Octopus body language: body patterns of Abdopus capricornicus during social interactions.

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Abstract

Octopus are well known for their rapidly changing and diverse body patterning achieved through combinations of chromatic, textural and postural components. The function of octopus body patterns includes camouflage for prey ambush and predator avoidance, aposematic display to startle intruders and predators and potentially intraspecific communication. However, as many octopus species are often solitary animals, body patterning during intraspecific social interactions are largely unexplored. Here we start addressing this gap in one diurnal reef-dwelling species, *Abdopus capricornicus*, by providing the first detailed description of the body patterns and associated components expressed during social interactions in captivity. Importantly, this is the first study aimed at disentangling the body patterns used for camouflage from those used for communication. This was achieved by staging dyadic interactions between octopus pairs under controlled conditions in a bare sand environment devoid of rocks or algae. Furthermore, while most studies on octopus interactions focus on reproductive behaviour, here we recorded the body patterns expressed during both intrasexual (e.g. male-male, female-female) and intersexual interactions. We revealed that some body patterns and components are specifically expressed when octopuses are interacting. Furthermore, *A. capricornicus* shows the richest body patterning repertoire among coastal octopuses studied so far, including 10 body patterns which comprise 27 chromatic, 8 postural and 10 locomotory components. In addition, 19 types of social encounters were identified. We suggest that the complexity of the reef habitat and of the visual stimuli experienced by *A. capricornicus*, including social cues deriving from frequent interactions, may contribute to its patterning richness.

Introduction

Octopuses are renowned for their ability to rapidly change their body colour, skin texture and body posture, producing a wide variety of body patterns and shapes to emphasise their appearance, conceal body outline or communicate with conspecifics (Packard and Sanders 1969, 1971; Borrelli et al. 2006; How et al. 2017; Hanlon and Messenger 2018). As many coastal octopuses live in shallow waters and are under intense predatory pressure, they often spend most of their time hidden in effective camouflage to avoid potential threats and ambush prey. On the other hand, octopuses can easily switch colouration into high contrast patterns to startle predators. For example, the venomous blue-ringed octopus uses yellow and blue in an aposematic pattern to warn of a toxic bite and the algae octopus shows dark longitudinal stripes on the mantle and body to attract mates (Packard and Sanders 1969, 1971; Borrelli et al. 2006; Huffard 2007; Mäthger et al. 2012; How et al. 2017; Hanlon and Messenger 2018). The dynamic assembly of octopus body patterns is directly driven by its enlarged and complex visual and central nervous system, allowing almost instant response to various situations (Messenger 2001; Nixon and Young 2003; Barbato et al. 2007; Chung et al. 2022).

Octopus body patterns are constructed by a combination of chromatic, textural, postural and locomotory characters or “components” (Packard and Sanders 1969, 1971; Packard and Hochberg 1977; Borrelli et al. 2006; Hanlon and Messenger 2018). The chromatic components, responsible for octopus colouration, are produced by a multi-layered display system in the skin. Different colour classes of chromatophores (e.g., yellow, brown and red) located superficially in the skin are the most important elements for pigmentary colours. Under the chromatophores, two types of reflective cells, iridophores and leucophores, provide the structural colours which help match the ambient brightness and hue (Messenger 2001; Hanlon and Messenger 2018). Furthermore, within the octopus skin, muscle groups work in an antagonistic and agonistic manner, forming a dermal muscular hydrostat system which can extend or retract skin papillae to form stretchable textural features. Adding these textural components onto octopus chromatic displays, along with the associated body posture and locomotion, further increases the complexity of patterning in octopus, generating sophisticated changes in visual appearance adapted to respond to different stimuli (Packard and Sanders 1971; Borrelli et al. 2006; Hanlon 2007; Allen et al. 2014; How et al. 2017; Gonzalez-Bellido et al. 2018). One of the most common octopus body patterns for camouflage, the “Disruptive” pattern, is composed of 9 components in *Octopus bimaculoides*, including “White longitudinal central stripe” on the mantle, white “Transverse mantle bar”, “Frontal white spots”, “Mantle white spots”, “Dark hood”, “Extended eye bar” (chromatic components), prominent “Long mantle papillae”, “Eye papillae” (textural components) and “Coiled arms” (postural component) (Packard and Sanders 1969; Fig. 7,8 in Forsythe and Hanlon 1988).

Aside from enabling camouflage, dynamic body patterning has also been reported during inter and intra-specific interactions in octopuses (Packard 1961; Van Heukelem 1966, 1970; Wells and Wells 1972; Forsythe and Hanlon 1997; Huffard 2007; Huffard et al. 2010a; Scheel et al. 2016; Bello and Antunes 2020). Despite most octopus species studied so far being generally solitary for much of their life span, social interactions during competition for shelter or food were recorded in both natural habitats and captivity (Yarnall 1969; Boyle 1980; Mather 1980, 1982, 1985; Cigliano 1993; Forsythe and Hanlon 1997; Scheel et al. 2016; Bello and Antunes 2020; Humbert et al. 2022). Furthermore, mating competitions (e.g., male-male agonistic fight) and courtship displays (e.g., visual displays and physical contacts) have been repeatedly observed in a few coastal octopuses (Van Heukelem 1966, 1970; Wells and Wells 1972; Huffard et al. 2008a, 2010a; Caldwell et al. 2015; Cifuentes et al. 2023).

However, despite strong interest in octopus behaviour, description of octopus body patterns used during intra-specific interactions remains limited. For instance, body patterning during intra-specific interactions has been described in four species, and these accounts are mostly restricted to few interactions observed in captivity or opportunistically in the field (Van Heukelem 1966, 1970; Wells and Wells 1972; Huffard et al. 2008a, 2010a; Scheel et al. 2016). In addition, despite a growing number of in situ observations revealed a diversity of life modes and habits across octopus species (i.e. nocturnal or diurnal, partially social or solitary, reef or muddy habitat) (Jereb et al. 2014; Hanlon and Messenger 2018), most of our knowledge of octopus body patterns in general is limited to few coastal species (Hanlon and Hixon 1980; Huffard 2007; Mather and Alupay 2016; Hanlon and Messenger 2018), predominantly solitary and nocturnal or crepuscular species such as *Octopus vulgaris* (Packard and Sanders 1971; Packard and Hochberg 1977) and *Octopus bimaculoides* (Forsythe and Hanlon 1988). Even for the most thoroughly studied species, *Octopus vulgaris*, detailed description of intraspecific interactions and the associated body patterning remains incomplete (Packard and Sanders 1971; Borrelli et al. 2006; Bello and Antunes

2020). Furthermore, the signalling function of the patterns displayed during interactions, such as for example which patterns mediate dominance or submission, remains largely unknown.

Recent studies reported frequent intra- and inter-specific interactions in a few octopuses species (e.g., *Abdopus aculeatus* and the Large Striped Pacific Octopus) (Huffard 2007; Huffard et al. 2010a; Caldwell et al. 2015; Scheel et al. 2016). Additionally, in situ observation revealed that two diurnal reef octopus species, *A. aculeatus* and *Octopus cyanea*, possess more sophisticated social behaviours previously unseen in other octopus species. These include for example, the extended mate guarding and frequent social interactions associated with rich body patterning reported in *A. aculeatus* (Huffard 2007; Huffard et al. 2008a, a) and the sneaker mating behaviour in both *A. aculeatus* and *O. cyanea* (Tsuchiya and Uzu 1997; Huffard et al. 2008a). Another interesting case is the collaborative hunting observed between *O. cyanea* and reef fishes (e.g., wrasses, groupers and goatfishes) (Vail et al. 2013; Sampaio et al. 2021). Remarkably, the hunting relationship between *O. cyanea* and the coral trout on the Great Barrier Reef, where the coral trout performs a headstand gesture to signal the octopus where the prey hides, represents a case of referential gesture, a complex form of communication only reported in few non-human animals so far (namely corvids and apes) (Vail et al. 2013).

Delineation of the detailed ethogram of the reproductive behaviour in other cephalopod species (e.g. squid and cuttlefish) revealed that body patterns can be assembled in specific combinations to convey different meanings, suggesting they may represent a form of language (Lin et al. 2017; Nakajima and Ikeda 2017; López Galán et al. 2020). Similarly, the dynamic patterning during octopus interactions, especially in diurnal reef species showing more complex and frequent encounters, may comprise sophisticated forms of communication. Here we present the first detailed description of the body patterns and the associated behaviours of another diurnal reef octopus, *Abdopus capricornicus* (Norman and Finn 2001). *A. capricornicus* possesses an enlarged brain with distinct morphological changes in its visual and learning centres (additional foldings of the brain lobes) compared to those of nocturnal octopuses studied so far (i.e. *O. vulgaris*, *O. bimaculoides*) (Chung et al. 2022). These structural changes likely reflect advanced cognitive behaviours including sophisticated visual communication such as those demonstrated by its closely related sibling, *A. aculeatus*, mentioned above. In this study, we report the body patterns of *A. capricornicus* during interactions with a conspecific (male vs. male, female vs. female, male vs. female) under controlled conditions in captivity, along with some behavioural observations from their natural habitat (intertidal reef flats). Our findings revealed that *A. capricornicus* shows the richest body patterning repertoire among octopuses studied thus far, including 10 body patterns which comprise 27 chromatic, 7 textural, 8 postural and 10 locomotory components. In addition, 19 types of social encounters were identified.

Materials and Methods

Animal collection and care

Animal collections were conducted under a Great Barrier Reef Marine Park Permit (G17/38160.1) and a Queensland General Fisheries Permit (180731). The maintenance and experimental protocol used here were covered by an animal ethics permit (QBI/304/16). Animal handling and care was conducted following the general guidelines for care and husbandry of cephalopods in the European Union (Directive 2010/63/EU) and also the guidelines for the care and welfare of cephalopods in research by Fiorito et al. (2015).

Seventeen (8 males and 9 females, including 4 juveniles, 5 subadults and 8 adults) *Abdopus capricornicus* were collected in the days of the annual lowest tide at Coconut Beach, Lizard Island, Queensland, in August 2019 and August 2020 (Table S1). Animals were collected with hand nets and then housed in individual tanks at Lizard Island Research Station (LIRS). The opaque PVC housing tanks were enriched with sand, rocks and algae to partly replicate *A. capricornicus* natural habitat. Each tank was provided with a PVC pipe as a shelter. The number of arms of each individual were noted as this species is capable of arm autotomy (arm-dropping behaviour, Norman and Finn 2001) and may drop or lose arms during competition or predation. Octopuses were fed with frozen prawns at least twice a day. All individuals were allowed two days of acclimation in their own holding tank before starting the behavioural experiments. In order to minimize stress due to repeated handling, mantle length (size), gender and maturity of all individuals were examined under slight anaesthesia (2% magnesium chloride mixed with seawater) after completion of behavioural trials.

Behavioural observations

Behavioural experiments consisted of staged dyadic encounters between pairs of octopuses: the experiments took place in an experimental tank which contained only a 2 cm layer of sand and a PVC pipe placed in the middle of the tank as a shelter for the animals (to trigger competition over shelter). All behavioural interactions were recorded in the indoor aquarium with artificial light sources (ARLEC WLED230, 2700 Lumen). A limited habitat enrichment was chosen to reduce the display of cryptic body patterns and allow to separate body patterns used for signalling from those used for camouflage. A double-layered black curtain surrounded the experimental tank to avoid octopus behaviour being affected by visual stimuli outside the tank (i.e. the experimenter). The tank was divided in three compartments with opaque separators that could be raised manually to start the trial (Fig. S2). Two octopuses were placed separately in the acclimation compartment located at each side of the tank. Each individual was allowed at least two minutes of acclimation in its compartment without visual contact with the other individual. After acclimation, all dividers were removed to allow interactions for 30 or 50 minutes (in 2020 and 2019, respectively). Interactions were recorded with four high definition cameras (1080P resolution at 30 frames per second), including one focused on the dorsal view (Canon Powershot G1 X, Canon Inc., Japan) and three other cameras covering the lateral views (GoPro cameras (Hero 3Plus and 4), GoPro Inc., USA, Canon Camcorder Legria HF 200, Canon, Japan). After the trial, the animals were immediately returned to their original housing tank. A round-robin tournament design was employed each year in terms of each animal encountered every other animal collected in that year, resulting in a total 80 hours video for analyses (42 trials in 2019 and 90 trials in 2020).

Body patterns classification

The body patterns displayed by *A. capricornicus* individuals were analysed using the software VLC Media Player (VideoLan (2006), retrieved from https://www.videolan.org/vlc/index.html) (Fig. 1–3, Fig S1, videos S1-8 in supplementary material). Components, body patterns and the associated behaviours of *A. capricornicus* were identified following previous reports from Huffard and colleagues (2007, 2008a, 2010a) on the closely related *Abdopus aculeatus*, along with reports on the few other species described so far. In particular, we referred mainly to the reports from Packard and Sanders (1969, 1971), Packard and Hochberg (1977), Forsythe and Hanon (1988), Norman and Finn (2001), Roper and Hochberg (1988) and Borrelli and colleagues (2006). Terminology used to describe behaviours and body patterns follows that reported in the literature mentioned above. Previously-unknown body patterns were defined along with the detailed description of the arrangement of chromatic and textural components.

RESULTS

Analysis of the body patterns of *A. capricornicus* during interactions under restricted laboratory conditions led to the identification of 10 body patterns and 27 associated chromatic components (Figures 1-3). The 10 body patterns identified in *A. capricornicus* include one previously unknown pattern, Aggressive Banding (Fig 3c, Fig S1 c-d), and other 9 patterns which show some degree of similarity to the patterns described from at least one of the other coastal octopus species in the published literature (Table 2). The 27 chromatic components include 18 components that had already been described in other octopus species, of which 9 white or light components and 9 dark components (Table 1-2), along with 9 additional previously-unknown chromatic components (Table 1-2; Fig. 1-3, Fig S1). In addition, 7 textural components, 8 postural components, 10 locomotory components and 19 encounter types were also identified (Table 1).

Chromatic pattern components

New components

Nine new components were identified in *A. capricornicus*, however 5 of them were only observed in single individuals. Most of the new components were expressed in both females and males, with the exception of the 5 components observed only in a single individual each, either a male or a female, as described in detail later.

The four new components which were often seen in *A. capricornicus* include the dark components (1) mantle “Brown Dots" (BrDots), (2) "dark Eye Stripe” (ES), and the light components (3) “Ringed-White Spots on arms” (RWS), (4) “Cream Stripe” (CrStripe).

BrDots - orange-brownish spots expressed over the mantle and marking the position of major mantle papillae (Fig. 2j). BrDots were mostly observed when the animal was moving around and only rarely when interacting with the conspecific. This component was expressed continuously for a long time (i.e. several minutes) on a Uniform pattern with a Light Brown body colouration. BrDots were occasionally expressed when the animal was approaching another individual, during low-aggression interactions (i.e. simple arm touches) or during retreat.

ES - consist of dark stripes on the anterior part of the eye bulb extending vertically from the dorsal tip of the eye bulb downwards to its base (Fig. 1e, 2h). ES were observed in a few interactions in both male-male and female-female pairs. ES were expressed when a male approached another male to engage in a contest, along with a Mottle general Brown body pattern with the components “Dark Edge Suckers” (DES), “Raised lateral mantle papillae” (Rpap) and “long Mantle papillae” (Mpap) (Fig. 2h). ES were also expressed with the BWS pattern (“Pale background with dark longitudinal stripes”) and the “Chevron Stripes” (CS) component on a Clear body colour (retreating octopus) and with a weakly mottled body with other white components (i.e. “Mantle White Spots” (MWS), “White Mantle Bar” (WMB), “White Arm Bars” (WAB) and “Posterior White Triangle” (PWT, see below) or “White papillae” (Wpap) and MWS, Fig. 1e).

RWS - numerous bright white spots surrounded by a dark ring found at regular intervals along the arms starting from the arm crown just below the “Frontal White Spots” FWS (Fig. 1a-b, g, S1a,g-h). RWS were observed expressed mostly on a Mottle general body pattern during interactions with conspecifics.

CrStripe - a cream-coloured stripe extending from the anterior end of the mantle toward the location of the MWS (Fig. 1a). CrStripe was observed several times when the animal was stationary as part of a General Resemblance body pattern, or when it was moving around in the tank and rarely when approaching a conspecific. CrStripe was accompanied by a flattened body and head, WAB and a whitish mantle tip on an ochre or dark-mottled body with other indistinguishable blotches.

The remaining 5 new chromatic components identified in *A. capricornicus* were only recorded in single individuals, and included 3 light components - “Anterior White Triangle” (AWT), “Posterior White Triangle” (PWT), “White Mask” (WM) and 2 dark components - “Dark Eyebrows” and “Dark Medial Mantle Stripe”.

AWT - this small white triangle is located at the anteriormost part of the mantle where it has its base, while its apex ends in between the MWS (Fig. 1e). AWT was observed only in one female. It was observed in combination with MWS, WMB and Wpap, and together with these components provided a “Disruptive” appearance to the mantle.

PWT – this white blotch of approximately triangular shape is located at the posterior end of the mantle around the midline. PWT was observed only in one female, following physical contact from the conspecific and in a defensive posture with Arms spread and Raised body, Dark mantle, MWS, WAB, Wpap and ES (Fig. 1c), or just associated with Arms spread, MWS, WMB and a light body colouration (Fig S1e).

WM – this component is given by the homogeneous whitening of the dorsal part of the eye bulbs (Fig. 1d), and it is expressed along with the Longitudinal Mantle White Stripe running across the mantle midline (LMWS). WM was observed only in one male.

Dark Mantle Medial Stripe – thin dark stripe on the mantle from the eyes half way through the medial mantle. Expressed always on a “Mottle general Brown” pattern with Rpap, Mpap, “Supraocular papillae” (Spap), ES and DES (Fig. 2b). It was observed in one male while it attacked another male.

Dark Eyebrows - dark short longitudinal patches over the dorsal part of the eye bulbs extending slightly backwards towards the mantle. They were observed only in one female, when she was moving around in the tank after a few interactions with the conspecific (Fig 2i, S1f).

Chromatic components shared with other coastal octopus species

Among the 18 previously-known chromatic components identified, 11 had also been detected in the related *A. aculeatus* (Huffard, 2007) along with other coastal octopus species (see details in Table 2): 5 light components, “Frontal White Spots” (FWS), “White Arm Spots” (WAS), “White transverse Mantle Bar” (WMB), “dorsal Mantle White Spots" (MWS), “Longitudinal Mantle White medial Stripe" (LMWS); and 6 dark components, “Dark longitudinal Arms Stripes" (DAS), “Dark Arm Bars” (DAB), “Dark Edge Suckers” (DES), “Star Eye” (SE), “Eye Bar” (EB), and “Dark Lateral Stripe” on mantle (DLS).

DLS - DLS extends laterally from the posterior tip of the mantle to the dorsal part of the head bordering the LMWS (Fig. 2a). DLS can join the posterior part of the “Extended Eye Bar” (EEB) and when “Dark longitudinal Arms Stripes” (DAS) are also expressed these three components form a continuous dark stripe extending from the mantle to the arms (Fig 2d-e).

LMWS - a longitudinal white stripe extending medially from the posterior tip of the mantle to the head (Fig. 2a); it can also extend medially between the eyes and the first pair of arms (Fig 1d). LMWS was observed mostly on a Uniform Dark or Light Brown body colouration (i.e. “Bold Pied Stripes” pattern, Fig. 3d) often in combination with DLS (which was either unilaterally or bilaterally expressed) (Fig. 1d, 3c), and both when the animal was moving around the tank or during interaction with the conspecific. The LMWS was expressed also in combination with another component, WM, but this was observed in a single individual (Fig. 1d, 3c-d).

DAS - dark stripes extending vertically from the proximal base of the arm crown down along arms I and II (Fig. 1d, 2k, 3c,e, S1c-d). The first set of stripes extends from each eye down along the edge of the first arms (arms IR and IL); these longitudinal stripes can extend across the eye, thus merging with the chromatic component EEB (sensu Packard and Sanders 1971). The second set of stripes extends from the base of the second pair of arms downwards (arms IIR and IIL). This component is the characteristic feature of the BWS pattern.

The remaining 7 components observed in *A. capricornicus* had not yet been described for *A. aculeatus*, but are similar to those described in other octopus species (see Table 1-2). These components include “White Arm Bars" (WAB), “Pale Mantle”, “White papillae” (Wpap), “Reticulated Mantle”, “Dark Mantle”, “Extended Eye Bar” (EEB), and “Chevron Stripes” (CS).

WAB - in *A. capricornicus*, is given by groups of white transverse bars or patches at regular intervals along the arms which are formed by the coalescence of WAS. This component was expressed in combination with a variety of other components in various patterns. For example, WAB could be expressed as an additional component on a Uniform or Mottle general pattern with either a clear or dark body colour (Fig. 1a,f, S1b), as a main component of the Aggressive Banding pattern in alternation with DAB over the arms (Fig. 3c, S1c-d), and as a main component of the Disruptive pattern on a dark body.

Reticulated Mantle - is given by the expression of both the WMB and an additional transverse white bar more posteriorly on the dorsal part of the mantle (Fig. 1h). Reticulated mantle was only observed in a few occasions. For instance, it was expressed on a uniform Light Brown body colouration along with other white components (WAB, MWS), on a Mottle general Brown pattern with Wpap, WAB and DES, or when CS were expressed bilaterally.

CS - consist of transverse "aligned dark patches" along the sides of the mantle (Fig. 2d,k, 3e). These transverse dark patches can vary in their extension, and they can be expressed either unilaterally or bilaterally. The CS often appear on a uniform Clear (pale or ochre) body colour, often superimposed on the "Pale background with dark longitudinal stripes" pattern (BWS). CS were seen expressed mostly during contests with a conspecific. They can continue to be expressed for a few minutes also after the interaction has terminated.

Body patterns

Body patterns are given by various combinations of pattern components (e.g. chromatic and textural components). Ten body patterns were identified in *A. capricornicus*, including 9 previously known patterns and an additional new pattern "Aggressive Banding" which has been identified only in *A. capricornicus* so far. Of the previously known body patterns, 6 patterns had already been described both in *A. aculeatus* (Huffard 2007; Huffard et al. 2010; Norman and Finn 2001) and in other coastal octopus species. In addition, 3 more patterns had already been reported in other coastal octopus species but not in *A. aculeatus* (see Table 1 for composition details and Table 2 for comparison with other coastal octopus species). Any of the patterns described could be expressed either unilaterally or bilaterally. Three of the 10 body patterns identified were observed only in one sex (either in males or in females, see detailed description below).

New body pattern

A new body pattern, named "**Aggressive Banding**", was identified in *A. capricornicus*. This pattern, is characterised by a light brown body colouration (uniform, or weakly mottled with small white spots) with alternating WAB and DAB, and Dark longitudinal Stripes along the arms (DAS) with a pale colouration between them typical of the BWS pattern (chromatic components) (Fig. S1c-d, 3c, Video S2). Additional components that could be expressed with this pattern were MWS, WMB, DES (Fig. S1c-d), DLS, LMWS (Fig. 3c) (chromatic components), Spap (textural component) and the Raised Mantle (postural component). Aggressive Banding was expressed during interactions when approaching or attacking a conspecific.

Body patterns shared with other coastal octopus species

The pattern "***Pale background with dark longitudinal stripes***" (BWS), similar to the one reported by Huffard (2007) for *A. aculeatus*, is characterised by a uniform pale body colour (light ochre or white) with "Dark longitudinal Arms Stripes" (DAS) (Fig. 2d,k, 3e, Video S1,8); these stripes can extend also across the eye, thus merging with the EEB (sensu Packard and Sanders 1971) (Fig. 2d-e). The chromatic components CS or DLS were often expressed with BWS. The BWS pattern was normally expressed with a smooth skin, but "Supraocular papillae" (Spap) could be expressed as well (textural component).

BWS was observed only during social interactions. This pattern was usually expressed unilaterally towards the conspecific, often accompanied by CS on the same side of the body. The BWS pattern (with or without CS) expressed on a Clear or Light Brown body colouration with Spap was often displayed by males approaching a female reaching out with the third right arm or during mating (Video S1,8). The male increased the intensity of the black longitudinal stripes along the arms and often started expressing DAB in addition, if the female started moving during mating.

The "***Mottle Conflict"*** (Motcon) pattern is given by a brown or dark brown body colouration with large pale spots all over the body.

In *A. capricornicus*, various forms of this pattern have been observed: the pale large spots can be visible on a brown or dark background (i.e. Mottle Conflict Brown (MotconBr) or Dark (MotconDark)) (Fig. 3f, S1i, Video S5), or the pale spots can become much whiter and larger such as to leave only a thin dark border around them (Mottle Conflict Light, (MotconLight)) (Fig. S1j, Video S6,8). These patterns are accompanied by WAS, DES (chromatic components), usually a Smooth skin (textural component), and often "Web spread" (postural component). Occasionally, some "long Mantle papillae" can be expressed as well (Mpap). The Mottle Conflict patterns were only observed during contests with conspecifics or when the animal was disturbed in its tank, and were of brief duration (i.e. few seconds). The brown or dark brown version of the Mottle Conflict pattern (MotconBr/MotconDark) was observed expressed by the most dominant and largest male, in 2019. Lighter versions, MotconLight, were observed in males that were receiving an attack and that escaped and once in a female being approached by a male expressing the BWS pattern (Video S8).

The "**Bold Pied Stripes**" (BPS) pattern consists of a brown or dark brown uniform body colouration accompanied by a medial white longitudinal stripe along the mantle (LMWS) (chromatic component). This pattern was only seen in a few occasions when an *A. capricornicus* male was approaching or attacking (i.e. Leap or Chase) a male conspecific and never when the animal was stationary or moving around in the tank (Fig. 3d, Video S3). A variation of this pattern observed was a Light Brown body colouration with LMWS and unilateral darkening of one side of the body towards the conspecific and a Smooth skin (unilateral Bold Pied Stripes).

The “***Passing Cloud”*** (PC), consists of dark waves of chromatophores expansion from the medial mantle sidewards on the mantle and then to the arms. The PC was expressed mostly on a uniform Clear or Light Brown body colouration and a Smooth skin (textural component), but occasionally Rpap and Mpap could be raised as well. It was observed only in two females both during intra- and inter-sexual interactions. The PC was expressed several times during mating while the female was moving dragging the male around with his third arm in her mantle (Video S4).

The “***General Resemblance”*** (GenRes) pattern is usually characterised by a weakly mottled ochre or grey body with FWS, MWS, WMB, WAS (chromatic components), secondary lateral papillae (Rpap) (textural component), and often arms tucked in around the body (postural component). Occasionally, a white blotch of roughly triangular shape is also expressed just behind the head on the anterior dorsal mantle. This pattern allows the animal to resemble the surrounding environment, such as sand, pebbles or light-coloured algae.

During social interactions trials, General Resemblance was observed when the animal sat quietly usually at the beginning of the trial. Otherwise, General Resemblance was observed in the housing tank and in the field while the animal was resting camouflaged against sand, rocks or algae.

The “**Dymantic**” (Dym) pattern is characterised by a very pale or white chalk body with DAB, DES and a flattened posture with Web spread (Fig. 3b). It was expressed when the animals were startled or disturbed in the housing tank or by a male approached by another male.

The “**Uniform**” (U) body pattern consists of a uniform body colouration which could take various shades: bright white (Uniform White), light ochre or light grey (Uniform Clear), darker ochre with a yellow-orange shade (Uniform Light Brown), brown (Uniform Brown), and dark brown (Uniform Dark). This uniform body colouration was expressed without any additional spots or other chromatic components, and usually with a smooth skin (textural component), although papillae could be expressed in some cases (Rpap, Mpap, Spap). However, a variation of Uniform Light Brown with the single component Brown mantle Dots (BrDots) was observed at times when *A. capricornicus* was swimming and moving around rather than during interactions. Uniform patterns were exhibited in a variety of contexts, such as while swimming or resting, in agonistic encounters or in response to disturbance.

The “***Mottle General pattern”*** (Motgen) is characterised by a uniform body colouration of various shades (similar to the shades of the Uniform pattern: light ochre or light grey, light brown, brown or dark brown) and small white spots evenly expressed throughout the body (mantle, head and arms), including WAS (chromatic components) (Fig. 1a,f, 3a, S1a-b). This pattern was often also accompanied by WAB, DES, Rpap, Mpap and Spap. Occasionally, the chromatic components Star Eye, EB and ES could also be expressed (Fig. 2b,h). Mottle General, especially the darker shades (Motgen brown or dark), was often expressed with a Raised Body and Mantle (postural components) and when the animal was Standing tall (postural component). Mottle General was mostly expressed during agonistic interactions (Video S7).

"Disruptive-like" (or "***Acute resemblance"***) (Disr) body patterns are characterised by the expression of light and dark components including light blotches of various shapes and size producing high contrast. A common Disruptive pattern was given by a combination of MWS, WMB, Wpap, WAB and in some cases also AWT, PWT or WM, on a dark body colour (i.e. Fig. 1e, disruptive mantle). These patterns were observed only a few times, mostly when the animal was stationary in the housing tank, which provided a slightly more complex environment than the experimental tank.

Sex differences in expression of body patterns and components

Most body patterns were observed in both males and females in similar behavioural contexts. BWS was expressed in similar contexts by both males and females during intrasexual interactions, while in male-female interactions only males expressed BWS when approaching a female and during mating.

However, the body pattern Bold Pied Stripes (Fig. 3d) and the new pattern Aggressive Banding (Fig. 3c, S1c-d) were observed only in males; the Passing Cloud was observed only in females.

Most of the components described were observed in both males and females.

Components observed only in females include "CrStripe" (Fig. 1a), "Dark Eyebrows" (Fig. S1f), "AWT" and "PWT" (Fig. 1c,e, S1e). The latter two components were expressed by the same female; however, two white blotches of irregular shape in similar relative positions on the dorsal mantle were also observed in males and in other females. The component"Dark mantle Medial Stripe" (Fig. 2b) and "WM" (Fig. 1d) were both observed in one male each.

DISCUSSION

A total of 27 chromatic, 7 textural, 8 postural and 10 locomotory components were identified in *A. capricornicus* during social interactions under controlled laboratory conditions, which expressed in different combinations gave rise to various body patterns. Ten body patterns were identified in *A. capricornicus*: one previously-unknown pattern, Aggressive Banding, along with 9 patterns that share similar features with those described in other coastal octopus species.

Of the known body patterns, 6 are found also in *A. aculeatus* (Mottle Conflict named Dymantic in *A. aculeatus* by Huffard (2007) and Alarm Display by Norman and Finn (2001) in *A. capricornicus*, Dymantic named Alarm Display by Norman and Finn (2001) in *A. aculeatus*, Ochre resting camouflage or General Resemblance, BWS, Passing Cloud and Bold Pied Stripes named Dark brown with pale medial stripe by Huffard (2007) in *A. aculeatus*), while the remaining 3 had been reported in other octopus species (Uniform, Mottle General and Acute Resemblance or Disruptive).

Chromatic components

Amongst the 9 new components identified in *A. capricornicus*, “Eye Stripes” (ES), “Brown mantle Dots” (BrDots), “Cream Stripe” (CrStripe) and “Ringed-White Spots on arms” (RWS), were observed repeatedly in multiple individuals, while the other 5 new components, “Anterior White Triangle” (AWT), “Posterior White Triangle” (PWT), “White Mask” (WM), “Dark Eyebrows” and “Dark Mantle Medial Stripe”, were observed in single individuals (i.e. WM in *Abdopus* 10, AWT in *Abdopus* 7). Given the small number of individuals observed in this study, it is difficult to determine whether the latter five represent individual-specific chromatic components or components variations as noted in other cephalopods (Packard and Hochberg 1977- page 210; Huffard et al. 2008b; Byrne et al. 2010; Caldwell et al. 2015), or whether their less frequent observation is due to the restricted captive space and relatively simple surrounding scene.

BrDots were expressed mostly while the animals were not interacting; ES and RWS instead appeared to be expressed in higher aggression interactions often on a Mottle General pattern, hence they are more likely to mediate intra-specific signalling.

The DLS was considered as part of the BWS pattern in *A. aculeatus* (see Fig. 2B, Huffard 2007). However, we decided to classify DLS as a separate component as it can occur independently of BWS and of the Dark longitudinal stripes along the arms (DAS). Equivalent stripes from the mantle to the arms have been reported also in other coastal octopuses (see Table 2 for details).

The LMWS is equivalent to the “Pale medial stripe down the mantle” of *A. aculeatus* (Huffard 2007) and also found in other coastal octopus species reported under various names (see Tables 1–2 for details). In *A. capricornicus*, LMWS can be expressed on a uniform dark body colour similarly to what occurs in *A. aculeatus* (“Dark body with pale medial stripe”), in *O. bimaculoides* (“Weak Disruptive”), and in *O. cyanea* (“Bold Pied Stripes”) (Forsythe and Hanlon 1988; Hanlon et al. 1999; Huffard 2007).

The Wpap were reported as a sexual display in *O. cyanea*, expressed on a dark chocolate brown body colour prior to approaching females for mating (Mather 2004). However, in *A. capricornicus* this component was expressed during male-male interactions on a Mottle General pattern with DES and often WAB; in these cases Wpap expression may signal higher aggression intent or dominance.

The CS are equivalent to those described for *O. vulgaris* (Packard and Sanders 1971) and also reported in *O. rubescens* (Packard and Hochberg 1977). When expressed bilaterally along with Reticulated mantle, the medial pale area of the mantle resembles the "Mantle Shield" described for *O. vulgaris* (Packard and Sanders 1971).

Body patterns

The new pattern of *A. capricornicus*, Aggressive Banding (Fig. S1c-d, 3c, Video S2), shares several components with the most common “strong Disruptive” pattern displayed by *O. bimaculoides*, which is given by the combination of “White Patches” (*A. capricornicus* WAB), “White longitudinal central stripe” on the mantle (*A. capricornicus* LMWS), WMB, FWS and MWS, along with “Dark hood”, EEB (which extends along the arms longitudinally similarly to the DAS of *A. capricornicus*), prominent Mpap and Spap and “Coiled arms” (equivalent to “Arms Tucked in” of *A. capricornicus*) (Fig. 7,8 in Forsythe and

Hanlon 1988), and it may also include DAB (Fig. 9 in Forsythe and Hanlon 1988). Six out of the 10 components composing the strong Disruptive of *O. bimaculoides* are also present in the Aggressive Banding pattern of *A. capricornicus* (Fig. 3c, S1c-d). Interestingly, this pattern was observed expressed only for camouflage in *O. bimaculoides*, whereas *A. capricornicus* uses it during social interactions.

Among the patterns shared with *A. aculeatus*, the most notable is the Pale with Dark longitudinal stripes or BWS which, similarly to *A. aculeatus*, was shown by males towards the female both before and during mating (Fig. 2k, 3e, Video S1). It is worth noting that in *A. capricornicus*, BWS was also shown by both males and females during intra-sexual interactions either while approaching a conspecific, retreating or escaping from a conspecific.

A similar pattern, black longitudinal stripes extending from the eye bulbs vertically along the arms on a pale body colour, was also reported in *O. cyanea* during male-male aggression (shown by a large male when chasing a smaller male prior to a copulation attempt, Van Heukelem 1966; Wells and Wells 1972), as well as in male-female interactions shown by the male unilaterally towards the female prior to copulation (Fig. 29–31 in Van Heukelem 1966, and see Van Heukelem 1970 for high quality images) or when the female showed some resistance to mating (Van Heukelem 1966; Wells and Wells 1972). BWS was shown by *O. cyanea* when approaching another individual, irrespective of its sex, suggesting BWS functions as an aggression signal during inter and intra-sexual interactions. Furthermore, unlike *A. capricornicus* which can hold BWS for a few seconds or a few minutes, *O. cyanea* males flash BWS when approaching a female (Wells and Wells 1972).

Similar Striped patterns were reported also in *O. americanus*, a cryptic species of *O. vulgaris* in Bermuda (Cowdry 1911; Avendaño et al. 2020) and in *O. vulgaris* from the Mediterranean sea (Packard and Sanders 1969, 1971; Dominguez-Lopez et al. 2021). These Striped patterns were observed in various contexts, such as while the animal is swimming and in reaction to disturbance, but also during intra-specific interactions (Cowdry 1911; Packard and Sanders 1971; Dominguez-Lopez et al. 2021) as the BWS pattern in *A. capricornicus*, *A. aculeatus* and *O. cyanea*, although not during mating behaviour.

The BWS pattern of *A. capricornicus* differs from that of *A. aculeatus* and *O. cyanea* as it is often characterised also by Chevron Stripes (CS), similar to those described for *O. vulgaris* (Packard and Sanders 1971) and *O. rubescens* (Packard and Hochberg 1977 – Fig. 32d). These CS are displayed towards another octopus in both these latter two species as in *A. capricornicus*. For example in *O. vulgaris*, CS are expressed in the "Zebra crouch" pattern which is given by the combination of CS, EEB, DAB and WAS, arms fanned out and ogive mantle kept raised. This pattern is displayed while the octopus is approaching or moving away from a conspecific, thus it was suggested to be an intraspecific signal with a quite aggressive connotation (Packard and Sanders 1971; Moynihan 1975).

A. capricornicus BWS can also be expressed with a Dark Lateral Stripe on the mantle (DLS) in alternative to CS. This DLS is a component of the BWS pattern also in *A. aculeatus*, while in *O. cyanea* the dark longitudinal stripes have only been reported to terminate at the head region and do not extend on the mantle (Van Heukelem 1966, 1970; Wells and Wells 1972). The presence of either DLS or CS in *A.*

capricornicus may convey different meanings. Given the striking resemblance of the BWS pattern in these three species, these differences in its composition may aid in species recognition (although size difference between the larger *O. cyanea* and the smaller *Abdopus* species may be more relevant).

The Mottle Conflict pattern (Fig. 3f, S1i-j, Video S5-6,8) is shown mostly during high aggression interactions (i.e. Full attack, Arm whips), but also at times when the animal is disturbed in its tank, hence it might have a "threatening" function at least in its darker versions.

A similar pattern was called Dymantic by Huffard (2007) in *A. aculeatus*, and Alarm Display by Norman and Finn (2001) in *A. capricornicus*. However, a pattern with the same characteristics "combining dark and light uniform phases with the light areas as pale islands on a dark ground" with "papillae not extended, and arms partly extended and partly curled back" had also been previously designated Broad Conflict Mottle by Packard and Sanders (Figs. 7,14 and 8 in 1969, 1971, respectively, *O. vulgaris*) and Packard and Hochberg (1977, O. *vulgaris, O. rubescens* - Fig. 33b-d); therefore, we used the original definition and named this pattern in *A. capricornicus* "Mottle Conflict". This was done to address the lack of consistency in the literature in assigning names to similar body patterns and components, even across related species, which was also recognised by Borrelli et al. (2006). The broad Conflict Mottle of *O. vulgaris* was also suggested to be equivalent to the Acute Mottle of *O. bimaculoides* described by both Packard and Hochberg (1977, see Fig. 19) and Forsythe and Hanlon (1988, see Fig. 11) (as well as the Acute Mottle of *O. burryi*, Hanlon and Hixon 1980) and may be similar also to the Deimatic of *O. cyanea* described by Hanlon and colleagues (1999) (see also Borrelli et al. 2006).

Packard and Hochberg (1977) noted that the "conflict mottle represents a neat balance between dark and light, as if the processes of excitation and inhibition were in equilibrium". They reported that *O. vulgaris* shows this pattern when there is a "psychological conflict between a positive learned response and a negative learned response"; however, they also observed this pattern expressed unilaterally towards an approaching conspecific (Packard and Sanders 1971), suggesting that *O. vulgaris* may use this pattern during agonistic interactions as found in *A. capricornicus*.

The Bold Pied Stripes pattern identified in *A. capricornicus* (Fig. 3d, Video S3) was called "Dark with pale medial stripe" by Huffard (2007) in *A. aculeatus*. However, a similar pattern described as "a bright white longitudinal stripe running mid-dorsally from the mantle apex between the eyes and onto the arms" displayed on a very dark body colouration was previously reported by Hanlon and colleagues and named "Bold Pied Stripes" (Figs lA, 4D in Hanlon et al. 1999). Therefore, we again selected the original definition. In *A. capricornicus*, Bold Pied Stripes was observed only a few times but always when the displaying octopus was approaching, chasing or reaching towards a conspecific. Similarly, in *O. cyanea*, Hanlon and colleagues (1999) reported that Bold Pied Stripes was displayed during agonistic encounters. Unilateral expression of a similar pattern, named "weak Disruptive", was also reported in *O. bimaculoides* hatchlings with the darker side towards the conspecific (Forsythe and Hanlon 1988). Therefore, this pattern may have an intraspecific function, possibly signalling aggression. Instead, in *A. aculeatus*, this pattern was displayed with an upright mantle and was only observed in individuals drifting or crawling among the seagrass, suggesting a camouflaging function in this species (Huffard 2007). As in our study *A. capricornicus* was mostly exposed to a bare sand environment (experimental tank), it is unlikely that this pattern had a crypsis purpose in this context.

The Dymantic pattern identified in *A. capricornicus* (Fig. 3b) includes several features which are part of the classic Dymantic (i.e. extremely white body, dark edges, body flattened and web spread) (*O. vulgaris* - Packard and Sanders 1969; Packard and Hochberg 1977; Mather and Alupay 2016), although it lacks the Eye Ring typical of the Dymantic of *O. vulgaris* (Packard and Sanders 1969, 1971 - Fig. 14; Packard and Hochberg 1977) and DAB are expressed instead. Furthermore, it also seems to occur when the animal is startled. In addition, interestingly a pattern characterised by a "pale grey/green base colour with regular narrow transverse black bars along the entire length of the arms" was reported as an Alarm Display in *A. aculeatus* by Norman and Finn (Fig. 4a in Norman and Finn 2001). Therefore, it is possible that a similar pattern is also displayed by *A. capricornicus* when the animal feels threatened.

It is worth noting, that Packard and Hochberg (1977) reported that there can be both intra- and inter-individual variation in the combination of pattern components composing a specific body pattern, as some individuals show the postural components of the Dymantic pattern with a Broad conflict mottle (Fig. 14 in Packard and Sanders 1969; Fig. 26b in Packard and Hochberg 1977) instead of with the typical Dymantic pattern (dark Eye Bar, Eye Ring, DES and paling of body). It is also possible that two forms of Dymantic exists in *A. capricornicus* as it has been suggested for other species (*O. vulgaris, O. bimaculoides*, Packard and Sanders 1969; Packard and Hochberg 1977): a "mature Dymantic" where the body blanches, and an "immature Dymantic" which is more similar to the Mottle Conflict. However, it is more likely that in this case these are two very different displays as the Mottle Conflict, unlike the potential Dymantic, is often expressed during intra-specific aggressive interactions.

The Passing Cloud of *A. capricornicus* (Video S4) is similar to the PC reported for an undescribed species of *Abdopus* and for two other reef-dwelling species *O. hummelincki* and *O. briareus* (How et al. 2017), although Hanlon and Hixon (1980) described the PC of *O. briareus* as originating at one eye instead of from the mantle. In contrast, in *O. vulgaris* the PC proceeds as "a dark flush" from the head outwards over the dorsal region of the arms and web (Packard and Sanders 1971), and in *O. cyanea*, the PC starts as "a small oval" at the posterior mantle or on the head and then expands as it proceeds forward across the arms (Mather and Mather 2004).

In *A. capricornicus*, the PC was observed only in females both during intra- and inter-sexual interactions. The PC was shown by a female during mating, but its expression did not seem to alter the male body pattern or behaviour. It is thus unclear whether females display the PC as a mating rejection signal. However, in *O. cyanea* strong colour flashes (PC) were expressed by females attempting to terminate a copulation (Van Heukelem 1966).

Apart from its main function as a "distracting" signal to startle or capture the attention of potential prey (*O. cyanea*, *O. vulgaris*, Packard and Sanders 1969; Mather and Mather 2004), the PC was also reported during interactions in other species. In *O. briareus*, the PC seemed to be used in establishing dominance, as it was shown unilaterally towards a conspecific prior to contact if the conspecific did not respond (Hanlon and Wolterding 1989). In *O. bimaculoides*, Forsythe and Hanlon (1988) observed the PC expressed only by aggressive individuals during social interactions. Therefore, the PC may signal aggression intent or dominance.

The Mottle General pattern of *A. capricornicus* (Fig. 1a,f; 3a; 2b,h; S1a-b; Video S7) resembles the chronic General Mottle described by Packard and Sanders for *O. vulgaris* (1969, 1971) and by Packard and Hochberg (1977) for *O. rubescens*. In these species, the chronic General Mottle was described as given by a "fine mottling of all the skin, small light and dark patches/spots present but at low intensity". The authors also noted that the "Eye bar, Arm bars, Arm spots and the hood - especially at low intensities – are often superimposed upon the general mottle" (Packard and Hochberg 1977). This chronic General Mottle was reported as employed for camouflage, during rest, walking or swimming.

Similarly, in *A. capricornicus*, several chromatic components could be superimposed on the Mottle General, including EB and WAB (as in *O. vulgaris* and *O. rubescens*), as well as DES, Star Eye, Rpap, Mpap and Spap and the new components ES and RWS.

However, given the simple experimental environment (i.e. bare sand), Motgen was clearly not used for camouflage in *A. capricornicus*. Instead, Motgen - especially when displayed with the additional components mentioned above - was mostly expressed during agonistic interactions. Possibly in a similar way, a chronic mottle pattern characterised by high contrast, raised papillae and vertical ogive mantle was reported displayed by *O. vulgaris* juveniles towards conspecifics (Mather and Mather 1994).

As noted by Packard and Hochberg (1977), "the most highly differentiated of the patterns are achieved by combination of one basic pattern with another". It may be that this "enriched" Mottle general pattern of *A. capricornicus* is a combination of a pattern used for crypsis (the basic Mottle general) and components used for intra-specific signalling. Packard and Sanders (1969) also noted that although Acute patterns are generally short-lasting and directed towards conspecifics or disturbing stimuli, some can also be maintained for longer periods at low intensity and employed for camouflage (Packard and Sanders 1969; Packard and Hochberg 1977). Thus, the Mottle general described here may be employed for both camouflaging and signalling, depending on the context. *A. capricornicus* shares the most patterns with *A. aculeatus* (6) followed by *O. cyanea* and *O. vulgaris* (5), and the most skin components with *Octopus* vulgaris (15) followed by *O. cyanea* (12), *A. aculeatus* (11) and *O. bimaculoides* (10). In contrast, the related *A. aculeatus* was reported to share the most components with *O. bimaculoides* (Huffard 2007).

Phylogenetic studies have suggested that *O. cyanea* is a sister taxon to *A. aculeatus* and that *Abdopus* is more closely related to the *O. vulgaris* group (which includes *O. bimaculoides*) than *Amphioctopus, Hapalochlaena* and *Callistoctopus* (Guzik et al. 2005; Huffard et al. 2010b; Lindgren et al. 2012); hence these similarities in patterning may reflect shared evolutionary history and/or similar selective pressures as *Abdopus, O. cyanea, O. bimaculoides* are all fully or partially diurnal and inhabit intertidal coral (*Abdopus* and *O. cyanea*) or rocky reefs (*O. bimaculoides*); *O. vulgaris* is mostly nocturnal but was also reported as able to switch to primarily diurnal activity when needed (Meisel et al. 2006).

However, we need to note that *O. vulgaris* is the most intensively investigated octopus species, therefore more of its components and patterns may have been identified compared to other species. Detailed investigations of body patterns in a diverse range of octopus species, such as that attempted here, will allow us to determine the interplay between phylogenetic relationships and ecology of shared features (Hanon and Hixon 1980; Huffard 2007; Huffard et al. 2010b).

A. capricornicus displayed 27 different chromatic components and 10 different body patterns during intra-specific interactions, showing a patterning repertoire richer than that of all octopus species studied so far (Hanlon and Messenger 2018). The field observations also suggest that the camouflage patterns in this species are extremely rich and complex and can easily fool predators with good colour vision. Thus, the complexity of the reef habitat and of the visual stimuli experienced by *A. capricornicus*, including social cues deriving from frequent interactions and complex spatial information, may contribute to its patterning richness and the underlying morphological changes in its brain structure (Chung et al. 2022). This was originally suggested by Hanlon and Messenger (2018). They reported that combinations of chromatic and textural components differ among species, depending on many factors such as habitat, activity pattern, and behaviour (Barbato et al. 2007; Hanlon and Messenger 2018). For example, octopus species inhabiting murky habitats show less sophisticated and varied body patterns and components (i.e. *Eledone cirrhosa* shows only 1 major body pattern, “Mottled”, Boyle and Dubas 1981) than species inhabiting coral or rocky reefs (i.e. *O. vulgaris* or *O. cyanea*, 14 and 9 body patterns, respectively, Packard and Sanders 1969, 1971; Roper and Hochberg 1988; Forsythe and Hanlon 1997; Hanlon et al. 1999), and nocturnal octopus species have more limited patterning repertoire than diurnal species. Similarly in squid, social species (loliginid) show rich patterning likely due to the extensive intra-specific signalling these patterns are employed for (Lin et al. 2017; Hanlon and Messenger 2018).

Habitat complexity affects signal design in other animals as well (Barbato et al. 2007; Laidre and Johnstone 2013; Hanlon and Messenger 2018; Stoddard and Osorio 2019; Hulse et al. 2019; Nakajima and Ikeda 2017; Baling et al. 2020). For example, the body patterns of darters – a group of freshwater fish, match the visual statistics properties of their natural environment (Hulse et al. 2019), the complexity of dorsal patterning in skinks is higher with increased vegetation cover (Baling et al. 2020), and increased patterning is found in felids inhabiting more complex environments (Allen et al. 2011). However, habitat complexity can affect patterning also in the opposite direction. For example, in chameleons, species occupying more physically complex habitats (high density of stems) show reduced colour change (Stuart-Fox and Moussalli 2008) but an increase in submissive signal conspicuousness. This is possibly due to the increased cover from predators given by such a habitat, allowing the evolution of more detectable signals. Indeed, signal conspicuousness is driven by a trade-off between the need to hide due to high predation risk and the need to be detected by conspecifics especially important in highly variable and complex environments.

It is possible that the complexity of *A. capricornicus* habitat, the coral reef flat, along with a diurnal activity pattern in well-lit shallow waters and further opportunities for social interactions, has driven the evolution of complex body patterning to camouflage on diverse substrates and to convey different types of information to conspecifics. In addition, living in a complex habitat may have at the same time promoted the design of a very conspicuous intraspecific signal such as the BWS in order to enhance detectability by conspecifics.

Limitations and future directions

Limitations of the study include the small number of individuals examined which prevented further characterisation of some components and patterns. In addition, the study was conducted in captivity under controlled conditions and mostly focused on intra-specific interactions. Field observations of *A. capricornicus* are needed to corroborate the behaviours and patterns observed here and to provide a complete ethogram for this species.

This study represents the first part of a more comprehensive investigation of body patterns associated with intraspecific interactions in *A. capricornicus*. In the following study, we will describe the sequence of patterns and associated behaviours (i.e. dominance) during male-male interactions in this species.

Declarations

COMPLIANCE WITH ETHICAL STANDARDS

Animal collections were conducted under a Great Barrier Reef Marine Park Permit (G17/38160.1) and a Queensland General Fisheries Permit (180731). The maintenance and experimental protocol used here were covered by an animal ethics permit (QBI/304/16). Animal handling and care was conducted following the general guidelines for care and husbandry of cephalopods in the European Union (Directive 2010/63/EU) and also the guidelines for the care and welfare of cephalopods in research by Fiorito et al. (2015).

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Competing interests

The authors declare no competing interests.

Author contribution

G.S. conceived and designed the study, carried out the experiments and analysed the behavioural videos. W.-S.C. provided feedback on the experimental design and data analyses. All authors carried out animal collection from the field. G.S. drafted the manuscript with feedback and support from W.-S.C.. W.-S.C. and J.N.M. supervised the study, revised the manuscript draft and contributed to the final version of the manuscript. All authors provided critical feedback and helped shape the research, analysis and manuscript.

Data availability

Supplementary material is available online at https://espace.library.uq.edu.au/view/UQ:0ff1ff4. Data will be made available on reasonable request.

Ethics approval

Animal collections were conducted under a Great Barrier Reef Marine Park Permit (G17/38160.1) and a Queensland General Fisheries Permit (180731). The maintenance and experimental protocol used here were covered by an animal ethics permit (QBI/304/16). Animal handling and care was conducted following the general guidelines for care and husbandry of cephalopods in the European Union (Directive 2010/63/EU) and also the guidelines for the care and welfare of cephalopods in research by Fiorito et al. (2015).

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Tables

Tables 1-3 are available in the Supplementary Files section.

Figures

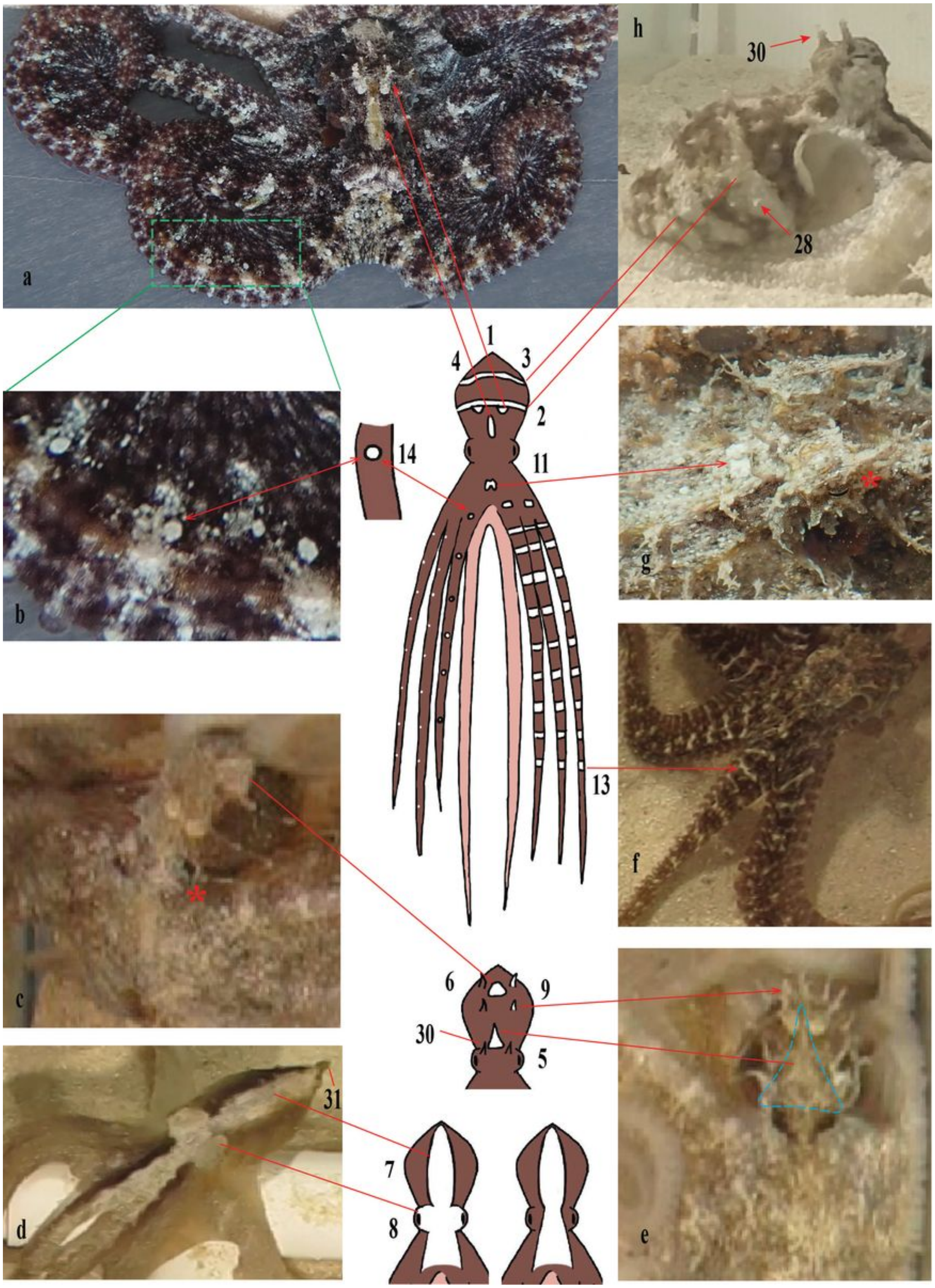

Figure 1

White components of *A. capricornicus*. a) White components Mantle White Spots (MWS) (1), Cream Stripe (CrStripe) (4) and Ringed-White Spots (RWS) (14) on a Mottle general pattern; b) close-up of Ringed-White spots (RWS) (14); c) Posterior White Triangle (PWT) (6) (the position of the eyes is indicated by a red asterix); d) Longitudinal Mantle White medial Stripe (LMWS) (7), White Mask (WM) (8) and Posterior papilla (Ppap) (31); e) Anterior White Triangle (AWT) (5) and White Papillae (Wpap) (9) on a

Disruptive mantle; f) White Arm Bars (WAB) (13) on a Mottle general pattern; g) Frontal White Spots (FWS) (11) on a General Resemblance pattern (the position of the eye is indicated by a red asterix); h) White transverse Mantle Bar (WMB) (2), Reticulated Mantle (3) and Supraocular papillae (Spap) (30)

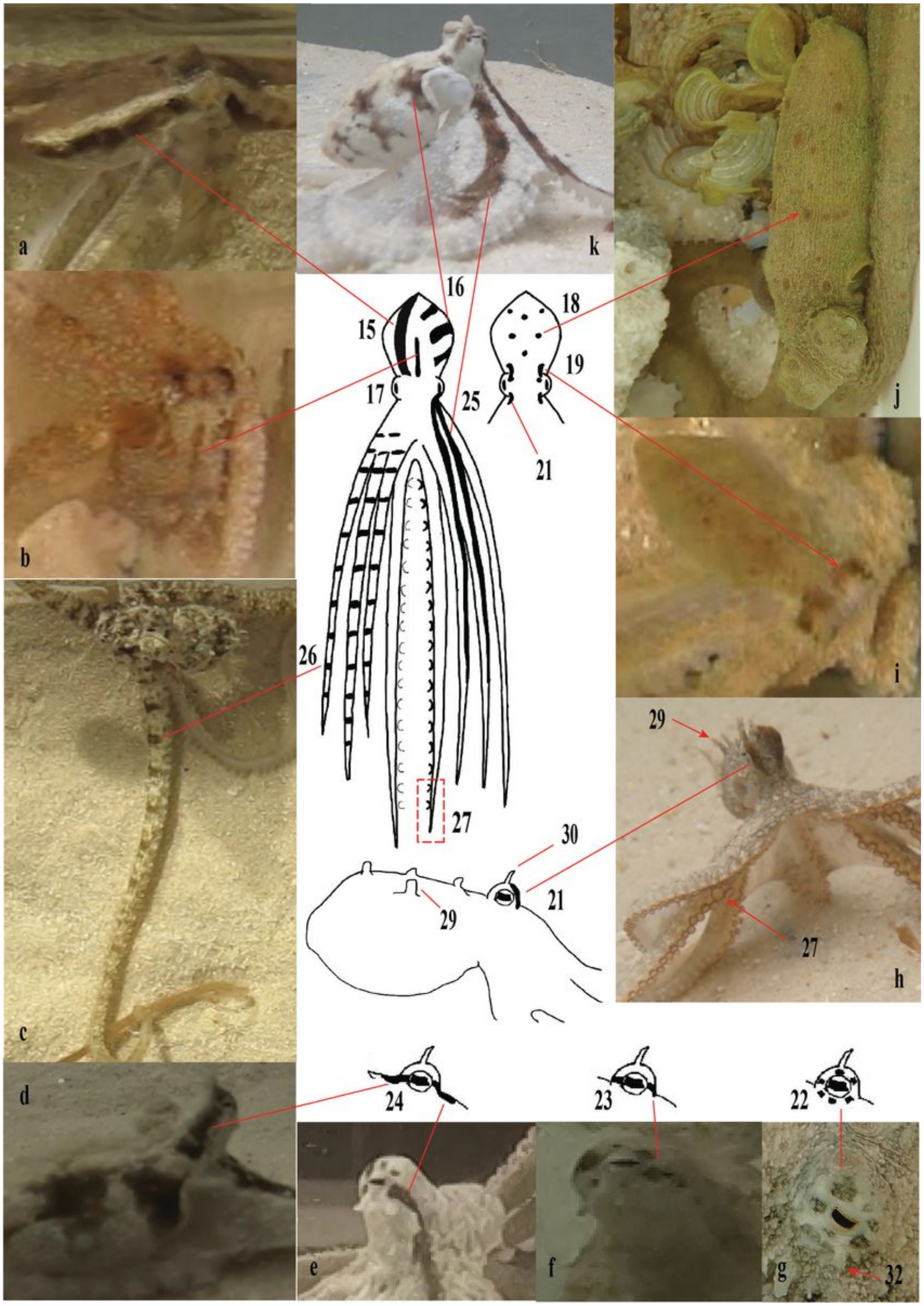

Figure 2

Dark components of *A. capricornicus*. a) Dark components Dark Lateral mantle Stripe (DLS) (15); b) Dark Mantle Medial Stripe (17); c) Dark Arm Bars (DAB) (26); d-e) Extended Eye Bar (EEB) (24) (in d) Chevron Stripes (CS) on the mantle can be seen as well); f) Eye Bar (EB) (23); g) Star Eye (22) and Sub-ocular papilla (32); h) Eye Stripes (ES) (21) and Dark Edge Suckers (DES) (27); i) Dark Eyebrows (19); j) Brown mantle Dots (BrDots) (18); k) Chevron Stripes (CS) (16) and Dark longitudinal Arm Stripes (DAS) (25) (BWS pattern)

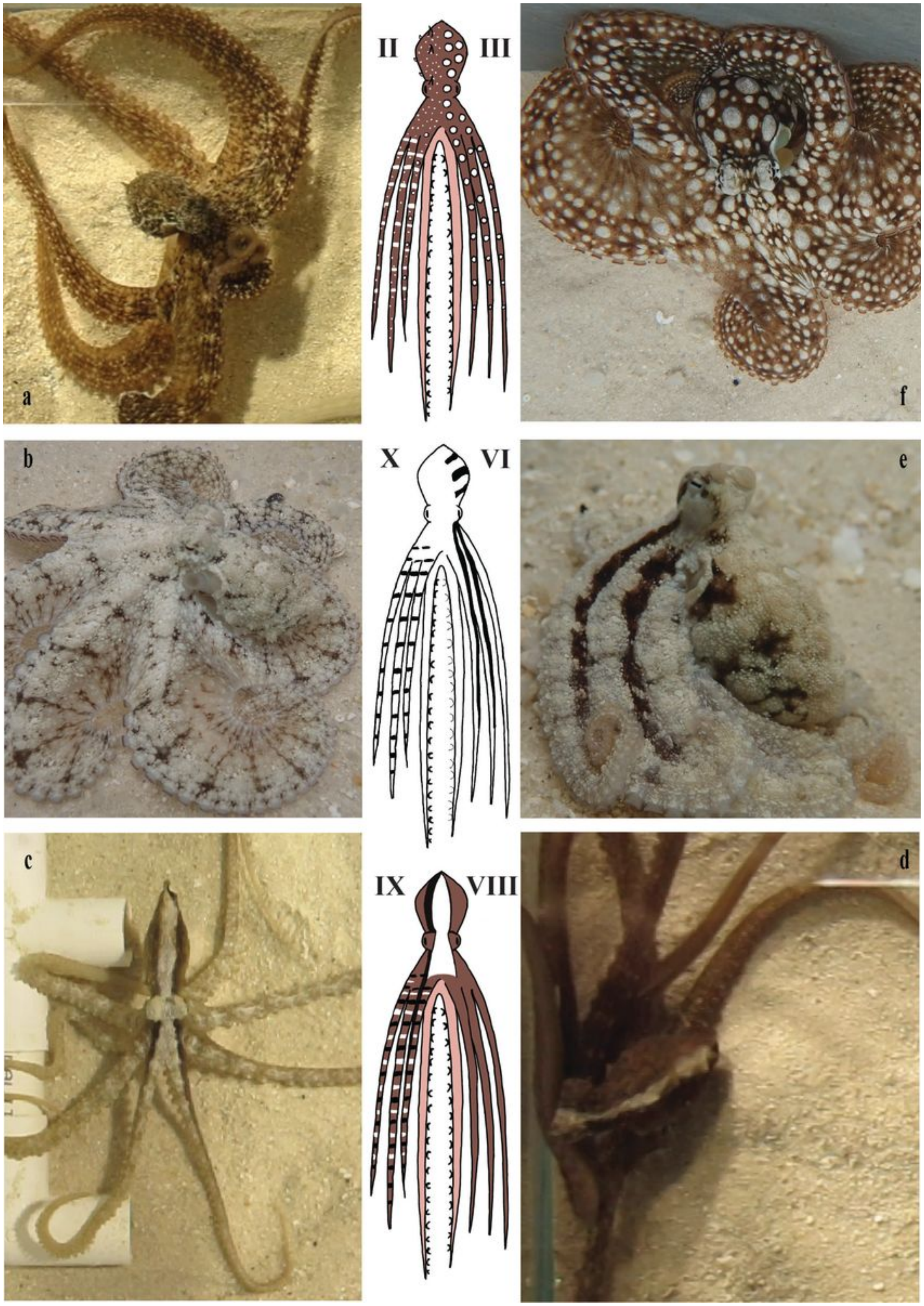

Figure 3

Body patterns of *A. capricornicus*. a) Mottle general brown (Motgen) (see also Video S7) (II); b) Dymantic (X); c) Aggressive Banding (AggrBand) with Posterior papilla (Ppap) visible at the posterior tip of the mantle (IX) (see also Video S2); d) Bold Pied Stripes (VIII) (see also Video S3); e) Pale with dark longitudinal arm stripes (BWS) (VI) (with Chevron Stripes (CS)) (see also Video S1,8); f) Mottle conflict dark (III) (see also Video S5,6,8)

Supplementary Files

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