SKIN COLOURS AND PATTERNS OF JUVENILE OCTOPUS VULGARIS (MOLLUSCA, CEPHALOPODA) IN BERMUDA

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VIE MILIEU, 1994, 44 (3/4) : 267-272

SKIN COLOURS AND PATTERNS OF JUVENILE *OCTOPUS VULGARIS* (MOLLUSCA, CEPHALOPODA) IN BERMUDA

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COLOUR PATTERN
SKIN TEXTURE
POSTURE
OCTOPUS VULGARIS
CEPHALOPODA

ABSTRACT – Juvenile *Octopus vulgaris* were observed from dawn to dusk in surface waters of Bermuda. Skin patterns, colours and textures were catalogued and studied in association with particular situations. Significant associations were observed between Hunting and the Mottle Pattern, Resting or "Sleep" with Grey-green-purple, Jet Swimming with Tan and Stripe, and Disturbance with Pale. In contrast to other patterns known from aquarium observations, the posture and pattern termed Dymantic (or Deimatic) was not seen in the field.

LIVRÉE CHROMATIQUE
TEXTURE DE LA PEAU
ATTITUDE
OCTOPUS VULGARIS
CÉPHALOPODES

RÉSUMÉ – Des juvéniles d'*Octopus vulgaris* (Cephalopoda) ont été observés du lever du jour au crépuscule dans les eaux de surface des Bermudes. Les « patterns », les couleurs et la texture superficielle de la peau ont été répertoriés et étudiés en relation avec des situations particulières. Des associations significatives ont été observées entre les patterns « chasse » et « tacheté », « repos » et « gris-vert-violet », « nage rapide » et « rayé » « perturbation » et « pale ». Contrairement aux « patterns » connus à partir d'observations en aquarium, l'attitude et le « pattern » « dymantic » (ou « deimatic ») n'ont pas été observés *in situ*.

INTRODUCTION

One of the most obvious and fascinating aspects of cephalopod behavior is the patterns and colours which are produced on the skin surface. No other animals change their appearance so quickly and in as wide a range as the near-shore cephalopods (Packard & Sanders, 1971; Moynihan & Rodaniche, 1982; Hanlon & Messenger, 1988), using many of the patterns described by Cott (1940). Because the displays are the result of muscle contraction guided by motoneurons in the brain of the animals, they are really a subgroup of behavior and may be Modal Action Patterns (Barlow, 1968; see Hanlon, 1988). Such behaviors are relatively fixed, stable across environmental variation and easily observable. It is important to catalogue them because they may be species-specific and an indicator of phylogenetic diversity, or widespread amongst the group and indicative of the conservative retention of patterns (Moynihan, 1975).

But the attempt to describe even the skin patterns for one species is not easily realized. They are combinations of localized components, which may be contributors to a whole pattern or the most important feature of it. They are caused by contractions of chromatophore muscles, which spreads the elastic sac with yellow, red or brown pigment to express these colours. And they are also caused by the relaxation of these muscles, which allows underlying components to appear (Packard, 1988). These are the blue-green iridophores and the white leucophores, which reflect background colour and allow the colour-blind octopod (Messenger, Wilson & Hedge, 1973) to match the colours of its background (Messenge, 1974). In addition, specific skin texture changes and postures accompany many of the displays, so the skin patterns cannot be considered in isolation.

One of the first approaches must be to catalogue the components and patterns and their accompanying postures and textures. Packard & Sanders (1971) have described the repertoire of *Octopus vulgaris*, Hanlon & Hixon (1980) of *O. burryi*, Boyle & Dubas (1981) of *Eledone cirrhosa* and Roper & Hochberg (1988) of *O. cyanea, O. ornatus*, and *Hapalochlaena maculosa.* The observations in the present study offer two opportunities. First, the repertoire can be compared to that of Packard & Sanders (1971) on *Octopus vulgaris* and to the descriptions of Bermuda octopuses by Cowdry (1911). The Bermuda octopuses may be representative of a different species than *vulgaris*, or at least a separate population (Mangold & Hochberg, 1990). Second, the data result from many hours of observation of octopuses in the

field, with a wide range of behavior patterns observed. This gives the authors the opportunity not only to catalogue the colours, patterns and postures but also to relate their occurrence to behavioural states (see Mather, 1988) of the octopuses.

METHODS

Juvenile *Octopus vulgaris*, ranging in size from approximately 50 to 400 gm, were observed in Bermuda during the months of June-September, from 1984 until 1990. Octopuses lived from the intertidal to a depth of 2 m, in areas of open rock, rocky rubble and small sand patches. The water temperature ranged from 25 to 28 °C. The co-authors were the observers, assisted by volunteers from Earthwatch in 1984, 1985 and 1989. During 1985, two or more octopuses were followed continually from dawn to dark, which gave ample opportunity for observation of skin colours and patterns. An observer floated on the water surface while breathing through a snorkel, taking notes on an underwater slate. Observations of octopuses at home during the night were made by the first author in 1990; they refused to move when illuminated and could not be followed on foraging trips.

Since these patterns were an obvious aspect of the octopus' behavior, they were commonly recorded by all observers. Two aspects of the octopus' colours and skin patterns were recorded. One was simply their repertoire what patterns, colours, postures and motions were observed. Some of these were common, others such as signals to conspecific were very unusual. The second aspect was more quantitative, the pairing of common colours or patterns with specific behaviors or states.

Before observation began, only the senior author was familiar with colours and skin patterns of octopuses. To minimize bias and yet produce some consensus on particular patterns, volunteers were not informed about octopus displays. After a few days, the authors met with members of each team and discussed octopus behavior in general, including skin patterns and colours, and agreed on categories. Each description was recorded in the data files verbatim. As in any observational study, rare events such as Passing Cloud and Split body patterns were likely over-reported (Altmann, 1974). As well, duration of patterns was not re-

Table I. – The repertoire of skin colours, patterns, textures, postures, and associated behaviors in juvenile *Octopus vulgaris* in Bermuda. A * indicates a component was mentioned in Packard & Sanders (1971) and a # in Cowdry (1911).

COMPONENTS		
Chromatic	White Components	*Frontal white V (1), eye flash (2), #longitudinal stripe (3)
	Dark Components	*Eye ring (4), *#eye bar (5), #longitudinal stripe (6), *passing cloud (7), frontal hood (8)
Skin texture		*#Smooth (9), *#raised papillae (10), *#long head papillae (11), *#long mantle papillae (12)
Postures	Arms	*#Upturned (13), down (14), *spread (15), *outstretched (16), *curled (17), #trailing (18), *curled tips (19)
	Head & Body	*Flattened (20), *head raised (21), body raised (22), mantle vertical (23), spread web turned (24)
	Mantle	*Rounded (25), *ogive (26)
	Funnel	Directed under web (27), *#directed into water (28), *directed towards external stimulus (29)
Movements	Mantle & Funnel	*#Water jet (30), *#ink puff (31)
	Head	*Head bob (32)
	Arms (number used in brackets)	Arm slap (1-2) (33), probe (1-8) (34), arm shake (6) (35), arm spread (4-8) (36), pull (4-8) (37), feel (2-8) (38), push (2-4) (39)
	Whole body	*#Jet (40), *#Crawl (41), *Shrink (42), Extend (43)
Skin Patterns	Chronic	#Grey-green-purple (44), *#chronic mottle (45), *#disruptive blotch (46)
	Acute	#Pale (47), purple (48), #reticulated (49), #pale mudbrown (50), unilateral (pale/dark) (51), #redbrown (52), grey (53)

corded at all, so the percentage of reports of colours or patterns does not represent the percentage of time during which they were maintained.

To track associations of pattern with behavioral state, the second author extracted notations of colour or pattern from observations during 1985 (520 animal-hours). There were 574 instances. When common colours or patterns were noted, 511 came from the four octopuses that had been watched throughout the day. The behavioral state of the octopus during which the patterns occurred ("Asleep", Alert, Eat, Hunt, Jet and React to Disturbance) was also recorded. The association between common skin patterns (Grey-Green-Purple, Tan, Mottled, Stripe, Dark Purple-Brown) and these behavioral states were analyzed by two chi-square analyses, one for observations on the most frequently observed octopus and one on all four. From the chi-square analysis, the deviation from expectation was converted to Z scores, and the significance of the Z-scores was computed. A significant Z score would indicate that pattern and behavior were much less or much more often associated than would be expected by chance (Kennedy, 1983). Because many (235) of the observations were from a single octopus (# 2), these analyses were done first for it alone and then for all four together.

RESULTS

Components of the octopus' skin patterns, colours and textures were catalogued in a similar manner to those of Packard & Sanders (1971) and Roper & Hochberg (1988). These were divided into Chromatic Components, Skin Textures, Postures, Movements and Skin Patterns (Table I). There were eight Components, including a Frontal white V, Eye Flash (Fig. 1D), Eye Bar (Fig. 1E) and Passing Cloud (Fig. 1A) (we did not see the lateral arm striping (8) of Packard & Sanders (1971), though Cowdry (1911) did). Skin texture varied from smooth to highly papillated. Postures, including those of Arms, Head, Mantle and Funnel, showed a great range, and the extended period of behavioral observations allowed us to catalogue a wide variety of movements of body parts. Skin patterns were also very varied, from the chronic Grey-Green-Purple during rest to the acute Mottled patterns which appeared to produce camouflage. As in other cephalopods, these components were often combined. Common combinations have been described in Table II; such combinations would produce the visual impression which an octopus gave to a vertebrate observer.

Table II. – Combinations of skin colours, patterns, textures and postures commonly observed in juvenile *Octopus vulgaris* in Bermuda.

CIRCUMSTANCE	COMPONENTS AND COMBINATION
(1) Resting	Dorsal body surface grey-green, purple chromatophores visible on ventral arm surfaces (44), arms upturned (13), skin texture smooth (9)
(2) Alert	Disruptive blotched body surface pattern (pale yellow-brown and dark purple-brown)(46), head raised (21), arms down (14), head bob (32)
(3) Hunting	Chronic mottle (45), movement by crawl (41), arms probe (34), feel (38), pull (37), web spread (36), and turned (24) in web-over, sometimes raised papillae (9) often with frontal V (1), occasionally dark (48), unilateral (51)
(4) Feeding	Disruptive blotched body surface pattern in home (46), arms pull (37), arm slap (33) and water jet (30) at scavenging fish (29), water jet (30) under web (27) and arm push (39) to expel prey remains
(5) Reaction to Disruption - in home	Body pale (47) and Shrink (42); eye bar (5) or eye flash (2)
(6) Reaction to Disruption - out	Arms spread and oriented (15), reticulated pattern (50), water jet (30) with funnel to external stimulus (29) of territorial fish Arms down (14) head raised (20) passing cloud (7) down partially spread web (15) to prey or source of disturbance
(7) Home alteration	Arms outstretched (16) and probe (34) to investigate, arms down (14) to pull (37) or push (39) rocks; water jet (30) from funnel directed under web (27)
(8) Jet Swim	Body surface pale mudbrown (51) at liftoff from bottom, adds dark stripes (6) and pale stripes (3) longitudinally down mantle and arm web after 1 second; mantle ogive (26), arms trailing (18) or with curled tips (19)
(9) To Conspecifics	(a) Body surface chronic mottle (45) with high contrast, raised papillae (9), mantle vertical (23) and ogive (26)
	(b) Body surface red (52) or grey (53), body flattened (20), web spread (36) but not turned to other octopus
	(c) Body surface red (52) body raised (22) from substrate, arms down (14) but spread (36). (Mature male approaching female)

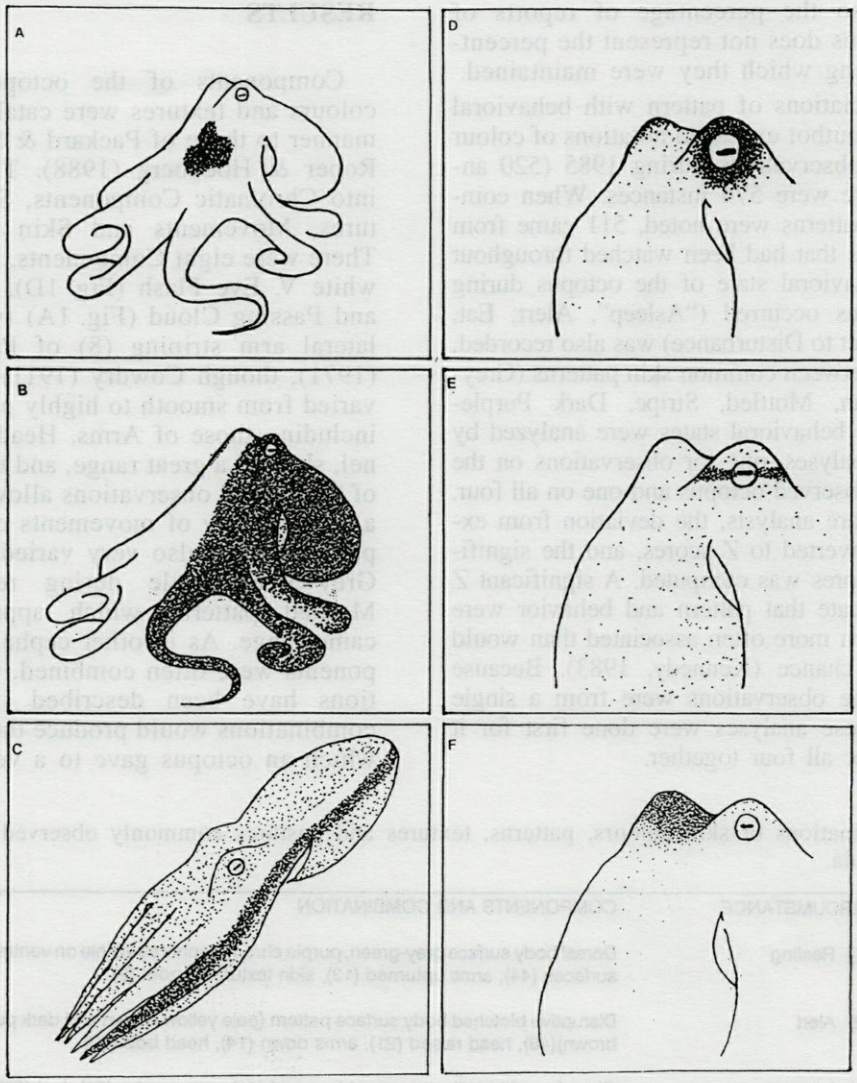

Fig. 1. – Some skin colours and patterns of juvenile *Octopus vulgaris* from Bermuda (drawings by Janet Mather).A, Passing Cloud (note that motion would be downward across the arm web).B, Half and Half. C, Stripe (note that number of stripes ranges from one to three). D, Eye Flash. E, Eye Bar. F, Frontal Hood.

The chi-square analysis was significantly different from chance both for Octopus # 2. X2 (30) = 293.4 $p < 0.001$, and for all four octopuses together X2 (30) = 351.4, $p < 0.001$. The follow-up analyses showed that four pattern-behavior associations were associated at far above a chance level ($p < 0.001$). Tan ($Z = 7.09$, $Z = 8.51$) and Stripe ($Z = 8.00$, $Z = 15.00$) were highly likely to occur during a Jet. They were present regardless of the event which precipitated the movement. Pale skin colour ($Z = 8.00, 8.51$) was highly likely to occur after a disturbance of the octopus in its home; it was not associated with spread arm web in this situation (see Table II). Grey-Green-Purple was closely associated with "Sleep" ($Z = 6.36$, $Z = 4.52$), and again had accompanying postures (see Table II). A grey-green colour was also displayed by octopuses during night-time when they were alert and part way out of their homes. The association of Mottled patterns with Hunting was less clear, significant for all the octopuses together ($Z = 3.50$) but not for the observations on # 2. This is likely because observations by many individuals, with name labels including speckled, dotted, dappled and blotched, were pooled to make this category. Subsequent observations suggest three important sub-categories: Mottled (background matching, and used when hunting), Blotched (see when the octopus was alert in the home entrance) and Reticulated (in response to the attack of small territorial fish) (see Table II).

DISCUSSION

One of the interesting aspects of patterns on the octopus skin is their associations with partic-

ular situations. Sometimes the quantitative data confirmed our impressions that a given pattern was usually expressed when an octopus was in one behavioral state. This was particularly true for the combination of Greygreen over the dorsal body with purple chromatophores visible on the ventral sides of the upturned arms, very common during "sleep" and also seen by Cowdry (1911) in this situation. It did not appear communicative; the colours may have resulted from reflection of the background by leucophores (Messenger, 1974), if the chromatophore muscles were relaxed and the pigment sacs contracted. However, this does not account for the expanded chromatophores and purple colour on the ventral surfaces of the arms (which were also noted by Cowdry (ibid) and can be seen in Packard & Sanders' (1971) Figure 9 in the same context).

A repertoire of patterns allows comparison with other species, which is especially important as the Bermuda octopuses may not actually belong to the species *O. vulgaris* (Mangold & Hochberg, 1990). Some distinctive patterns, including the Passing Cloud (Fig. 1A), were seen across species. The cross-group commonalities led Moynihan (1975) to comment on the conservatism of Cephalopod displays. The horizontal Eye Bar (Fig. 1E) is common across *O. vulgaris* (Packard & Sanders, 1971), *O. cyanea* (Roper & Hochberg, 1988) and *Eledone cirrhosa* (Boyle & Dubas, 1988). The white V spot was also noted by Packard & Sanders (1971), but there were differences in the two groups of octopuses. White areas on the frontal mantle were noticeable, but octopuses from the Mediterranean showed them as two white spots and those from Bermuda as a distinctive V. And the Mediterranean octopuses had other conspicuous white spots on the dorsal mantle, whereas these animals did not (see Hanlon's (1988) figure 2 of a juvenile *O. vulgaris* from the Gulf of Mexico).

There were differences between the two repertoires, which may have been due to the stage of maturity of octopuses or to different contexts of observation. Bermuda octopuses showed a conspicuous Eye Flash (Fig. 1D) when "annoyed" yet protected by the shelter of their home. This was not a longer-term maintained dark ring around the eye, but a very quick (less than 1 second) paling and darkening of the area immediately surrounding the pupil, similar to that seen in threatening baboons (Hall & de Vore, 1965). It might not have been seen in the laboratory or by an intrusive human observer. These octopuses showed no Hood, as described by Packard & Sanders (1971); the nearest to this was a dark extensions down from the eyes by a male adult octopus (Fig. 1F), similar to that shown by an *O. vulgaris* from the Bahamas in Hanlon's (1988) Figure 1. This pattern may only be displayed by mature octopuses. One component which may be population or species specific is the Stripe pattern (Fig. 1C). It was only seen during jet-propelled swimming, and its presence depended on the duration of the swimming. Perhaps it appeared automatically, like the red skin of *O. rubescens* during jet-propelled leaps (Warren *et al.*, 1974). This particular pattern, dark brown and white along both body and arms, varying from one to three stripes, was also seen on swimming *O. vulgaris* by Cowdry (1911), in the only other paper which described the colours and patterns of Bermuda octopuses, and is longer in extent from the horizontal striping seen on *O. cyanea* (van Heukelem, 1983, Fig. 16.1).

The extended observations allowed us to catalogue the complexity of many postures and behaviors. We saw a great variety of movements of the flexible arms, ranging from the Pull, Feel and Probe used when exploring for food (Mather, 1991) to the Shake of curled arms which appeared to shed sucker skin and the Slap which repelled scavenging fish. Some components which had been suggested as stereotyped showed variability. The Spread Web was described by Yarnall (1969) in *O. cyanea* while it was hunting (as Speculative Pounce) and by Hanlon (1988) in *O. briareus* (as a Parachute Attack). It was a common component of hunting behavior in the Bermuda octopuses (Mather, 1991), both as an initial approach to surround a rock and after an octopus had apparently contacted a prey animal with an outstretched arm tip. The octopus usually spread all the arms, but could spread only the left or right ones. And the spread web was also used when octopuses were attacked by territorial damselfish, but in this case the web was stretched widely and oriented so that its maximum area would be visible to the fish. These different used of Web Spread were accompanied by different skin pattern, a brown and white blotched Reticulated when the octopus was attacked, and an extreme paling that gave an impression of shimmering green-white in feeding. Such details of display components are important because they suggest this is a not a stereotyped Modal Action Pattern (see Barlow, 1968; Hanlon, 1988), but separate behaviors combined according to the needs of the octopus.

It was surprising not to see a single instance in the field of the Dymantic (or Deimatic (Hanlon, 1988)) posture and pattern, which has been reported for other octopuses and squid. This was in contrast to its relatively common display in captivity by octopuses from the same population. Behavior in captivity may represent a different repertoire from that in the normal environment. An example is the formation of dominance hierarchies by octopuses in captivity (Mather, 1980), when animals of the same species in the ocean were solitary and asocial (Mather, 1982). Very small *O. vulgaris* do not display the Dymantic, rather a camouflaging Flamboyant posture (Packard & Sanders, 1971). But these octopuses were larger, 100-300 gm., and capable of displaying the Dymantic in the laboratory. Oc-

topuses in their home reacted to disturbance by paling, without any postural change. When attacked by a territorial damselfish, they spread the arms and web, but the accompanying pattern was a blotchy brown and white, much like the one shown in Packard & Sanders' (1969) Figure 14 for an immature octopus. Perhaps the lab situation, with its unique combination of enclosure and threat, drew out a combination of two patterns seen in the field; Cowdry (1911) recorded the Dymantic in Bermuda octopuses but did not describe the situation.

Despite the extensive observations, there remains much to be learned about the skin colours and patterns of even this small population of octopuses. They appear to have many communicative functions, probably "aimed" at predators, prey, scavengers and even conspecific. Some, such as Stripe, seem invariant and tightly linked to a behavior, while others such as the camouflaging Mottle were very variable and may be either background matching or disruptive. And others like the Eye Flash and Passing Cloud were seen so seldom and in equivocal situations that their function can only be speculated upon. But the addition of this repertoire and these observations from the field will assist us in ultimately understanding the extent and meaning of these fascinating skin patterns.

ACKNOWLEDGEMENTS – This research was carried out with the financial assistance of N.S.E.R.C. and the Earthwatch Center for Field Research, and with the support of the Bermuda Biological Station. We would like to thank the Earthwatch volunteers who served as members of the research teams, Dr. J. Vokey for statistical advice, and Drs. F.G. Hochberg and L. Delude for critical reading of the manuscript.

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Reçu le 13 juin 1994; received June 13, 1994
Accepté le 26 juin 1994; accepted June 26, 1994