal Stripe. Each may initiate the signal and it may or may not be answered by the other. (Note: Moynihan called what we identify as Saddle by the name Pied; this is confusing to its appearance so it has been renamed. He also saw it as a repellent signal, which was not confirmed in our studies). This pair of signals can be produced by squid in the late juvenile stage who do not appear to continue with other activity, by a pair as the initiating signals for potential mating and as the final signals after they have mated and are returning to lesser activity and pair maintenance. Full Saddle and Stripe are performed with the female over the male and the pair 1/4 m or less apart. Full Saddle is paling of all the mantle surface to white, with the exception of a strip anteriorly which is left brown, giving the impression of a saddle over the body; there may also be some brown extending posteriorly mid-dorsally and brown dorsally on the head, as well as yellow on the fins and the sides of the head. Partial Saddle is spatial, as the whitening 'peels forward' from the posterior mantle, and it may be emitted as just a small pale patch during consortship. Full Stripe consists of shining silver reflectiveness extending longditudinally mid-dorsal along the mantle, dividing wide chocolate-brown longditudinal stripes; these are echoed by smaller parallel brown stripes along the bases of the fins. It may be expressed partially as the two wide stripes of lesser contrast, but also the fin stripes by themselves are seen during consortship. These variations do not appear language in the sense of Moynihan's components, rather indications of intensity, but this needs further investigation.

When a pair is in consortship, the male may emit Half and Half. This was called Lateral Silver by Moynihan, and again the name is an inadequate descriptor. As well, the expression of colour or patterns that differ laterally is common in Cephalopods and described as Half and Half in octopuses (Packard & Sanders, 1971). The side of the mantle towards the consorted female is brown, as is the side of head and arms (possible only arm tips). The side away from her is shiny silver white, and on this side only the area above the eyes is bright green (hence Green Eyebrows). If a male shifts to the other side of a female during this display, the appearance of his two sides is quickly reversed. Males apparently emit this when their consortship is more stable and has caused a displacement from the group of approximately 2 meters, thus it is late in pairing. If other members of the group drift closer, near 1 m, the male may put some Zebra stripes over the white half (thus effectively 'saying' three things at once). The signal may change into partial, giving one Green Eyebrow and pale at the posterior mantle called Rear Light--again the partial is spatial.

When a male is about to attempt spermatophore transfer to a female with whom he is consorting, he turns pale (though not the silvery pale of Half and Half) and increases and decreases the intensity of this signal rapidly; we have designated this Flicker and hope to establish the phase change timing by video analysis. It is an honest signal of mating intent, but the action can be interrupted by several actions. After mating a male will likely continue Flicker and attempt mating again, usually not successfully.

Another male (possibly a larger one, not necessarily) can emit an aggressive Zebra signal and approach; this is usually then matched by the Flickering consort male. The female can remain close and become Pale herself, if so they may do a back-and-forth swim of about 2 meters that has been called Rocking, and mating ensues. She may swim away and they Chase, she may emit an aggressive Zebra signal, she may Dodge, swim to the ocean bottom or assume a linear 60 degrees-up posture. Some of these may be testing for male 'quality', others appear genuinely repulsion. While the Flicker is unmistakeable, there are other visual signals during this process that need more details and video analysis for evaluation. A bright pebbled mantle in blue, green and silver that we designated Cheap Industrial Carpet may be a positive signal of mating readiness by females. But a larger and less distinct pebbling is seen during hunting, and the lack of brown countershading at dawn and dusk produces a blue-green pattern which is still less pebbled.

The signal designated Zebra is the most complex and linguistically the most interesting; it is also similar to an aggressive signal of *Sepia* (Hanlon & Messenger, 1988; Adamo & Hanlon, 1996) and *Loligo* (Hanlon & Messenger, 1987). A Full Zebra is a ritualized exchange of visual signals between two males. The 'winner' swims below, puts black Zebra stripes on white over all the dorsal surface of mantle, head and arms, as well as a black line along the base of the fins. His arms are spread laterally over 260 degrees, with the tentacles folded back along the body. The 'loser' is above, with Zebra stripes on brown body, arms spread 60 degrees at maximum, fin base stripe and possibly Zebra striping on white mantle ventral surface. The two animals are very close and contact of the posterior mantle is common, pushing is probably a component of the interaction. An extreme, seen once, is for the two squid to grapple with the arms. Such a display can last up to a couple of minutes and the squid rise in the water almost to the surface and are oblivious to other stimuli. The 'winning' and 'losing' display suggests that the outcome is obvious before they start the visual display, but while this is usually true it is not always so. Instances are being collected (and Hanlon, in Hanlon & Messenger, 1987, has videotaped sequences) to evaluate the meaning of signal and behaviour.

Even more interesting is that the Zebra is variable both in extent and situation. It can be demonstrated on brown, yellow-brown or white background and on part of the mantle, all of it, head and part or all of the arms (some of this is spatial, directional broadcasting, some appears to be signal strength). This Low Zebra manifestation seems to be a signal of 'annoyance' aimed at fish as well as conspecifics, and emitted at times by females though commonly by males to other males. The Zebra with paler background or over larger area does not always 'win', as the size and consortship arrangement in progress modulate its result. Between the signal of 'annoyance' and the ritualized Full Zebra, there may be a Challenge Zebra on yellow-white, all body and arms but arms fanned out yet compressed at the tip, which indicates aggression and a willingness to escalate to Full Zebra. Of all the visual signals given to conspecifics, this one comes closest to a 'language', and is particularly interesting in its progression from what appears to be an emotional expression to a ritualized male-male exchange. Further study of the exact context, extent and outcome of Zebra exchanges will be necessary to put forward a case for a language-type communication.

During 1998, the videotapes will be analyzed to begin the spatial mapping of signals that is a first step in their description. Information about mating strategies will be assessed in preparation for a conference presentation at the annual meeting of the Animal Behaviour Society in 1999. Data on the Zebra display will be collated, but another year of observation will be needed for a complete contextual description. This will be carried out during spring of 1999 as part of my six-month Study Leave (approved in 1997). James Wood will prepare the manuscript on the shrimp and anemone commensalism for presentation and publication.

RESEARCH REPORT: 1999.

DO SQUID MAKE A VISUAL LANGUAGE ON THEIR SKIN?

PHASE II: DETAILED ASSESSMENT.

The topics of research in this second year of study of the *Sepioteuthis* squid skin communication system (Moynihan & Rodaniche, 1982) were both more specialized and more diverse. The basic observation in 1998 had pointed out feasible observation and interesting types of skin displays. In addition, the award of Study Leave for Spring of 1999 allowed me to increase the study duration from four to six weeks, from May 1st to June 15th, 1999.

Exploration in 1998 had revealed that the area in front of the dive resorts of Bonaire was home to several schools of squid and easy of access and for observation. Thus we concentrated on this area, again in front of the Oceanside Restaurant (Captain Don's Habitat Resort) but also near the Sand Dollar Dive Resort. Volunteers again came for two-week periods. The first team consisted of Roland Anderson, Seattle Aquarium, David Sinn, a graduate student at Portland State University and Ulrike Greibel, a postdoctoral researcher in Cephalopod behaviour at Konrad Lorenz Institute of Ethology in Vienna. The second team consisted of Jack de Metro of Kearney, New Jersey, a long-time volunteer assistant to us, and three graduate students. They were Theia De Long of Mississippi State University, Gabrielle Mowlds of Western Washington State University and Fiona Tibbitt of University of Southampton. The third team consisted of two University of Lethbridge students, Jason Chinn and Domenica Smid-Provost, and our son and daughter-in-law, David and Ariane Mather, all of whom had participated in previous field research..

Phase II of the study planned to gather observation about two specific skin patterns. The first was the agonistic Zebra display, which has been simplistically described by Adamo and Hanlon (1996) as a male-male contest in *Sepia* but was seen in a wide variety of circumstances for *Sepioteuthis* in Phase I. The second was the responses by squid to a variety of fish predators; nearly 200 observations were gathered in 1998 but the range of fish predators and the skin colours, avoidance and escape behaviours was only partially documented. For each of these situations, the ten volunteers and I were able to collect several hundred instances in Phase II. Analysis of the data by Factor Analysis of the fish responses and an Assessment/Management approach of the Zebra exchanges (see Owings & Morton, 1998) will begin in Fall of 1999. Presentations are planned at the Conference on Comparative Cognition and the Animal Behaviour Society meetings in 2000.

Because of the increased opportunities with more time and volunteers, other data have been gathered. There were several schools of *Sepioteuthis* in the area with squid at different sizes and thus different ages of the 18-month lifespan. Observations from a developmental view on reaction to fishes, school cohesion, actions and postures and reactions to conspecifics have thus begun, especially with Ulrike Greibel. She and I plan eventually to develop an ethogram of the species *Sepioteuthis sepioidea*. We were also able to concentrate on the Flicker pre-mating display of adult male squid. We plan to establish its communicative value by assessing the reactions of conspecifics, as the 'goal' of communication must be to change behaviour of receivers (Guilford & Dawkins, 1991). I suggested to the graduate students that they might single out an area of behaviour on which to concentrate. Theia De Long has taken up the challenge and we found another display on which to focus, the Dymantic startle pattern. As a result we have collected several hundred instances of this pattern, which consists of dark dots on the lateral posterior mantle, similar to that of other Cephalopods (Hanlon &

Messenger, 1997). This data will be analyzed in Winter of 1999-2000. David Sinn is interested in spatial organization of squid schools and we have also collected some data on spacing; this will be augmented in the future. In addition, David was able to produce some videotape of squid displays which will also be evaluated in Winter of 1999-2000.

One important advance was made in this period of observation. We were able to identify individual squid without any invasive marking techniques. Adult male squid have a relatively permanent pattern of dots along their fins, and these patterns are individually recognizable. Along with our observations of fin and mantle damage from earlier encounters with potential predators, this allowed us to follow individuals for weeks. For instance, the adult female Wavy and male Bald were identified in the first few days of the study and were still followed in their post-reproductive period six weeks later. Such tracking of individuals will allow me to describe both the social organization of the schools and the mating strategies carried out by males and females. We were also able to witness the final aspect of reproduction, egg-laying by female squid, in several instances. I expect to present these data as an outline of Squid Reproductive Strategies at the Cephalopod International conference in Aberdeen, Scotland in summer of 2000.

The project is expected to continue, with one month's observation study in May-June 2000. One goal is to further develop the outline of mating strategies, including the transition of schools into reproductive maturity and the egg-laying phase of female squid. Another is to return to analysis of the skin signals that males and females emit during courtship. While we have a fairly complete assessment of the male Stripe and female Saddle, both these displays are variable in extent and we need to delineate the 'meaning' of partial as opposed to full-body signals. We expect to continue the developmental approach. Some signals, such as the Dymantic change over the lifespan while others such as the Zebra appear only with maturity (see Hanlon & Messenger, 1988, for similar observations in *Sepia*). This will be combined with more data in the ethogram of *Sepioteuthis*.

RESEARCH REPORT: 2000

DO SQUID MAKE A VISUAL LANGUAGE ON THEIR SKIN?

Moynihan & Rodaniche (1985) proposed that squid could make a visual language on their skin. They summarized some observational data on the ability of *Sepioteuthis sepioidea* to produce different spatial pattern components at the same time, which could be the equivalent of words in human language. Unfortunately they did not follow up on these preliminary observations, leaving the important idea hanging. With Moynihan's death in 1996, it looked as if this exciting idea would remain unproven, and we would not know whether this could add a third example to those of to human language (see Sebeok, 1990) and bee dances (von Frisch, 1967). This research has been taken up with the idea of proving or disproving that squid make a visual skin language. Understanding the pattern production asks for observation in the natural environment (see Lehner, 1996 for methodology), it also requires a substantial period of time to unravel the components.

As the animal itself was poorly understood, much basic work had to be done to set the foundation for unraveling the meaning of skin patterns. *Sepioteuthis sepioidea* is a common species near shore in the Caribbean (Roper, Sweeney & Naun, 1984), so the choice of study site was based on ease and convenience. Bonaire, Netherlands Antilles, was chosen for three aspects of what might be describes as security. The island is part of the Netherlands and Dutch efficiency assures adequate transportation, policing and health procedures. Its nearshore has been National Park for 25 years (it is a notable dive location) so that the marine animals are protected. And the crescent shape of the island enclosed a lee side away from prevailing winds that is fairly calm, a good environment for snorkelers. In fact, cooperation from dive resort owners and workers has meant that we have worked in comfort off the resorts for the three summers of observation, and they have also contributed hints about animals and watched out for our safety.

Again in 2000, the main focus of research has been observation of squid in the shallow (up to 5 m) narrow (40 m) nearshore strip. While the 1998 observations allowed us to obtain a baseline description of where the squid were and what they were doing, further work has extended past this. In 1999 we discovered how to identify individual animals, and focused observation on one skin signal, the dark lateral slashes called the Zebra. Over 1200 observations were accumulated and two reports, to the American Malacological Society at Pittsburgh in 1999 and to the joint meeting of CSBBCS and the British Psychological Society in Cambridge, England in 2000, have reported different aspects of the squid Zebra. More data on this signal remain to be analyzed. In addition, the interspecific signals are mostly in the context of reproduction, so it was necessary to piece together the mating strategies of this species to form a backdrop for the signals. This topic has been reported in many different locations, including to the Animal Behaviour Society in Lewisburg, PA, in 1999 and the Cephalopod International Conference in Aberdeen, Scotland in 2000. A paper with this title has been submitted for publication in a conference volume of Bulletin of Marine Science and is under review.

Each year of the study provides an opportunity to focus observation on a single skin display, and in 2000 it was the female sexual signal called Saddle. Over 600 observations of this signal have been collected and will be submitted to analysis in the Fall of 2000. Saddle varies in terms of area of the mantle, and appears to be a signal of a particular level of sexual interest, attraction, damping down or maintaining male interest. In addition we collected more data on the sequence of communication following the male Flicker display, which indicates readiness to pass spermatophores to a chosen female and is the context for male-male aggression, as well as female choice. We also collected more data on the startle Dymantic display, which will add to and be assessed by a 1999 team member, graduate student Theia deLong.

Again in 2000 we rented a three-bedroom house above the main town of Kralendijk, and my husband acted as base manager. We studied the squid for a month and were accompanied by assistants from many areas for two-week periods. For the first two weeks Dr. Uli Griebel returned from her postdoctoral studies in Vienna, and was accompanied by her student Ruth Byrne. In addition Suzanne Boom, a graduate student from the Netherlands currently working at Oban, Scotland, and Miranda Lubbers, an ex-student of mine presently residing in Calgary, assisted us. For the second two weeks we had Beth Zimmer, a recent graduate in Marine Biology from Miami and Bryan Bugler, similarly just finished undergraduate work in Massachusetts. One of our current students in Psychology, Terra Taylor, was also part of this team and plans to assist me with data analysis in Fall 2000 while taking an Applied Study course. The second team was rounded out by Jack Demetro, our long-time volunteer from Kearney, New Jersey.

As the first team of graduate student was ambitious and idea-focussed, we had many discussions about possible foundations of squid behaviour. This led to a side topic of research, that of group formation (see Ritz, 1994). Squid appear to be obligate members of groups but proving that assumption has seldom been tackled quantitatively. As a result, we designed a reporting format and collected information on the distribution of all squid, whatever their ages, within a 400-m stretch of the waterfront out to the drop-off. This was carried on by a daily survey for four weeks, and by a single-day 11-hour focussed observation on one group, as well as construction of a detailed map of the area. The graduate students will assist in data analysis through Fall of 2000 and spring of 2001, and expect to present results at a conference in Summer of 2001, probably the International Ethologic Congress in Germany in August.

During November, 1999, a hurricane took an unusually southern route in the Caribbean. While it did not hit Bonaire the storm waves generated a twelve-hour impact on the normally lee side, destroying much of the shallow coral reef system and also several dive resort docks. The impact of this storm on the squid appeared to be a population reduction. Adult groups were more sparsely distributed along the shore, and there were particularly fewer adult males. The result of this was our ability to isolate and follow one group, which stayed in front of the Harbour Village dive resort. *Sepioteuthis* squid live 12-16 months (LaRoe, 1971), and their semelparous reproductive strategy means that their reproductive period is less that a month at the end of this time. We were able to follow the adult females of the group as they passed through this period and trace female reproductive strategies for the Mating Strategies focus, adding it to previous information for the report and paper in 2000. This confirmed in a different phylum Trivers' (1972) prediction that small-gamete producing males would generate Competition and large-gamete producing female would emphasize Choice.

Such relatively low population density meant that there was little new to report about the Zebra display. It is apparent that this signal, designated more for its general resemblance to that of the cuttlefish *Sepia* Zebra (Hanlon & Messenger, 1988; Adamo & Hanlon, 1996), is a complex one. At maximum the Zebra becomes a formal ritualized contest between adult males. Far more often, it is apparently a quantitative signal of aggression or mood, generated by males as well as females. In 2000 I took the approach of forming a quantitative scale of area and contrast to come up with an Intensity score, regardless of location of display, and this appears to account for some of the cross-situation differences in the Zebra display. The data about the area on which the signal is produced are in the computer and need to be analyzed by this approach; to see if, for instance, a Mantle Zebra means something distinct from a Fin Zebra. In addition, further evidence must be collected to see whether the signal is always an honest indication of mood or dominance. Can a squid 'lie with a Zebra display'? They may indeed do so, indicating that while it is not a language, it is a complex and abstract signalling system (see Owings and Morton, 1998).

For 2001 the specific signal on which I hope to focus observation is the male sexual signal called Stripe2. Like all squid signals, this varies quantitatively, but in a different way than Zebra and Saddle. There are two pairs of longitudinal dark stripes, a wide one mid-dorsally and a narrow one just above the median fins. Only a large number of observations accompanied by video analysis will allow us to find out how these are combined or displayed separately, and in what circumstances. Since Stripe2 is generally combined with female Saddle, these observations will complement those of 2000.

Information is being gathered slowly in several different areas. We have centered our investigation of complex information transmission in a spatial signal array approach. Dr Griebel has noted that squid can 'double signal', producing two messages at once for two different receivers. We have noted, and Ms deLong will assess, that the Dymantic dot pattern of startle seems to stem from the juvenile display called Plaid, that there are potentially four dots and different ones are shown in different situations, as well as being recruited for camouflage in foraging situations. Owings and Morton (1998) remind us that information transfer is not frozen in time but is part of an interactive flow of communication between sender and receiver, who must be kept in mind (see Guilford & Dawkins, 1991). We hope to assess the sequence of information passage across time in two situation, after a male Flicker and during a dual-Zebra interaction of two males. As well, Dr Griebel and I are working on an ethogram of the species, and the availability of animals of different ages in the same area mean we will be able to evaluate behaviour from a developmental viewpoint. This is particularly important because Coleoid Cephalopod skin signalling capacity likely evolved for camouflage from fish (Packard, 1988) and was secondarily recruited for intraspecies communication. In *Sepioteuthis*, skin patterns appear to function for camouflage in the juvenile period and only act as signals to conspecifics in the short adulthood.

Research conducted during this time will be reported in several different venues. In August 2000 I will report to the Animal Behaviour Society meting in Atlanta about a spin-off of the 1999 data, squid responses to threatening fish. In the summer of 2001, the American Malacological Society and the World Malacological Congress meet in Vienna; Dr Griebel and I may led a Workshop on Cephalopods in their World, focussing on behaviour and ecology. The International Ethological Congress overlaps by two days and is near, in Germany, I will probably present some more of the Zebra analyses there. Since the Animal Behaviour Society meeting is conveniently near in Corvallis, Oregon, in June, I tentatively plan to present some of this work there as well. There is much to report, as well as much that investigation will continue to uncover.

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