

Signaling to the Enemy? Body Pattern Expression and Its Response to External Cues During Hunting in the Cuttlefish *Sepia officinalis* (Cephalopoda)

SHELLEY A. ADAMO^{1,*}, KELLY EHGOETZ², CHERYL SANGSTER²,
AND IVY WHITEHORNE²

¹ *Department of Psychology and* ² *Department of Biology, Dalhousie University,
Halifax, Nova Scotia B3H 4J1*

Abstract. Cuttlefish can rapidly alter their appearance by using neurally controlled chromatophore organs. This ability may provide a window into their cognitive capacity. We test whether the changes in body pattern that occur during hunting depend on context. If they do, then it may be possible to use these changes to study cephalopod cognition while the animal is engaged in ecologically relevant tasks. We found consistent individual differences in the tendency of cuttlefish to hunt with the first two arms raised. We also found that cuttlefish usually darken their skin after they seize a prey item. This darkening is observed regardless of the identity of the prey (fish, crab, or shrimp), prey context (buried in sand, in a bare tank, or on top of a rock pile), or the presence of a sudden stimulus. The sudden stimulus was created by presenting an overhead model bird to the cuttlefish. The model induced components of the Deimatic Display, which is a form of antipredator behavior, suggesting that the model was perceived as a potential threat. Passing Cloud displays and the Darkening of the arms were significantly reduced after exposure to the model bird. The effect of a potential predator on body pattern expression during hunting suggests it may be possible to use these changes as a sensitive indicator of ecologically relevant learning.

Introduction

Cephalopods are the only invertebrates that have large, encephalized central nervous systems (Budelmann, 1995). For this reason they are an important group in which to test

hypotheses about the evolution of different nervous system structures and the relationship of these structures to advanced cognitive abilities (see Budelmann, 1995; Karson *et al.*, 2003). Cephalopods, such as the cuttlefish *Sepia officinalis* (Linnaeus, 1758), have brain:body weight ratios larger than that of most fish and reptiles (Packard, 1972). However, they appear to lack some of the cognitive abilities frequently observed in fish (see Mather, 1995; Boal, 1996; Boal *et al.*, 2000; for fish, see Kelley and Magurran, 2003; Laland *et al.*, 2003; Warburton, 2003). Cephalopods do have some advanced cognitive abilities, especially when performing tasks that are ecologically relevant (*e.g.*, spatial learning; see Mather, 1995; Karson *et al.*, 2003). Therefore, studies that focus on behaviors that are central to a cephalopod's life history and in which the animal has devoted a large amount of neural tissue may provide the best indicators of cephalopod cognition. For example, the body patterns produced by the chromatophore organs are critical for cuttlefish survival (Hanlon and Messenger, 1988, 1996), and cuttlefish appear to require their large brains, in part, to control their chromatophores (Budelmann, 1995). In this paper we examine whether changes in body patterns during hunting may prove useful for studying cephalopod cognitive ability.

Chromatophore organs are controlled by innervated muscle fibers, giving *S. officinalis* the ability to rapidly change both the pattern and color of its skin (Messenger, 2001). These muscles are innervated directly from the chromatophore lobes of the brain (see Messenger, 2001), at least for chromatophore organs in the fin (Gaston and Tublitz, 2004). However, only by stimulating higher brain centers such as the optic lobe can the cuttlefish be induced to display a coherent body pattern (Boycott, 1961).

Received 26 October 2005; accepted 26 January 2006.

* To whom correspondence should be addressed. E-mail: sadamo@dal.ca

Although cuttlefish can produce many body patterns in theory, in practice they use only some combinations frequently (Table 1; Hanlon and Messenger, 1988). The main function of these patterns appears to be crypsis (Hanlon and Messenger, 1988). Body patterns are also used for communication signals in males (Adamo and Hanlon, 1996) and probably females (Boal *et al.*, 2004; Palmer *et al.*, 2006). Body patterns may also play a role in foraging behavior, because some body patterns, such as Passing Cloud (Table 1), are frequently observed during hunting (Hanlon and Messenger, 1988, 1996). Hanlon and Messenger (1996) suggest that these body patterns may distract or lure prey.

Producing appropriate body patterns during foraging behavior probably requires advanced cognitive abilities. Cuttlefish are generalist predators (Hanlon and Messenger, 1996) and if body patterns are important during hunting, the optimum type and frequency of display will probably vary depending on the identity of the prey. Being able to exploit new prey items and becoming more efficient at catching old ones should select for cuttlefish that can alter body pattern use during hunting depending on context. Learning plays a role in the hunting behavior of cuttlefish (*e.g.*, Darmaillacq *et al.*, 2004), although there is no evidence that body patterns related to hunting change as a result of experience or external factors. Moreover, showy displays may attract predators as well as prey. Therefore, such displays should also be sensitive to the risk of predation. Learning when to be “cautious” has been observed in fish (Kelley and Magurran, 2003).

To determine whether body patterns observed during hunting may be useful in ecologically relevant studies of cephalopod cognition, we examine whether their expression

changes depending on prey type, prey context, or the presence of a sudden stimulus (*i.e.*, potential predator).

Materials and Methods

Cuttlefish

Cuttlefish were housed as previously described (King *et al.*, 2005). Briefly, we obtained cultured animals from the National Resource Center for Cephalopods, Galveston, Texas. Cuttlefish were maintained in the Aquatron marine facilities of Dalhousie University. Each tank (78 × 62 cm; water depth 25.5 cm) was divided in half by an opaque barrier, and each section contained a piece of PVC piping (about 25 cm long) for a cuttlefish shelter. A plastic disk (diameter 30 cm) was also placed in each tank, providing a more “enriched” environment (see Dickel *et al.*, 2000). Each tank received water from an open seawater system. Salinity ranged from 27.5 to 30.5 ppt. The water was maintained at 21 °C in experiment 1, 16 °C in experiment 2, and 15 °C in experiment 3. Animals were maintained on a 12:12 h light/dark cycle and fed frozen shrimp or fish *ad libitum* daily. Cuttlefish that were used in experiments received their daily feeding after the experimental trial. Cuttlefish size (mantle length) was measured at the time of the experiment, and sex was determined during necropsy. Cuttlefish from different generations were used in each of the three experiments (*i.e.*, no cuttlefish were used in more than one experiment).

To avoid cueing by the experimenters, opaque curtains were hung around all experimental tanks. Cuttlefish were observed *via* a camera attached to a monitor. Trials were recorded on Hi8 videotape. The introduction of any material

Table 1

Description of body patterns and postural components*

Element	Description
Body Pattern	
Dark Mottle	Coarse-grained dark and light areas appear across mantle
Deimatic	Animal flattens and pales with two eye spots at back of mantle
Disruptive	Bold transverse and longitudinal dark and white bars and shapes
Light Mottle	Similar to Dark Mottle, but with less contrast between dark and light
Passing Cloud	A broad transverse wave of light or dark that travels across the animal
Stipple	Uniform tone with small specks of darker color across the mantle
Uniform Blanching	Animal suddenly turns pale
Uniform Darkening	Animal suddenly turns dark
Uniform Light	Animal maintains overall pale coloration
Weak Zebra	Stripes across mantle. Low contrast
Postural elements	
Dark arms	First pair of arms are raised and darkened
Splayed arms	All arms held apart, often irregularly curved
Raised arms	First pair of arms are raised
Waving arms	First pair of arms raised, each in S-shaped curve. Swayed gently from side to side. Arms usually dark.

* Descriptions are based on Hanlon and Messenger (1988).

into the experimental tank was done remotely by the observer from behind the blinds. The experimental tanks used to test the cuttlefish were located in a room adjacent to that containing the home tanks. Cuttlefish were moved from their home tanks to the experimental tanks by gently scooping them into clear plastic bags. The cuttlefish, and their surrounding seawater, were then transported to the experimental tank in the adjoining room. Cuttlefish spent less than 2 min in the plastic bags during the transfer.

Data analyses

Data were analyzed using nonparametric tests (Sokal and Rohlf, 1981; Meddis, 1984). The alpha criterion was adjusted when more than one statistical test was performed on the same data set. Because body patterns are somewhat subjective, random sequences (chosen by lot) were tested for inter-observer reliability. Inter-observer reliability scores were $r > 0.85$ (Pearson correlation). Values are given as medians and first and third quartiles.

Hunting behavior in cuttlefish

Cuttlefish hunting behavior can be divided into three phases: attention, positioning, and seizure (Messenger, 1968). During attention, the cuttlefish aligns itself with the prey item. During positioning, the cuttlefish moves until it is about 1 mantle length from its prey. Seizure, the final phase, can be accomplished by two different maneuvers. During a tentacle strike, two tentacles are ejected and grab the prey. During an "arm-grab," the cuttlefish jumps on its prey and wraps its arms around it. Table 1 describes some of the body patterns commonly observed during hunting.

Experiment 1. Effect of Prey Type on Hunting Behavior and Body Patterns

Procedure

To test whether cuttlefish ($n = 7$) alter their hunting tactics and body pattern use depending on the type of prey, cuttlefish were presented with live green crab (*Carcinus maenus*, carapace widest width, 4–7 cm), live goldfish (*Carassius auratus*, 5–8 cm, rostrum to tail), or frozen tiger shrimp (*Penaeus monodon*, about 7 cm, rostrum to tail); and their hunting behavior was videotaped. Cuttlefish in this experiment had never experienced live crab. Cuttlefish were sexually mature adults ($n = 3$ males, 4 females) and ranged from 11 to 17 cm in mantle length.

The experimental tank ($91 \times 61 \times 44$ cm, water depth 37 cm) had an opaque plastic shelf (61×17 cm) above the outlet pipe, creating a shelter for the cuttlefish. At the start of a trial, cuttlefish were placed under this shelter in the experimental tank and left undisturbed for 30 min. At 30 min, a prey item from one of the three prey types was introduced into the tank at the opposite end from the shelter.

Crabs were tied between their fourth and fifth walking legs and lowered into the tank. Goldfish were placed in a container that was tipped into the tank (*via* a pulley system). Shrimp were tethered to a weighted nylon filament and lowered into the tank. Trials lasted a maximum of 10 min or until the cuttlefish had consumed the prey. Cuttlefish were given no more than one trial per day.

All cuttlefish were presented with each prey type twice, in separate trials. The order that the prey types were presented was randomized to prevent order effects.

Results

Cuttlefish always seized fish using a tentacle strike (7/7 cuttlefish, all trials). Crabs were seized using an arm-grab (4/7 cuttlefish attacked a crab, 4/7 used an arm-grab). In all but one attack, the cuttlefish approached the crab from the posterior end, away from the claws. In one trial, a cuttlefish attacked the crab laterally. Shrimp were seized using a tentacle strike (5/7 cuttlefish attacked, 5/7 used tentacle strike, both trials).

During hunting, cuttlefish displayed a variety of body patterns prior to seizure (*i.e.*, attention and positioning stages). Cuttlefish expressed the patterns Disruptive, Light Mottle, Stipple, Weak Zebra, and Uniform Light. They also exhibited the postural display of Raised arms. There were no consistent differences related to prey type (Test for trends for frequency data; Meddis, 1984; $Z < 1.0$, $P > 0.1$, all tests). No Passing Cloud displays were observed. During the seizure phase, cuttlefish frequently expressed the Dark Mottle, regardless of prey type (7/7 cuttlefish expressed Dark Mottle during at least one seizure event). Interestingly, frame-by-frame analysis revealed that this change in pattern occurred after the prey had been caught by the tentacles.

Experiment 2. Effect of Prey Context on Hunting Tactics and Body Pattern Use

Procedure

Cuttlefish hunted live sand shrimp (*Crangon septemspinatus*) under the three treatments described below. The test tank (134 cm length \times 55 cm width \times 29 cm water depth) was divided into two sections (one 85 cm in length and one 49 cm in length) by an opaque black partition. The partition could be raised remotely. Shrimp (6–8 cm, rostrum to tail) were placed in the tank at least 3 min prior to the addition of the cuttlefish. Cuttlefish were sexually mature (mantle length: 11–14.5 cm; $n = 11$; 5 males and 6 females).

Treatment 1: Bare Tank. Cuttlefish were presented with a shrimp in the center of a bare tank. The shrimp was tethered by tying a nylon filament just anterior to the telson. The shrimp was unable to camouflage itself against the blue-green color of the tank.

Treatment 2: Rock Pile. A shrimp was tethered to the

top of a pile of small rocks. The rocks were 5 to 20 cm in length along their longest axis, and each rock was no more than 2.5 cm in height. The total height of the rock pile was 12 cm. If untethered, the shrimp could have hidden between the rocks. The shrimp were clearly visible to a human observer, and presumably to the cuttlefish as well. Cuttlefish are visual predators with excellent acuity (Messenger, 1968).

Treatment 3: Sand. The experimental tank was filled 0.5 to 1.5 cm depth with fine brown sand, into which the shrimp buried themselves. Shrimp were tethered under the sand.

To start a trial, cuttlefish were placed in the larger of the two sections of tank. We found that after 15 min, cuttlefish adopted a resting pattern and settled on to the bottom of the tank. After a 15-min acclimation period, the partition was raised and the cuttlefish entered the treatment area. Each trial lasted 10 min after the partition was raised or until the shrimp was eaten. Cuttlefish were given four trials with each treatment. The order of presentation of each treatment was randomized. Cuttlefish were given no more than one trial per day.

Results

No cuttlefish exhibited the Passing Cloud display during any of the three treatments, although in one of the sand trials one cuttlefish expressed a pulsating dark pattern on its arms that resembled a Passing Cloud display. All cuttlefish (11/11) expressed the Dark or Light Mottle body pattern during seizure of the shrimp in 3/3 treatments in at least 1/4 trials. Frame-by-frame analysis revealed that the change in body pattern occurred after the seizure of the shrimp.

Cuttlefish had never experienced sand-covered tank bottoms prior to this study. In their first Sand trial, none of the cuttlefish used their funnels to blow sand away from the shrimp to aid in its capture. For 5/11 cuttlefish, the shrimp was plainly visible during their first Sand trial, and all but 1 of the cuttlefish successfully captured the shrimp. For 3/11 cuttlefish, the shrimp was invisible (*i.e.*, completely buried) during their first Sand trial. In these trials, none of the cuttlefish engaged in hunting behavior. For the remaining 3/11 cuttlefish, the shrimp was partly visible during their first Sand trial. In 3/3 of these trials, the cuttlefish attempted a tentacle strike in the sand but only 1 was successful in catching the shrimp. By the last two sets of Sand trials, of the six trials in which 5/11 cuttlefish were exposed to shrimp that were completely or partially covered with sand, in two of these trials no hunting sequences were initiated until the experimenter moved the shrimp remotely, removing it from the sand. In the other four trials, all initial tentacle strikes failed to capture the shrimp. In one trial, the cuttlefish blew the sand off the shrimp after its first tentacle strike was unsuccessful, and the shrimp remained partially

covered in the sand. The cuttlefish then successfully seized the shrimp.

Cuttlefish ($n = 11$) required the least amount of hunting time (*i.e.*, start of the attention stage to extrusion of the tentacles) in the Bare Tank treatment (median, 2 s; first quartile, 1 s; third quartile, 3 s), followed by the shrimp on the Rock Pile (median, 9 s; first quartile, 7 s; third quartile, 16 s), and finally shrimp in Sand (median, 14 s; first quartile, 13 s; third quartile, 20 s; Test for trends, repeated measures; Meddis, 1984; $Z = 2.63$, $P < 0.001$).

Over the four sets of trials, cuttlefish showed a decrease in the duration of hunting time in the Rock Pile trials (Test for trends, repeated measures; Meddis, 1984; $Z = 1.92$, $P < 0.05$, $n = 11$). Test for trends in the Sand treatment was not possible because of the variability in the degree to which shrimp buried themselves in the different trials.

Despite extensive variability in the body patterns expressed both within and between animals, the postural component Raised arms was used significantly more often when cuttlefish were hunting in the Sand and Rock Pile treatments than in the Bare Tank (Fig. 1; Repeated measures test for trends; Meddis, 1984; $Z = 2.73$, $P < 0.01$, $n = 11$).

Strong individual differences in the frequency of the use of Raised arms were consistent over the four sets of trials and over the three different treatments (Fig. 2; Frequency test; Meddis, 1984; $Z = 2.03$, $P < 0.01$). Some cuttlefish almost always raised their arms while hunting (max. >80% of all trials), while 1/11 never used this postural component regardless of context.

Experiment 3. Hunting in the Presence of a Sudden Stimulus

Procedure

Ten juvenile cuttlefish (mantle length 9.0–13 cm; male $n = 6$, female $n = 4$) were exposed to an overhead model

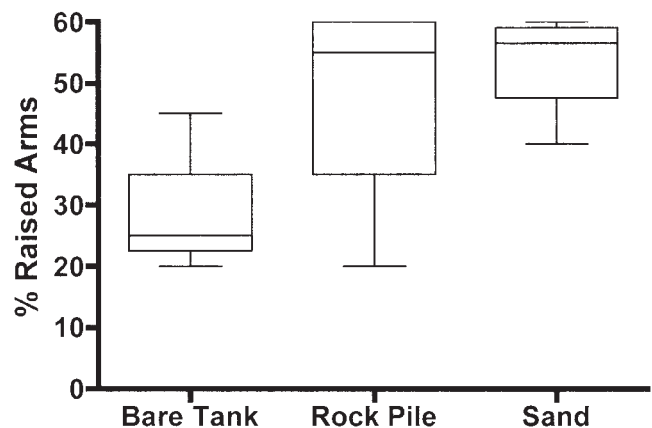


Figure 1. The percentage of trials in which cuttlefish exhibited Raised arms. Box and whisker plot. Values are taken from the median value of the 11 cuttlefish for each set of trials. Error bars denote the most extreme value per group; the line within the box denotes the median value.

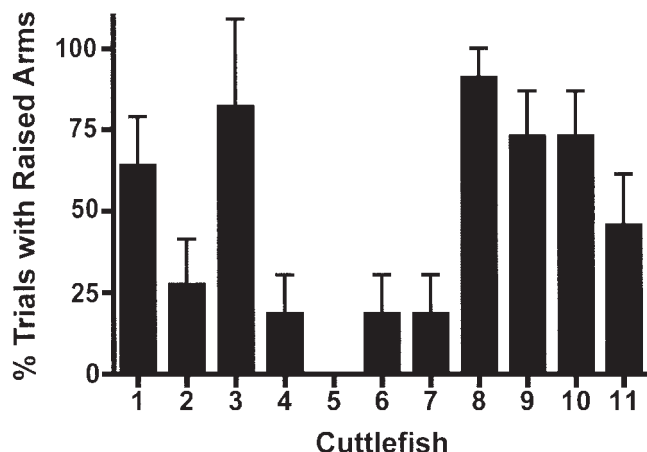


Figure 2. Individual differences in the tendency to use Raised arms during hunting. Each bar represents the median percentage of all trials ($n = 12$) in which each cuttlefish exhibited Raised arms. The error bars denote 95% confidence intervals.

bird while they were hunting. To begin a trial, a cuttlefish was transferred from its home tank to the experimental tank ($91 \times 61 \times 44$ cm; water depth 37 cm). The bottom of the experimental tank was covered with coarse sand and large rocks. At one end of the tank, just above the water line, was an opaque cup (8 cm in diameter) that held a live sand shrimp (*Crangon septemspinosus*) collected locally. The shrimp (50–75 mm, rostrum to tail) was tethered to a line and a small weight. The shrimp could be lowered into the water by pulling on a line. The model bird was seagull-shaped and made of black Bristol board (wing span, 45 cm; length, 41 cm) attached to a wire that ran above the experimental tank. The black Bristol board stood out against the white ceiling above. The lighting came from fluorescent lights in the ceiling; therefore, the model bird was seen as a silhouette from the tank. The end of the wire was attached to the cement-block wall behind the tank. A piece of wire terminated the model's movement down the wire track. After traveling down the wire track, the model remained suspended above the end of the tank containing the shrimp for the remainder of the trial. At this point, the model was 47 cm above the water surface. The model was directly above any cuttlefish that was in position to seize the shrimp. We used a bird model because birds are thought to prey upon cuttlefish in the field (Blaber and Wassenberg, 1989; Lipinski and Jackson, 1989). The water surface was calm during trials. Using data gathered from the video, we determined that the model moved at approximately 0.5 m/s.

To determine whether the cuttlefish could potentially see the model, an experimenter entered the water-filled tank, positioned her head to be about 20 cm from the posterior edge (striking distance for the cuttlefish from the shrimp) and looked up. To the human observer, the model was clearly visible from underneath the water, both while it was

sliding along its track and once it stopped at the end of its run. However, because cuttlefish eyes are differently placed than human eyes, this information does not demonstrate that the cuttlefish could see the model, only that the image of the model penetrated into the tank. However, in another study using a similar apparatus, cuttlefish produced robust behavioral and physiological responses to an overhead bird model (King and Adamo, 2006). Therefore, we know that cuttlefish are capable of responding to visual stimuli located in the air above them in an experimental set-up very similar to ours and completed in the same laboratory.

After 30 min of acclimation in the experimental tank, the shrimp was lowered into the tank. Cuttlefish were then given 10 min to initiate a hunting sequence. If the shrimp was not attacked within that time, the trial was terminated. During the first trial, cuttlefish were allowed to attack and consume the shrimp without the model bird being present (pre-bird trial). In the three bird trials, as soon as the cuttlefish had adopted the attention stage of hunting, the model was released and allowed to fly over the tank, producing a sudden novel stimulus. The model stopped above the end of the tank containing the shrimp and was left there for the remainder of the trial. After three bird trials, the cuttlefish were given one trial without the model bird being released (post-bird trial). There were always 2 to 4 days between any two trials.

Results

Body patterns observed during foraging. Prior to orienting toward the prey, cuttlefish expressed a Stipple body pattern (10/10 cuttlefish, all trials). This cryptic pattern allowed the cuttlefish to blend in with the coarse sand substrate (Hanlon and Messenger, 1988). Most cuttlefish (8/10 in at least 2/5 trials) maintained a Stipple pattern as they raised themselves from the substrate and oriented toward the prey (*i.e.*, the attention stage of hunting). The pattern often darkened as the cuttlefish approached the shrimp (positioning stage, 8/10 cuttlefish in at least 1/5 trials). Orienting cuttlefish extended their fourth arms forward (8/10 cuttlefish, at least 1/5 trials) or sometimes splayed them out to the side (6/10 cuttlefish, at least 1/5 trials). All cuttlefish ($n = 10$) seized the prey using a tentacle strike. During prey seizure, the cuttlefish usually adopted a darker body pattern, such as Light or Dark Mottle (Table 2); however, 1/10 cuttlefish showed Uniform Blanching during the attack instead of a darker body pattern (Table 2). Frame-by-frame analysis demonstrated that the body pattern darkened either at the same time as the tentacles contacted the prey or immediately after. Most cuttlefish (7/10) returned to Stipple within 15 s of seizure in at least 2/5 trials.

Effect of the model bird on cuttlefish foraging. All of the cuttlefish (10/10) made some response to the appearance of the bird model (Table 2) and temporarily ceased approaching the

Table 2

Number of cuttlefish exhibiting different body patterns in Experiment 3*

Foraging stage	Pre-Bird (<i>n</i> = 10 cuttlefish)		Bird (<i>n</i> = 10 cuttlefish)		Post-Bird (<i>n</i> = 10 cuttlefish)	
	Pattern	<i>n</i>	Pattern	<i>n</i>	Pattern	<i>n</i>
Pre-Attention	Stipple	10	Stipple	10	Stipple	9
Attention and Positioning	Stipple	9	Stipple	7	Stipple	7
	Dark Mottle	3	Dark Mottle	3	Dark Mottle	3
	Other†	8	Other†	10	Other†	7
	Passing Cloud	8	Passing Cloud	7	Passing Cloud	6
	Raised arms	10	Raised arms	10	Raised arms	8
	Dark arms	6	Dark arms	7	Dark arms	5
Reaction to Model	—		Deimatic	10	—	
			Ink	2		
Attention and Positioning (2)— While Bird Model Above Tank	—		Stipple	7	—	
			Dark Mottle	2		
			Other†	8		
			Passing Cloud	3		
			Raised arms	7		
			Dark arms	2		
Seizure	Light/Dark Mottle	9	Light/Dark Mottle	10	Light/Dark Mottle	9
	Uniform Blanching	1	Uniform Darkening	1		

* Most animals exhibited more than one body pattern during each stage. In Bird trials, Body patterns listed were observed in at least 1/3 trials.

† Includes Light Mottle, Disruptive, Uniform Light and the postural components Splayed arms and Waving arms.

shrimp; 10/10 cuttlefish exhibited some components of the Deimatic pattern in at least 1/3 trials. Components of the Deimatic Display were never seen during hunting trials in which the model bird was not present. Two cuttlefish inked (2/3 trials and 1/3 trials) when the bird appeared above the tank. Both of these cuttlefish resumed hunting the shrimp under the ink. Cuttlefish often reinitiated hunting and seized the shrimp (7/10 animals in 3/3 model trials). The other 3 cuttlefish reinitiated hunting in at least 1/3 trials. Cuttlefish reinitiated hunting 2 min 18 s (1st quartile, 1 min 12 s; 3rd quartile, 5 min 48 s, *n* = 10, median bird trial value used for each cuttlefish, averaged over only those trials that included seizure) after the presence of the model bird. Once they reinitiated hunting, cuttlefish exhibited body patterns similar to those observed in the pre- or post-bird trials (Table 2), except for a decline in Passing Cloud displays (Fig. 3; Repeated dichotomous data; Meddis, 1984; $Z = 4.56$, $P < 0.01$) and a decrease in the use of Dark arms (Repeated dichotomous data; Meddis, 1984; $Z = 4.04$, $P < 0.01$). The time required to capture the shrimp after hunting was reinitiated (attention to seizure) was not significantly different from the time required to hunt the shrimp (attention to seizure) in the non-bird trials (median time across trials used for each cuttlefish, Matched Pairs test; Meddis, 1984; $Z = 1.3$, $P > 0.1$). Therefore, the decline in Passing Cloud Displays and the use of Dark arms

was not an artifact of a difference in hunting duration between bird and non-bird trials.

Discussion

Presentation of an overhead model resulted in the production of fewer Passing Cloud displays (Fig. 3). The de-

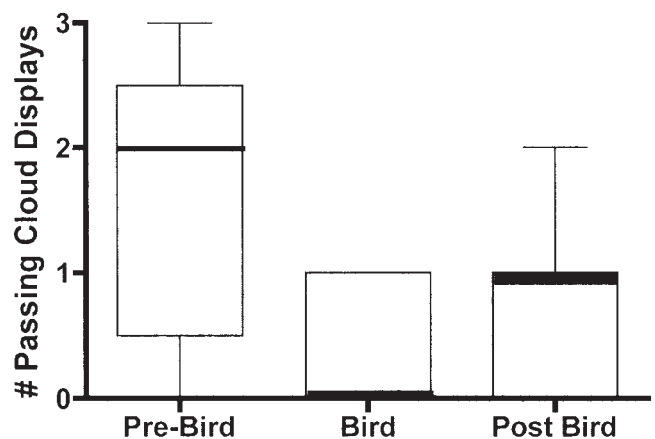


Figure 3. Passing Cloud displays decrease after exposure to the bird model. Box and whisker plot. The line in the box represents the median value of the 10 cuttlefish for each group. The median value and 3rd quartile are 1 for the Post-Bird group. Error bars denote the most extreme value per group.

cline in the number of displays was not due to a habituation process, because the number of Passing Cloud displays increased during the final trial without the overhead model (Fig. 3). Moreover, the number of Passing Cloud displays remained high in all trials prior to the appearance of the model bird (Table 2). Furthermore, in squid, habituation does not occur towards model predators unless there are a large number (>15) of model presentations in one day (Long *et al.*, 1989). Cuttlefish appeared to perceive the sudden appearance of the model bird as a potential threat. All 10 cuttlefish expressed at least some components of the Deimatic Display during the “bird” trials. The Deimatic Display is thought to be an anti-predator response (Hanlon and Messenger, 1996). Therefore, cuttlefish appear to suppress the conspicuous Passing Cloud display (Packard and Hochberg, 1977) in the presence of a potential predator.

However, further studies, such as showing that Passing Cloud displays increase predation in the field, must be completed before we can conclude that decreasing this display reduces predation on cuttlefish. Nevertheless, indirect evidence supports this hypothesis. Dark arms, another conspicuous display, is also reduced after exposure to the model bird (Table 2). Fish can alter their foraging behavior when predation risk is increased (Kelley and Magurran, 2003), as can non-cephalopod molluscs (Serra *et al.*, 1997). Therefore, this ability in cuttlefish would not be surprising.

Unfortunately the function of the Passing Cloud display is unknown. In juveniles, Hanlon and Messenger (1988) noted that young cuttlefish expressed the Passing Cloud display during hunting, when approached by large fish, and when swimming. In the context of hunting, it is thought to distract or mesmerize prey (Hanlon and Messenger, 1996). Other cephalopods also exhibit Passing Cloud displays, typically during hunting (*e.g.*, Mather and Mather, 2004). Interestingly, we did not see Passing Cloud displays in adult cuttlefish. Whatever function it may have during hunting, adults appear to use it less than juveniles.

The observation that all cuttlefish (10/10) responded to the overhead model demonstrates that they were capable of perceiving it. We assume that the cuttlefish used visual cues to perceive the model. The model's track apparatus was not attached to the experimental tank and, therefore, it probably did not produce vibrational cues.

The conspicuous change in body pattern that occurs at the time of seizure (typically Dark or Light Mottle) was observed in all experiments, regardless of prey type, context, or the presence of a potential predator. Messenger (1968) also noted that cuttlefish express color changes during seizure, although he described it as Uniform Dark. Crypsis is usually the cuttlefish's major defense against predation (Hanlon and Messenger, 1988, 1996), and the sudden change in contrast and color that occurs during seizure probably puts them at risk. Given that this display is often performed after the prey has been seized, it is unlikely to be

a signal designed to confuse or startle the prey. Mauris (1989) found that a related cephalopod, *Sepiola affinis*, also makes a number of striking body pattern changes at the time of prey seizure. Mauris (1989) suggests that these pattern changes serve to “startle” potential predators while the cephalopod is attending to its attack on the prey and not watching for predators. Hanlon and Messenger (1988) noted that the only predation events they witnessed on juvenile *Sepia officinalis* in the field occurred when the cuttlefish's attention was directed at their video camera, leaving them oblivious to predators. Further field studies are required to test whether predators are startled by the display and whether expressing this display results in increased survival for cuttlefish. The sudden change in appearance that occurs during seizure does fit the description of a Deimatic Behavior (Hanlon and Messenger, 1996), which is a behavior designed to deter predation. However, this explanation seems incomplete because it does not explain why cuttlefish in a sizable minority of trials (about 10%–15%) did not exhibit a dramatic change in body pattern contrast at the time of seizure. Regardless of its functional significance, this result demonstrates that not all body patterns used during hunting are equally plastic.

We have little evidence that the body patterns used during hunting differ depending on context or the identity of the prey used in this study. Even though Raised arms did differ between prey contexts (Experiment 3), the tendency to exhibit Raised arms correlated with the length of the hunting bout. It is possible that Raised arms may be more likely to occur the longer the foraging event lasts, regardless of the context of the target.

This study corroborates earlier work (*e.g.*, Messenger, 1968) that also found that cuttlefish tend to use tentacle strikes on fish and arm-grabs on crabs, depending on crab size and other factors (Messenger, 1968; Duval *et al.*, 1984). Our naïve cuttlefish positioned themselves away from the claws of the crab on their first attack. Boal *et al.* (2000) found similar results, but only if crab odor was present. These authors suggest that the smell of crab can induce a state of food arousal, heighten the animal's attention, and decrease the chance that it will attack the crab facing the claws. Our cuttlefish were probably exposed to crab odor from earlier trials in the same tank, even though there was constant water flow in the experimental tank. However, their lack of experience with crabs may explain why 3 of the 7 cuttlefish never attacked the crabs, even though they always attacked the fish.

Cuttlefish have been observed using their funnel to remove sand covering prey (shrimp, see Tinbergen, 1969 who cites a personal communication by Dutch zoologist Jan Verwey; crab, see Mather, 1995). After four repeated trials, we observed this behavior only once, after a failed tentacle strike. Possibly our cuttlefish required more experience hunting in sand to learn this technique. Having experience

with sand may be important for cuttlefish to learn how to manipulate it (Poirier *et al.*, 2004).

Strong individual differences existed for at least one body pattern used during hunting (Raised arms; Fig. 2), even though the animals were reared in the same laboratories, under the same conditions. *S. officinalis* appears to show other individual differences as well (Calvé, 2005), as do other cephalopods (*e.g.*, Mather and Anderson, 1993). The function, if any, of Raised arms during hunting remains an area of active research (*e.g.*, see Hanlon and Messenger, 1996). However, if it does serve some function, as suggested by preliminary studies (Hanlon and Messenger, 1996), then individual differences in its use may reflect differences in hunting strategies between individual cuttlefish. Such differences could arise because of a combination of early learning and genetic influences. These same factors are thought to produce individual differences in fish (Warburton, 2003), in other cephalopods (*e.g.*, Sinn *et al.*, 2001), and in non-cephalopod molluscs (*e.g.*, West, 1986). Differences in body pattern use during hunting may be helpful for exploring how environmental influences can produce individual differences.

This study suggests that body pattern production may serve as a sensitive indicator of ecologically relevant learning (see also Mather, 1995). For example, it may be possible to use changes in body pattern expression to test whether cuttlefish can learn to associate cues with the presence of predators. Studying the effect of potential predators on the foraging behavior of fish has proven a useful paradigm for examining their cognitive ethology (*e.g.*, Kelley and Magurran, 2003). Use of body pattern changes as a measure of learning also has the advantage that the brain areas controlling their expression are under active investigation (Messenger, 2001; Gaston and Tublitz, 2004).

Acknowledgments

We thank the staff of the Aquatron for assistance in animal maintenance. This work was supported by a grant from the Natural Sciences and Engineering Council of Canada (NSERC) to S. Adamo.

Literature Cited

- Adamo, S. A., and R. T. Hanlon. 1996. Do cuttlefish (Cephalopoda) signal their intentions to conspecifics during agonistic encounters? *Anim. Behav.* **52**: 73–81.
- Blaber, S. J. M., and T. J. Wassenberg. 1989. Feeding ecology of the piscivorous birds *Phalacrocorax varius*, *P. melanoleucos* and *Sterna bergii* in Moreton Bay, Australia: diets and dependence on trawler discards. *Mar. Biol.* **101**: 1–10.
- Boal, J. G. 1996. Absence of social recognition in laboratory-reared cuttlefish, *Sepia officinalis*, L. (Mollusca: Cephalopoda). *Anim. Behav.* **52**: 529–537.
- Boal, J. G., K. Wittenberg, and R. T. Hanlon. 2000. Observational learning does not explain improvement in predation tactics by cuttlefish (Mollusca: Cephalopoda). *Behav. Proc.* **52**: 141–153.
- Boal, J. G., N. Shashar, M. M. Grable, K. H. Vaughan, E. R. Loew, and R. T. Hanlon. 2004. Behavioral evidence for intraspecific signaling with achromatic and polarized light by cuttlefish (Mollusca: Cephalopoda). *Behaviour* **141**: 837–861.
- Boycott, B. B. 1961. The functional organization of the brain of the cuttlefish *Sepia officinalis*. *Proc. R. Soc. Lond. B* **153**: 503–534.
- Budelmann, B. U. 1995. The cephalopod nervous system: what evolution has made of the molluscan design. Pp. 115–136 in *The Nervous System of Invertebrates: An Evolutionary and Comparative Approach*, O. Breidbach and W. Kutsch, eds. Birkhäuser, Basel.
- Calvé, M. R. 2005. Individual differences in the common cuttlefish, *Sepia officinalis*. Master's thesis, Department of Biology, Dalhousie University, Halifax, NS. 73 pp.
- Darmaillacq, A. S., L. Dickel, M. P. Chichery, V. Agin, and R. Chichery. 2004. Rapid taste aversion learning in adult cuttlefish, *Sepia officinalis*. *Anim. Behav.* **68**: 1291–1298.
- Dickel, L., J. G. Boal, and B. U. Budelmann. 2000. The effect of early experience on learning and memory in cuttlefish. *Dev. Psychobiol.* **36**: 101–110.
- Duval, P., M. P. Chichery, and R. Chichery. 1984. Prey capture by the cuttlefish (*Sepia officinalis* L.): an experimental study of two strategies. *Behav. Proc.* **9**: 13–21.
- Gaston, M. R., and N. J. Tublitz. 2004. Peripheral innervation patterns and central distribution of fin chromatophore motoneurons in the cuttlefish *Sepia officinalis*. *J. Exp. Biol.* **207**: 3089–3098.
- Hanlon, R. T., and J. B. Messenger. 1988. Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): the morphology and development of body patterns and their relation to behaviour. *Philos. Trans. R. Soc. Lond. B* **320**: 437–487.
- Hanlon, R. T., and J. B. Messenger. 1996. *Cephalopod Behaviour*. Cambridge University Press, Cambridge.
- Karson, M. A., J. G. Boal, and R. T. Hanlon. 2003. Experimental evidence for spatial learning in cuttlefish (*Sepia officinalis*). *J. Comp. Psychol.* **117**: 149–155.
- Kelley, J. L., and A. E. Magurran. 2003. Learned predator recognition and antipredator responses in fishes. *Fish Fish.* **4**: 216–226.
- King, A. J., and S. A. Adamo. 2006. Ventilatory, cardiac and behavioural responses to sudden visual stimuli in resting cuttlefish (*Sepia officinalis* Linnaeus). *J. Exp. Biol.* in press.
- King, A. J., S. M. Henderson, M. H. Schmidt, A. G. Cole, and S. A. Adamo. 2005. Using ultrasound to understand vascular and mantle contributions to venous return in the cephalopod *Sepia officinalis* Linnaeus. *J. Exp. Biol.* **208**: 2071–2082.
- Laland, K. N., C. Brown, and J. Krause. 2003. Learning in fishes: from three-second memory to culture. *Fish Fish.* **4**: 199–202.
- Lipinski, M. R., and S. Jackson. 1989. Surface-feeding on cephalopods by procellariiform seabirds in the southern Benguela region, South Africa. *J. Zool.* **218**: 549–563.
- Long, T. M., R. T. Hanlon, A. Ter Maat, and H. M. Pinsker. 1989. Non-associative learning in the squid *Lolliguncula brevis* (Mollusca, Cephalopoda). *Mar. Behav. Physiol.* **16**: 1–9.
- Mather, J. A. 1995. Cognition in cephalopods. *Adv. Study Behav.* **24**: 317–353.
- Mather, J. A., and R. C. Anderson. 1993. Personalities of octopuses (*Octopus rubescens*). *J. Comp. Psychol.* **107**: 336–340.
- Mather, J. A., and D. Mather. 2004. Apparent movement in a visual display: the 'passing cloud' of *Octopus cyanea* (Mollusca: Cephalopoda). *J. Zool.* **263**: 89–94.
- Mauris, E. 1989. Colour patterns and body postures related to prey capture in *Sepioida affinis* (Mollusca: Cephalopoda). *Mar. Behav. Physiol.* **14**: 189–200.
- Meddis, R. 1984. *Statistics Using Ranks*. Blackwell, Toronto.
- Messenger, J. B. 1968. The visual attack of the cuttlefish, *Sepia officinalis*. *Anim. Behav.* **16**: 342–357.

- Messenger, J. B. 2001. Cephalopod chromatophores: neurobiology and natural history. *Biol. Rev.* **76**: 473–528.
- Packard, A. 1972. Cephalopods and fish: the limits of convergence. *Biol. Rev.* **47**: 241–307.
- Packard, A., and F. G. Hochberg. 1977. Skin patterning in *Octopus* and other genera. Pp. 191–231 in *The Biology of Cephalopods*, M. Nixon and J. Messenger, eds. Academic Press, San Diego.
- Palmer, M. E., M. R. Calvé, and S. A. Adamo. 2006. Response of female cuttlefish *Sepia officinalis* (Cephalopoda) to mirrors and conspecifics: evidence for signaling in female cuttlefish. *Anim. Cogn.* **9**: 151–155.
- Poirier, R., M. P. Chichery, and L. Dickel. 2004. Effects of rearing conditions on sand digging efficiency in juvenile cuttlefish. *Behav. Proc.* **67**: 272–279.
- Serra, G., G. Chelazzi, and J. C. Castilla. 1997. Effects of experience and risk of predation on the foraging behaviour of the South-eastern Pacific muricid *Concholepas concholepas* (Mollusca: Gastropoda). *J. Anim. Ecol.* **66**: 876–883.
- Sinn, D. L., N. A. Perrin, J. A. Mather, and R. C. Anderson. 2001. Early temperamental traits in an octopus (*Octopus bimaculoides*). *J. Comp. Psychol.* **115**: 351–364.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W.H. Freeman, New York.
- Tinbergen, N. 1969. *The Study of Instinct*. Oxford University Press, London.
- Warburton, K. 2003. Learning of foraging skills by fish. *Fish Fish.* **4**: 203–215.
- West, L. 1986. Interindividual variation in prey selection by the snail *Nucella emarginata*. *Ecology* **67**: 798–809.