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Behaviour Development: A Cephalopod Perspective

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This paper evaluates the development of behaviour from the viewpoint of the intelligent and learning-dependent cephalopod mollusks as a contrast to that of mammals. They have a short lifespan, commonly one to two years, and most are semelparous, reproducing only near the end of their lifespan. In the first two months of life, *Sepia officinalis* cuttlefish show drastic limitation on learning of prey choice and capture, gradually acquiring first short-term and then long-term learning over 60 days. This is paralleled by development of the vertical lobe of the brain which processes visually learned information. In the long nonreproductive adulthood, *Octopus* species show major flexibility in prey choice and continued mobility across the sea bottom. This results in large behaviour variability within and between individuals and both exploration and simple play-type behaviour. During the short reproductive period, *Sepioteuthis sepioidea* squid gather for choice and competition, including flexible strategies in use of their skin display system. At the end of the life cycle, *Sepia officinalis* cuttlefish have a swift decline in memory capacity and also brain degeneration during their short period of senescence. The emphasis on different behaviour capacities during these four stages is contrasted with those of the mammalian model of behaviour development.

Because we have a normal model of mammals, we assume that learning-dependent animals have a long life, parental care, and strong social organization (Humphrey, 1976). Yet the cephalopod mollusks are heavily dependent on learning (Mather, 1995; Wells, 1978) and have none of these. How is their learning and behaviour affected across the lifespan? Behaviour and learning capacity are not the same over any animal's life, as a view of any lifespan development text (e.g., Santrock et al., 2003) will reassure the reader. Thus we can read in humans about sensitive periods in childhood, brain-behaviour development linkages, the transition of adolescents from parental care to adulthood, the rise and recession of gender differences, and the acquisition of wisdom in old age. All these aspects of lifespan development of behaviour take the mammalian model for granted (see Gandelman, 1992). It is assumed that these lifespan differences are the normal ones for any animal that relies heavily on learning, yet this need not be the case. Cephalopod molluscs such as octopuses and squid (Hanlon & Messenger, 1996) change throughout their lifespan, not necessarily in the same pattern as the social mammals. This paper attempts to look at behavioural development from the perspective of these cephalopods and see what lessons can be learned from this different model.

The cephalopod lifespan and natural history are not the same as the mammalian one (see Figure 1). First, octopuses and squid have short lives, somewhere between three months and two years. It is logical to ask why animals with such a short life should rely heavily on learning and to what extent their learning is shaped by this short duration. Second, they have little to no parental care (in con-

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trast see Fleming & Blass, 1994). Female octopuses care for their eggs but die shortly after they hatch and most squid die shortly after egg laying (Boyle, 1987). This means no parental care, no imprinting (Bischof, 1994), little buffering of young from the harsh environment and no transitions of weaning and adolescence (Gandelman, 1992, Chapter 9). This difference is made even larger as the cephalopods are generally solitary. Some squid swim in schools, by Ritz's (1994) definition, but their social interaction appears limited and most have little or no social contact for much of their lives (Hanlon & Messenger, 1996). Thus they have environment-dependent rather than social-dependent learning (Humphrey, 1976, but see Milton, 1988). This means no social pressure, no status interactions, no imitation and little need to learn parental behaviour (e.g., Hauser, 1988, for alarm calls). All this is imposed on a different reproductive strategy as cephalopods are semelparous and thus reproduce only once, at the end of their lives. They usually produce many small offspring and the young octopuses or squid are at high risk of mortality, a risk that extends for much of their lifespan.

Mammalian Model



Cephalopod Model



Figure 1. A comparison of the division of the lifespan of a representative mammalian and coleoid cephalopod species into 'childhood', early and reproductive adulthood and senescence.

Figure 1 demonstrates that the lifespan of any animal can be divided into four sections, childhood, nonreproductive adulthood, reproductive adulthood and senescence. The proportion of the lifespan that is allocated to the different stages is quite different between the mammalian and cephalopod models, with the majority of time of the cephalopods spent in prereproductive adulthood and the mammals in the reproductive part. This paper will focus on each of the four life stages in turn and evaluate where possible what pressures and capacities might be emphasized for cephalopods in each stage.

Childhood

Eggs of many cephalopods species are tiny, a couple of millimeters long (Boletzky, 1998), and the newly-hatched paralarvae drift off in the plankton where many live for several months until they settle out near the shore. While the demand of this part of the life history must be interesting and the transition offers specific challenges (Boletzky, 1987), this makes them very hard to study.

Such a transition may resemble the sensitive period of young mammals after birth, as social and olfactory cues determine mammals' later dietary and sexual preferences (Gandelman, 1992, Chapter 4). One possibility to trace change through this transition is the relatively large egged *Octopus joubini (mercatorius)*. They are initially pelagic but settle to the bottom and assume the adult nocturnal activity pattern and den occupancy within a couple of weeks (Mather, 1984). Presentation of different settlement substrates and available prey at this time would offer them an opportunity to learn responses that might guide their future choices across the 6-month lifespan.

In contrast the young of the cuttlefish *Sepia officinalis* are relatively large at 1-2 cm length and occupy the same near-shore sandy bottom habitat as adults. The cuttlefish has been a good species in which to study learning because it has a relatively simple visual attack on shrimp or prawn prey (Messenger, 1968). Two elastic extensible tentacles are shot out to grasp the prey, and the third of three attack phases (attention, positioning, and tentacle ejection) is open-loop. Adult cuttlefish can learn fairly quickly to cease attacking a prawn that has been placed in a glass test tube (Messenger, 1977), as attacks in this situation result in (possibly painful) strikes on the glass and no prey capture.

When the visual attack was evaluated in newly-hatched cuttlefish, Wells (1962) found that they were somewhat different from adults. Young cuttlefish readily attacked their common prey, *Mysis* crustaceans, yet the visual search image was quite narrow and they would fail to attack a visual image that was unlike that of mysids. The first capture attempts shortly after hatching were accurate and effective, so release of the behaviour did not depend on learning. However, when a mysid was placed in an appropriate-sized test tube the little cuttlefish continued striking at the prey—they could not learn to modify their attack behaviour. Wells (1962) found that by the age of one month cuttlefish could learn to stop this behaviour and begin to take prey other than mysids. Thus the restricted preprogrammed and automatic behaviour found at birth was modifiable by one month of age.

Messenger (1973b) was able to add anatomical evidence to this story. A series of studies of learning in octopuses (Wells, 1978) had established their extensive learning capacity (though see Boal, 1996, for a critique of these studies), and that the neural basis for visual learning was established in a special area of the brain, the vertical lobe. Cuttlefish with the vertical lobe removed could not hunt visually for prey (Sanders & Young, 1940). When Messenger (1973b) evaluated the amount of development of the vertical lobe in newly-hatched cuttlefish, he found that there was very little. They could not learn to stop futile attempts at prey capture because they did not have the area of the brain by which to learn it.

Dickel has recently taken up a more detailed study of the behaviour development. He found that predatory behaviour did not develop for the first three days of life, during which cuttlefish were nourished by the inner yolk sac (Dickel, Chichery, & Chichery, 1998). Pursuit behaviour, which might need short-term memory, took several days to develop. He charted the gradual increase in the volume of the vertical lobe during this time, and found that the maturation of the vertical-subvertical lobe tracts appeared to be correlated particularly well with the appearance of pursuit of prey and thus short-term memory.

Messenger (1973a) had earlier studied the long-term retention of information in memory by adult cuttlefish and he found a biphasic response function that suggested both short-term and long-term memory. Dickel, Chichery, and Chichery (1998) refined this approach with young cuttlefish to look at the two memory systems. After training to withhold tentacle strikes, cuttlefish from 8 days onward were significantly less likely to strike 5 min after training and this difference was not affected by age up to 90 days (of a 22-month lifespan). In contrast, retention at 60 min delay was not significant until 30 days, and it was significantly better than that at 60 days. In other words, short-term memory was present a week after birth but long-term memory took weeks more to develop. Looking in detail at brain anatomy, Dickel, Chichery, and Chichery (2001) found that relative growth of the vertical and superior frontal lobes of the brain was strongly correlated ($r > 0.8$) with this improvement in long-term memory.

While this suggests a major role of preprogrammed development in the maturation of memory, further research (Dickel, Boal, & Budelmann, 2000) has suggested that the environment does have an effect. Cuttlefish were reared in an impoverished environment (singly in bare, opaque tanks) or an enriched one (grouped and with sand, rocks, shells, and plastic seaweed). Those reared in the enriched condition grew significantly more in the first month than those reared in the impoverished one, a parallel to findings with rats (Gandelman, 1992, Chapter 6). At one month the cuttlefish reared in enriched conditions showed signs of long term memory and their performance was better than that of the impoverished group even at 3 months. This strongly suggests an effect of environment on plasticity and also sends a message long known for those studying vertebrates (Würbel, 2001), that lab animals may be significantly impeded by the impoverishment of their standard environment. This plasticity can be a specific rather than a general effect. Poirier, Chichery, and Dickel (2005) found that cuttlefish raised in the laboratory in tanks that provided a sandy bottom were both more likely to dig into the sand in a novel tank and more effectively covered themselves when doing so. Similarly, although diversity in prey choice switched in for cuttlefish after one month, exposure to alternate prey, such as crabs, could rapidly modify this preference (Darmaillacq, Chichery, Poirier, & Dickel, 2004).

The conclusions drawn from the information in this section will be of no surprise to researchers studying behaviour development in mammals (see Renner & Rosenzweig, 1987). What is surprising is the clear parallel between cephalopods and mammals. Both groups show the presence of preprogrammed behaviour near birth, then the advent of learning and the loosening of such programming. This parallel in unrelated groups suggests that it is the single best way to produce a learning-dependent animal who has to survive infancy first. Such preprogramming of early behaviour seems necessary even despite mammalian parental care.

Nonreproductive Adulthood

Much of the lifespan of cephalopods is spent in this stage (Boyle, 1987). Before the relatively short period of reproduction, they use their excellent conversion efficiency of food of 50%, compared to the mammalian 10%, to gain weight and grow body tissue. During this time they are relatively uninterested in members

of the other sex and most species are solitary and asocial (Hanlon & Messenger, 1996). In this period, development and use of their intelligence is not concerned with conspecifics but with coping with predator pressures and finding and consuming prey. This section will evaluate some of the ecological pressure and responses that octopuses make during the long nonreproductive period of their lives.

The near-shore ocean environment, particularly that of the tropical coral reefs, is one of the most complex on the planet and thus contains a large array of potential predators for a vulnerable octopus. Randall (1967) examined the stomach contents of fishes in the Caribbean and found that 29 species had remains of octopuses or squid. Most did not have a large percentage of them in their diet, which means that they were opportunistically preying on the cephalopods. The predatory behaviour of each may be different. Thus barracuda stay motionless in the water until potential prey cease to notice them, groupers dart out from hiding under a rock, peacock flounders emerge from hiding in the sand and moray eels snake through rock crevices. Marine mammals also prey on octopuses, and Scheel (2002) found that octopuses were absent in the subtidal region of the coast of Prince William Sound in Alaska, likely removed by the pressure of sea otter foraging. This implies that octopuses are always in danger and must avoid predation all the time and by a wide range of species and techniques.

Predator pressure by fish in particular has shaped the excellent camouflage of the chromatophore based skin display system in octopuses; Packard (1972) suggested that fish were the designers of cephalopod skin. Direct neural control means that chromatophores can contract and skin appearance change in 30 ms and over an area as small as one square millimeter (Messenger, 2001). But many animals, such as stonefish and flounder in the ocean and moth and sloth in the forest, have the ability to blend into the background. Octopuses can not only blend but also change their appearances quickly over time (see Figures 2a and 2b), they can eject ink as a screen or pseudomorph and disappear into cracks and holes in the background. Hanlon, Forsythe, and Joneschild (1999) followed escaping *Octopus cyanea* and showed that their kaleidoscope of display changes in appearance were both many (3 times per minute) and unpredictable. Such a sequence can effectively break a predator's search image (Curio, 1976); what was striped is now mottled, and through the ink screen what used to be a dark shape is now a quite different pale one. The authors point out that such sequencing of appearances must involve choice of behaviour, assessment of results and repeated choice until the octopus is caught or escapes, quite a different matter from simply appearing like the background. Such evaluation and choice of programs must use learning to assist them.

An equally demanding situation for octopuses is the choice and consumption of prey. Octopuses are generalist foragers; Ambrose (1984) found that *O. bimaculoides* took 55 species on Bird Rock in California, Mather (1991a) that *O. vulgaris* selected 28 in one small bay in Bermuda over a few weeks. Such selection also varies from region to region in *Enteroctopus dofleini*, the giant Pacific octopus, across the west coast of North America (Hartwick, Thorarinsson, & Tulloch, 1978; Vincent, Scheel, & Hough, 1997). Nevertheless, the prey remains discarded by specific individuals are often of one or a few species, suggesting they might be learning specific prey availability and becoming specializing generalists. In order to find the snails, clams, and crabs that comprise their diet, octopuses become cen-

tral place foragers. An octopus hides in a central den, moves out to find prey and returns several times per day (Mather, 1991a). The lack of simple following along the outbound path indicates that octopuses may be using spatial memory (see Boal et al., 2000) to make these return trips (Mather, 1991b). When an octopus goes out for another foraging trip it does not return to an area it has already covered, indicating it may have some form of working memory of where it already hunted. In addition this suggests a win-shift foraging strategy, a reasonable one since having found prey hiding in crevices, algae or sand, octopuses cannot expect an immediate replacement. This ability suggests octopuses could be tested for spatial memory similar to that found by Roberts (1991) for rats on radial mazes (see Dyer, 1998; Sherry, 1998). Mather (unpublished results) tested *O. rubescens* on an aquatic analogue of a radial maze and was unable to find such ability. However, this species apparently does not return to specific den sites; *O. vulgaris* and *O. cyanea*, which do, would be better subjects.

Such pressure on a memory system (Laughlin & Mendl, 2004) may account for why octopuses have developed both a visually-based and a tactile-based memory system (see Mather, 1995), each in a separate area of the brain (Wells, 1978). But the pressure is even greater, as octopuses in this stage of the lifespan occupy small home ranges without any territorial defence and switch home ranges after an average of ten days' occupancy (Mather & O'Dor, 1991). Unlike territorial vertebrates who can learn paths and subareas of a larger area, octopuses must learn new locations, prey, and predators over and over again in this lifespan stage. Perhaps this is also a necessity in this variable environment (Wingfield, 2003). The ten days occupancy of a home range suggests that octopuses' spatial memory should not be long-term memory. West-Eberhard (2003) pointed out the importance not only of learning but also of forgetting, and it is possible that the duration of spatial memory in the octopus is restricted (as, for instance, bees' learning of flowers is much better with particular colours; Menzel, 1985).

Catching a prey animal does not assure easy consumption and once again adult octopuses have flexibility. To penetrate into a snail or clam shell, they have several options. *E. dofleini* can pull out the snail, pull apart the clam valves or break the shell with the pull of their strong arms, chip off the edge of a clam valve with their beak to open a hole for venom penetration or drill a hole in the shell with the salivary papilla to allow access for their paralytic toxin. *O. vulgaris* try the quick but energy-expensive technique of pulling first (Fiorito & Gherardi, 1999; McQuaid, 1994) by trial and error, only going to the time-consuming drilling if pulling fails. If the *Venerupis* clams which are normally pulled apart are kept closed with a twist of wire, the octopus switches its technique to drilling (Anderson & Mather, 2005).

Drilling is also not random in position, rather over the retractor muscle attachment of the snail and the body or the adductor muscles of the clam (Ambrose & Nelson, 1983; Cortez, Castro, & Guerra, 1998; Hartwick, Thorarinsson, & Tulloch, 1978; Wodinsky, 1969), depending on the octopus species. The accurate position is learned by small octopuses within a few trials (Anderson, personal communication) and can be relearned. Wodinsky (1973) blocked the spire of conch snails so holes could not be drilled. *O. vulgaris* drilled right through dental cement, pulled off a rubber coating and, when foiled by a metal coating on the spire, drilled

as close to the edge of the metal as they could. There appears to be some monitoring of the condition of one's own body in this choice of technique as well. Wodinsky (1973) found that female octopuses who were brooding eggs, and thus had lost the function of the posterior salivary gland that supplied the venom, simply pulled snails out of their shell without attempting to drill.

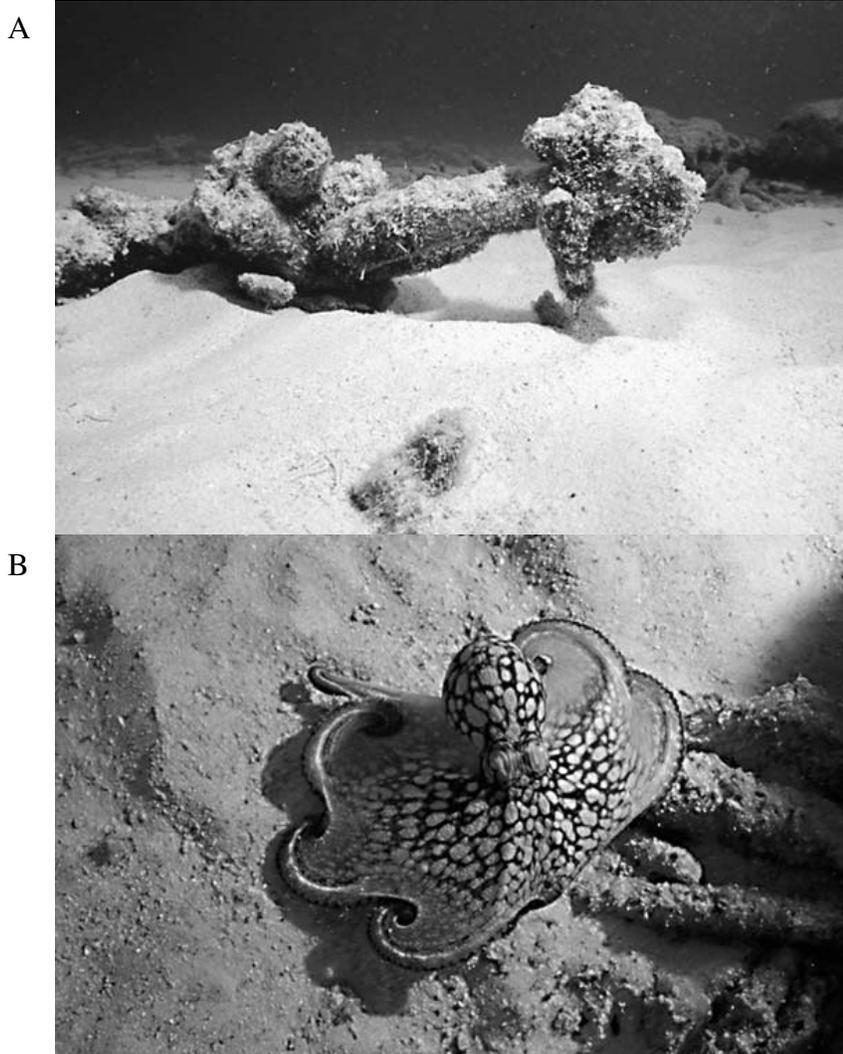


Figure 2. (A) Picture of a common octopus, *O. vulgaris* in camouflage on the end of the rusty beam. (B) Picture of a common octopus, *O. vulgaris*, in Bonaire taken 60 seconds after the picture in Figure 2 and taken from above shows the startle deimatic display. (Reproduced with permission from James B. Wood.)

What does this ecological pressure mean for behaviour in the laboratory? First, it means that octopus are highly exploratory. Octopuses are notorious for taking apart things in their tank, and Wells (1978) mentioned that the average life-span of a floating thermometer in a tank containing an *O. vulgaris* was 10 min. Anderson (personal communication) commented about an *E. dofleini* (named, per-

haps appropriately, Lucretia McEvil) that destroyed her support system overnight. She dug through a layer of sand several centimetres thick, bit through wires holding the undergravel filter plate to the corner of the tank, pulled the platform out of the sand, tore it into pieces and left the pieces floating in the aquarium tank. An octopus will approach any novel item that is dropped into its tank, grasp it with all arms, and explore with the suckers on the ventral surface of the arms. Such exploration is one of the critical components of learning (West-Eberhard, 2003).

When given such an article repeatedly, octopuses perform different behaviours over the period of eight days. As one might expect, they rapidly habituate to a “toy” (Kuba, 2004; Mather & Anderson, 1999). Yet after a period of several days the octopus returns to interaction with the object and sometimes shows activity that fits in the category of object play (see Burghardt, 2001, on criteria for play). Mather and Anderson (1999) watched two of their eight subjects send a floating pill bottle to the opposite end of their aquarium tank where it was picked up by the inflow siphon and returned, only to be blown away again—in one case, 20 times over. Kuba's (2004) in-depth analysis of such play-like behaviour showed that the only significant influence on its development was days of study, with a peak at days 3 and 4 of 8. Kuba (2004) had seven quite small (mantle length 3-4 cm) and seven nearly adult (mantle length 11-17 cm) subjects, and there was no difference in play-like behaviour between the two groups. This is very different from the situation in mammals, where play is generally a feature of juveniles although it can be seen in adults at a much lower level (Pellis & Iwaniuk, 1999).

Perhaps stimulated by the tendency to move into a new home range after a period of days, octopuses in the laboratory are also known for their escape behaviour. Their considerable arm strength (Trueman & Packard, 1968) can be utilized to push up an aquarium cover and their compressible soft body can be squeezed through a very small opening. The result is a notorious ability to escape from tanks (Wood & Anderson, 2004), sometimes to their death on the floor below. Following the win-shift foraging strategy demonstrated in the field (Mather, 1991a), an octopus in the Brighton Aquarium became well-known when it several times climbed out of its tank, slipped into the tank next door to it and returned after the capture and consumption of a lumpfish. Note that these were all very well-fed octopuses that had no “need” to go foraging for food but did so anyway.

The combination of exploratory behaviour, win-shift foraging, and individual differences is so strong that they can be called personalities (Mather & Anderson, 1993; Sinn, Perrin, Mather, & Anderson, 2001). This may lead researchers to have difficulty training octopuses in traditional tasks. Studies of octopus learning, ranging from Wells' (1978) with *O. vulgaris*, Boal's (1991) with *O. bimaculoides*, to Papini and Bitterman's (1991) with *O. cyanea* have all had difficulty getting the animals to reach a normal criterion of correct choices. Papini and Bitterman (1991) commented that octopuses could easily reach a criterion of 7/10 correct choices and yet did not go further, preferring to sample the previously unrewarded stimulus. Variability in choices is probably well fitted for an animal in a variable environment. The necessity to move to and explore a new area and the sampling of unrewarded choices in the laboratory makes sense when one realizes that win-stay strategies would not be appropriate for the natural history of the octopus in its normal environment. Darmaillacq, Dickel, Chichery, Agin, and Chich-

ery (2004) have demonstrated taste aversion learning in cuttlefish; it would be interesting to see if such aversion is long lasting.

What does this show in a comparison with adult learning in mammals? First, it reminds us that natural strategies, such as the emphasis on exploration and win-shift foraging of the octopus, will shape the learning of each animal and may be quite different from that of a mammal with a fixed territory and parental care duties as an adult—and note that parrots appear to learn some tasks well in a social context (Pepperberg, 2004). The difficulty of surviving in this complex environment with many different predators and prey and different challenges for capture and preparation are clearly a sufficient background for an environmental rather than a social basis for learning, which also controls some primate learning capacity (Milton, 1988). And the presence of simple play that is not different from early to late in the lifespan suggests that the blossoming of play in juvenile mammals is indeed made possible by the parental protection and care that allows the young time to play, possibly also necessary to help the young animal fit into its social context.

A less visible piece of information from this phase of the octopuses' lifespan is that, in contrast to mammals (Galea et al., 1994), no consistent differences in behaviour have been reported between the two sexes. This information is tentative both because negative results are not generally published and because animals may not have been identified to sex internally when they were used, as it would require the death of the animal. Nevertheless there are no sex differences reported for the long series of learning studies by Wells (1978), and for the personality research of Mather and Anderson (1999). It is logical that this should be the case as sex simply is not manifested at this time, but is a distinct difference from mammals, where sex differences in behaviour show themselves during the juvenile period and are enlarged thereafter (Field & Pellis, 1998).

Reproductive Adulthood

The switch from somatic to reproductive growth in semelparous animals like the cephalopods is a major transition. Cephalopods are permanently male or female although their sex does not manifest itself until maturity. The maturation is triggered by development of the optic gland (Wells, 1978), a hormonal gland which is under control of the pedunculate lobe of the brain. Light appears to activate its suppression, although many cephalopods are not strictly seasonal in reproduction and so it is not just day length that triggers change but also temperature and lifespan (Calow, 1987; van Heukelem, 1979). Somatic growth is constant and longer growth at the same general rate allows some cephalopods to live longer (Wood & O'Dor, 2000). When suppression is removed and the optic gland matures, protein synthesis in the muscles is much reduced, resulting in free amino acids that are taken up in the reproductive organs and ducts. Such a process results in gradual wearing away of the octopus' body and death, although Wodinsky (1977) was able to reverse this in brooding female *O. hummelincki (filosus)* by removal of the optic gland. Hormonal control is not so clear in males, as Wells and Wells (1972) were able to remove the gonads and even the ducts of males, and they still attempted to mate with females (as do male mammals, see Gandelman,

1992, Chapter 3). Nevertheless, reproduction generally shortly precedes death in cephalopods. A more detailed investigation of the hormonal control of behaviour in these animals is overdue. How do hormones mediate the appearance of squid sexual displays, octopus migrations, and male-male competition in cuttlefish? Could optic gland extract trigger the changes, and what brain areas would show growth or decline, in cell density or connections?

There has been surprisingly little investigation of the development of the switch in behaviour from growth-related to reproductive in cephalopods, although casual observation has reported that at maturity males octopuses become more active and females less so. Is there a two-stage tuning for and appearance of sexual behaviour as in mammals (Gandelman, 1992)? Some cephalopods, including octopuses and cuttlefish, migrate to a specific area for mating and egg-laying (Corner & Moore, 1980; Hall & Hanlon, 2002). Squid and cuttlefish form short-term consortships; males compete for access to females with tactics including female mimicry (Norman, Finn, & Tregenza, 1999) and are especially likely to show agonistic behaviour near egg masses (King, Adamo, & Hanlon, 2003). Female choice of which males to accept is important in some species, especially the cuttlefish (Naud et al., 2004).

The author's long-term observational field study of the display system of the Caribbean reef squid, *Sepioteuthis sepioidea*, in Bonaire has begun to give some answers about reproductive strategies (Mather, 2004). This is a particularly good species in which to study behaviour in the reproductive phase of life (Mather, 2004; Moynihan & Rodaniche, 1982) because these squid are found permanently in groups of up to 50 or so, normally approximately 20, and individuals can be identified. Young squid are attracted to and swim parallel with others but appear not to interact otherwise. The first indications of sexual behaviour are displays which seem critical in the information exchange before sperm transfer. The agonistic Zebra with irregular dark stripes is exchanged between males and the sexual Saddle (pale-mantle with brown ring) is produced, often without male response, by newly-mature females (Mather, unpublished results). Short-term consortships of up to several days (the group separates at night to feed) are maintained during the few weeks of sexual maturity. Sexual displays, including the male Stripe of longitudinal dark mantle stripes exchanged with the female Saddle and the male pre-mating on-off Flicker (see Figure 3) as well as the agonistic Zebra, appear to be very variable (Mather, 2004; Mather, Greibel & Byrne, in sub; Moynihan & Rodaniche, 1982), but there is little indication that their form is any different in subadults than in adults. However, subadults may produce displays out of the normal sequence (for instance, a Flicker without Saddle-Stripe first) or may produce them to an individual of the wrong sex (a Flicker to another male, resulting in a Zebra response). Females produce their agonistic Zebra quite late in their lifespan to repel males, after they presumably have mated a sufficient number of times that they have stored a good supply of sperm in their spermatophoric gland for fertilization of the eggs when they lay them.

Variability in the male Zebra display on mantle and arms comes from three sources: area on which it is produced, contrast between the dark stripes and the background (which can be varied in this sophisticated display system by darkening of stripes or paling of background), and increase of the apparent area by spread of

the arms (Mather, 2004). If this variation of display intensity (see Messenger, 2001, for a discussion of the chromatophore system's variability) is catalogued on a scale from 0.5 (half the arms on a pale brown background) to 10 (all arms and mantle on a white background, arms spread 280 degrees to alongside the mantle), the intensity can be related to which of a pair of males is the winner or loser. Is the display an honest one or is it, as Krebs and Dawkins (1984) suggest, manipulation of the receiver? A data base of 1,213 Zebra displays was collected from observations in the field during 1999 and 2000. Each display was scored for intensity, sex of receiver (closest individual or closest on the side of the Zebra display) and behavior of sender and receiver, before and after the display was produced. 71% of the displays were male-male and an additional 16% were female-male. When the behaviour after a male-male Zebra was catalogued, 73% of the time the winner made a more intense Zebra display.

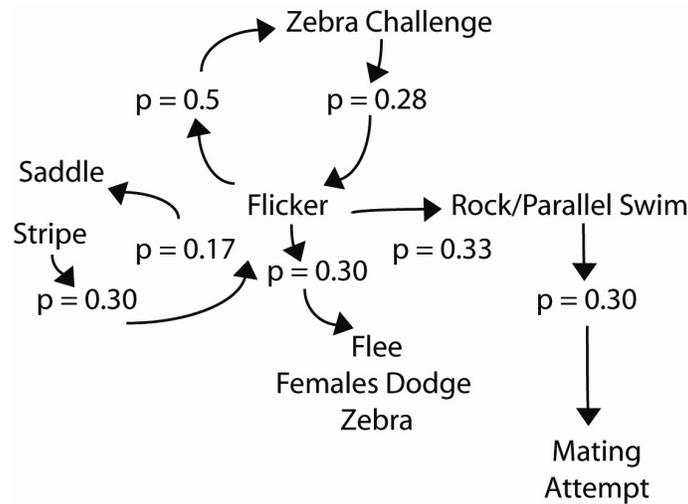


Figure 3. A flow chart of the sequence of behaviours and displays in the courtship of the squid *Sepiotheuthis sepioidea* and its interruption by peripheral males.

However, there is one interesting situation in squid in which the winner is not the one who produces the more intense Zebra display. A mature male, usually in a short-term consort pairing with a mature female, gives a specific Flicker display indicating his intent ($p = 0.3$) to pass spermatophores to a willing female (see Figure 3). In this situation there is a high ($p = 0.5$) probability that a subadult male will make a Zebra display and interrupt the courtship (see Shier, 2002, for eavesdropping). Given this challenge the courting male will break off, approach the subadult and often display Zebra in return. In this case the subadult may be less than “honest” as it will be much more likely (56% of the time) make a more intense Zebra display than the adult.

This display intensity may be a deceptive message of status by a subadult male who could not win a physical contest, which rarely happens in this species, or take over the consortship. Such deception can be evaluated for its fit into three categories (Guzeldere, Nahmias, & Deaner, 2002). Deception can be defined as “an agent producing or withholding an act or signal so that it is misinterpreted by

another to the advantage of the agent" (Guzeldere et al., 2002, p. 353). The first category is hardwired deception, where the deceptive animal simply has the perceptual message permanently, such as the camouflage of a moth on tree bark (Kamil & Bond, 2002). A second category of deception occurs where the deceiver assumes a deceptive communication because it has learned that it will result in a payoff. What payoff might the subadult squid acquire in this situation? Since female squid mate with approximately 10 males over a period of approximately three weeks and collect sperm from all of them, it might pay the subadult male to discourage courtship if it results in him gaining successful copulation later on when he is larger. Thus it is probably not the third category of deception, where the deceiver intends to deceive as it understands how its behaviour affects the receiver and thus manipulates the receiver's mental state. But it is difficult to tell precisely what a squid "knows" or "represents" with a visual display. There is obviously some sophistication of control of squid sexual displays, and see Adamo and Hanlon (1966) for those of cuttlefish.

We see from this section that this shift from a solitary or asocial to a sexual lifestyle plunges the squid into a demanding but short-term (approximately a month) lifestyle of courtship, choice and competition perhaps like an iteroparous mammalian female's short period of receptivity. It is much simpler than the mammalian long-term knowledge of social relationships (Seyfarth & Cheney, 2002), yet might also demand social cognitive ability.

Senescence

The short stage of senescence in the lifespan of cephalopods is the almost inevitable outcome of the physiological changes that accompany sexual maturity. As the focus of growth changes from somatic to reproductive tissues (O'Dor and Wells, 1978; Tait, 1987), the digestive glands cease to function properly and feeding slows or stops. As somatic growth ceases, brain tissue begins to degenerate (Chichery & Chichery, 1992a). In a relatively short time the body simply shuts down.

Senescence is probably much more noticeable and a longer period of a cephalopod's life in captivity than in the wild, and it is the aquarium keepers of octopuses who have brought this period of life to our attention (Anderson, Wood, & Byrne, 2002). Researchers or aquarists commonly see an octopus which seems to be in excellent health stop eating, develop skin lesions and decline over a period of weeks. This period is present in both sexes but is masked in females as they stay in their den and tend eggs, only coming out after eggs have hatched if they survive that long. Interestingly, senescent male octopuses both lose their normal activity rhythm and double the amount of time they are active, from around 40% to over 80% (Meisel et al., 2003). Such a pattern of activity would place an octopus in imminent danger of predation in the wild and senescent octopuses probably do not survive long.

Besides the changes in physical condition, senescent cephalopods change their behaviour. Aquarists report that senescent octopuses lose coordination and crawl through stinging sea anemones that they would have previously avoided (Anderson et al, 2002), as well as drastically cutting their food intake. In the wild,

senescent female squid which have presumably laid their eggs give agonistic Zebra displays to all comers and often end up either solitary or schooling with one or two other females. Senescent large males move from group to group, challenging other males with a Zebra display and perhaps exchanging a Stripe-Saddle display with the largest females, yet not moving further to Flicker displays or mating (Mather, personal observation). Such attenuation of behaviour sequences was also reported for senescent cuttlefish by Chichery and Chichery (1992a). In their two-week period of decline, cuttlefish first underestimate the distance to a prey item and thus undershoot with the tentacles, later detect but fail to pursue the shrimp prey and finally cease even to orient to the shrimp.

Such failures in behaviour sequencing were linked to brain structure by Chichery and Chichery (1992a, 1992b). Two-year old cuttlefish were both slower to learn the same avoidance task that they had used on the very young cuttlefish, had lesser retention and were also, as is found in human elders (Santrock et al., 2003), much more variable in learning than one year olds. Neurohistological analysis showed an accumulation of granules representing axon degeneration in the cuttlefish brains, particularly in the motor centers of the peduncle area and the basal lobes. Interestingly enough, despite the lack of learning the vertical lobe was spared but there were many degenerating fibres in the tracts leading to and from this structure. This degeneration of the motor output areas correlates nicely with the initial decline not in perception of prey but in response to it and may be a parallel to the initial degeneration of the hippocampus in Alzheimer's disease in humans (Santrock et al., 2003).

Cephalopod senescence appears to be similar to but much swifter than that of mammals (Promslow, 1991). It reminds us of the overwhelming role that physiology appears to play in guiding behaviour in these animals. Without the buffering of the social group in terms of assistance, increased status and continuing contribution to care of offspring, the cephalopod completes its semelparous reproductive effort and just dies. The physiological changes that shift the animals from growth to reproduction simply continue their shift to speedy decline and death (van Heulekem, 1979).

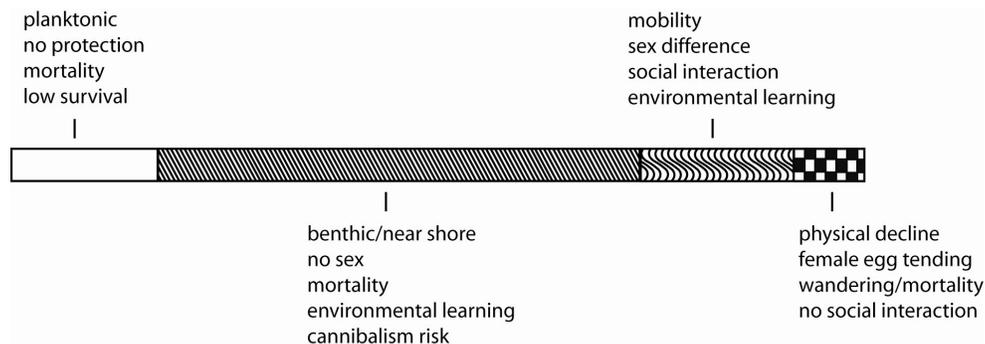


Figure 4. A depiction of the major features of ecology and behaviour in the lifespan stages of coleoid cephalopods.

Conclusion

This comparative look at development of behaviour (Figure 4) places the “normal” mammalian path in a wider perspective. The fixity of behaviour in young cephalopods makes it appear that the buffering of childhood by the presence and care of parents is not enough to erase the necessity for a learning-dependent animal to start off without learning. The extreme learning dependence of the mobile octopuses with wide prey choice and avoidance of many predators shows how environment can be the only pressure to make a learning-dependent animal. Nevertheless, in this prereproductive period play-like behaviour is at a low but constant level, suggesting that the protection of parents allows a young mammal to play at a fairly high level while its continuous presence in social groups may make it necessary. There appear to be few sex differences in behaviour during this long prereproductive period of cephalopods. Nevertheless, when the semelparous cephalopods do mature, due to a simple hormonal system, they assume the system of male competition and female choice that most other species groups do. Squid use this considerable behavioural flexibility to compete, court and mate. At the end of the lifespan, the cephalopods are unprotected by any social group and their swift decline and short senescent period seems the inevitable end point of physiology, the switch from somatic to sexual growth that began with their delayed maturation.

What cephalopod might be used as the model to study behaviour development? The subclass Coleoidea (most of the modern cephalopods) is a fairly diverse group and so there is no single choice for a model species. Octopuses, especially *O. vulgaris*, have had much research attention, mostly in the laboratory (Wells, 1978, but see Mather 1991a, 1991b). They adapt well to lab situations, are sometimes large but mostly have a planktonic young stage and are solitary. Both vision and chemotactile senses are important to them. Cuttlefish have had research attention in the laboratory but almost none in the field so the context of their behaviour is often completely lacking. They are very visual and their relatively large young are perfect for a focus on early stages of behaviour development; they are solitary until reproduction but our fragmentary knowledge of their reproductive strategies in the field (see Hall & Hanlon, 2002) blocks our understanding. Squid are the social cephalopods but they are open ocean species in many cases and that makes understanding their behaviour a practical problem. They are predominantly visual and use their display system for sexual interaction (Mather, 2004; Moynihan & Rodaniche, 1982) but are difficult to keep in the laboratory. The small sepiolid squid (Sinn & Moltchanowskyj, 2005), are easy to keep in the laboratory across their 5-month lifespan and might be an ideal group to use as a model. However, they are probably solitary although essentially nothing is known of their natural history and most are strictly nocturnal. As in any other group, the choice of a model cephalopod organism will have to depend on the specific question about development of behaviour. But there are many interesting questions to ask and much to learn from the cephalopods as models of behaviour development.

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