

# Cuttlefish camouflage: context-dependent body pattern use during motion

S. Zylinski<sup>1,\*</sup>, D. Osorio<sup>1</sup> and A. J. Shohet<sup>2</sup>

<sup>1</sup>*School of Life Sciences, University of Sussex, Brighton BN1 9QG, UK*

<sup>2</sup>*Stealth Materials Group, QinetiQ, Cody Technology Park, Farnborough GU14 0LX, UK*

It is virtually impossible to camouflage a moving target against a non-uniform background, but strategies have been proposed to reduce detection and targeting of movement. Best known is the idea that high contrast markings produce ‘motion dazzle’, which impairs judgement of speed and trajectory. The ability of the cuttlefish *Sepia officinalis* to change its visual appearance allows us to compare the animal’s choice of patterns during movement to the predictions of models of motion camouflage. We compare cuttlefish body patterns used during movement with those expressed when static on two background types; one of which promotes low-contrast mottle patterns and the other promotes high-contrast disruptive patterns. We find that the body pattern used during motion is context-specific and that high-contrast body pattern components are significantly reduced during movement. Thus, in our experimental conditions, cuttlefish do not use high contrast motion dazzle. It may be that, in addition to being inherently conspicuous during movement, moving high-contrast patterns will attract attention because moving particles in coastal waters tend to be of small size and of low relative contrast.

**Keywords:** motion; camouflage; dazzle; cuttlefish; vision

## 1. INTRODUCTION

It is not by chance that such highly developed creatures as frogs would starve amidst plenty if the prey did not move.  
(Julesz 1971, p. 105)

Even when the texture of a target and background match perfectly, movement attracts attention and allows rapid figure–ground segregation in the visual system of many animals (Julesz 1971; Srinivasan *et al.* 1990; Frost 1993; Smith & Snowden 1994). Animals that rely on camouflage may minimize visible movement through strategies such as stealth and deceptive resemblance (Cott 1940), but often this is not possible. How then do animals reduce the risk of predation as they move?

Given the difficulties of remaining undetected during movement, an alternative strategy is to concentrate efforts on avoiding capture once detected. High-contrast dazzle markings, or ‘motion dazzle’, are proposed to foil capture by interfering with motion detection mechanisms, and hence misleading the viewer as to the direction and/or speed of movement (Stevens *et al.* 2008; Troscianko *et al.* 2009). Despite their counterintuitive appearance, dazzle markings have a longstanding military application, used by the British and American navies in World War I to disguise the speed and direction of ships (Behrens 1999). Similar optical effects may be conveyed by the zigzag markings of snakes, which are believed to provide camouflage or aposematism (depending on viewing distance) to a stationary animal and a dazzle or flicker–fusion optical effect to a moving animal (Ruxton *et al.* 2004).

Although included in the seminal camouflage literature (Thayer 1909; Cott 1940), theories surrounding the role of high-contrast patterns in hindering recognition and/or

capture had until recently remained untested in the published literature. Stevens *et al.* (2008) gave empirical evidence that some dazzle markings hinder the targeting ability in human ‘predators’ attempting to capture artificial ‘prey’ in a computer game. They demonstrated that both background complexity and pattern configuration play important roles in thwarting capture. Certain conspicuous markings conveyed protection from targeting prey while others did not. However, it was clear that targets matched to the background in terms of mean luminance were significantly harder to capture than any target carrying conspicuous markings. In these experiments, the conspicuous markings did not act to break up the body outline, and differences in the detectability of static targets were not tested, but it might be assumed that certain dazzle markings could convey static disruptive camouflage to a target on more complex backgrounds. We return to the relationship between motion dazzle and camouflage in §4.

Cephalopod molluscs, particularly benthic species of cuttlefish and octopus, are masters of adaptive camouflage. These animals rapidly alter their body coloration and physical skin texture to match a given environment primarily via neurally controlled and visually driven chromatophores (Hanlon & Messenger 1996). Cephalopods often change their appearance when they move, presumably to avoid detection during or after the movement. For example, octopus uses a combination of stealth and rapid chromatic and textural changes as they move, apparently to match the changing background (Hanlon *et al.* 1999).

Here we use the capacity for rapid pattern change in the cuttlefish *Sepia officinalis* to investigate the potential for motion camouflage and/or dazzle by an animal that can alter its body pattern in less than a second (Hanlon & Messenger 1996). We assessed changes in

\* Author for correspondence (s.zylinski@sussex.ac.uk).

body coloration during movement over a periodic stimuli (checkerboard patterns), for which we have a good understanding of static body patterns. On a fine-scale checkerboard stimuli, these animals use a body pattern described as mottle (figure 2c(ii)), which is formed from irregular, alternating patches of light and dark skin of roughly the same scale as light and dark patches in the visual background, and therefore consistent with a background matching camouflage pattern (Barbosa *et al.* 2007; Stevens & Merilaita 2009a). On coarse-scale checkerboards, animals use the so-called disruptive body pattern (figure 2c(i)) (Chiao & Hanlon 2001; Barbosa *et al.* 2008), which consists of larger scale contrasting light and dark features with clear borders. The disruptive pattern may have a disruptive camouflage function (breaking up and/or distracting attention away from the body outline) at high levels of expression, but is most likely used in background matching at lower levels of expression (Hanlon *et al.* 2009; Stevens & Merilaita 2009b; Zylinski *et al.* 2009). Based on the current understanding of body coloration and movement, there are four separate strategies a cuttlefish might use during motion, which are outlined in figure 1. Briefly, an animal starting from a stable, static body pattern (a), assumed to be the most appropriate camouflage for the given background, might (b) maintain the same pattern during movement; (c) use another 'recognized' pattern less well matched to the background features; (d) use a conspicuous high contrast pattern that may be a 'motion dazzle' pattern or (e) attempt to dynamically match background features as it moves over them (if moving on a visually heterogeneous background). If the animal resettles on a visually similar background following movement then it might: (f) return to, or retain, the original stable body pattern or (g) use a different (presumably sub-optimal) pattern to reduce search image formation (whereby a predator learns characteristic features of prey and searches for these during hunting).

## 2. MATERIAL AND METHODS

### (a) Animals

Cuttlefish were hatched from eggs collected from the south coast of England and housed in purpose built facilities at the SeaLife Centre, Brighton, UK. Animals were fed ad libitum on mysids and naupliids, and maintained under a 12:12 L:D lighting regime. Subjects were approximately five months old at the start of experiments with mantle lengths 50–60 mm. Images of animal body patterns in response to stimuli were collected by digital video camera (Canon XL1S) in an enclosed filming tank designed to prevent any disturbance during experiments. Lights were arranged to give even illumination and images were taken from a mirror at a 45° angle above the tank. Test stimuli were placed under and around the edges of the circular test arena of 250 mm diameter, 100 mm deep in sea water. Individual animals were transferred from the holding tank to the test arena, with images collected after the animals had settled and the body pattern expressed had remained stable for at least 10 min. Ten naive animals were used in the experiment, and data were pooled as animals were housed together due to space limitations. Both stimuli were tested on three separate occasions, with individual animals not returned to the holding tank until all ten animals had been tested, thus ensuring

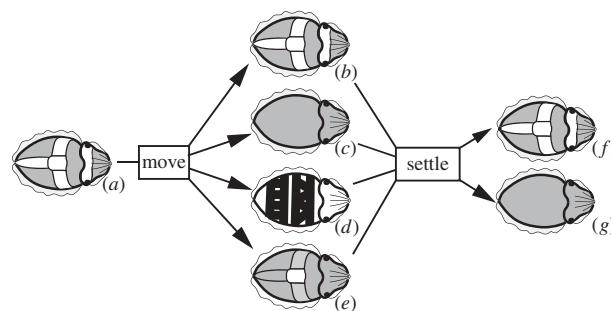


Figure 1. Schematic of possible 'solutions' for moving cuttlefish based on literature of camouflage and motion. (a) Settled animal produces a stable body pattern in response to cues in the visual environment, here represented by a disruptive pattern. When the animal moves, there are four main strategies it can adopt given its capacity for rapid adaptive coloration change: (b) it can retain the same body pattern as used when static; (c) it can use another of the main body pattern categories (i.e. mottle or uniform); (d) it can use a very different pattern, for example, high-contrast components in a striking configuration, which might function as motion dazzle markings; (e) it might use a range of components to attempt to maintain an exact match to the background it is moving over. On ceasing movement and settling back on the substrate, the animal might adopt one of two strategies (assuming the background is visually comparable to that settled on before movement): (f) it might use a pattern identical to that it started with; (g) it might take an 'apparent rarity' approach and use a pattern of another category.

no individual was tested more than three times on each stimulus.

### (b) Data collection

We used two stimulus types, consisting of high-contrast checkerboard patterns each of a size predetermined from work on static camouflage (Zylinski *et al.* in press) to promote either the mottle body pattern (small checks, 4 mm<sup>2</sup>) or the disruptive body pattern (large checks, 10 mm<sup>2</sup>), both at 0.80 Michelson contrast. Printed stimuli were placed on the floor and around the walls of the test arena. Images were taken of settled body patterns after ten minutes of stable expression, then animals observed and recorded using video if they subsequently began to move around the arena. If animals did not move within 30 min of observation, the trial was ended. Successful trials consisted of one recorded episode of movement; an episode was regarded as a single movement event, from an animal moving from a settled position to subsequently resettling. A further image was taken of the post-movement body pattern once this had remained stable for over a minute. Recorded episodes of movement lasted between 5 and 60 s, with an average of 17 s. Movement episodes of less than 5 s were discarded as these were often resettling forward-and-backwards movements not consistent with longer episodes. Any change in the body pattern observed tended to coincide with the start of movement. As the body pattern used by an individual during movement appeared to be stable, a single still frame from the midpoint of the video sequence for each movement episode and taken forward for analysis.

Twenty-seven movement episodes were recorded on the small check stimulus and 23 on the large checks. This resulted in 150 images: 50 episodes of movement, with three images per episode giving the body pattern before,

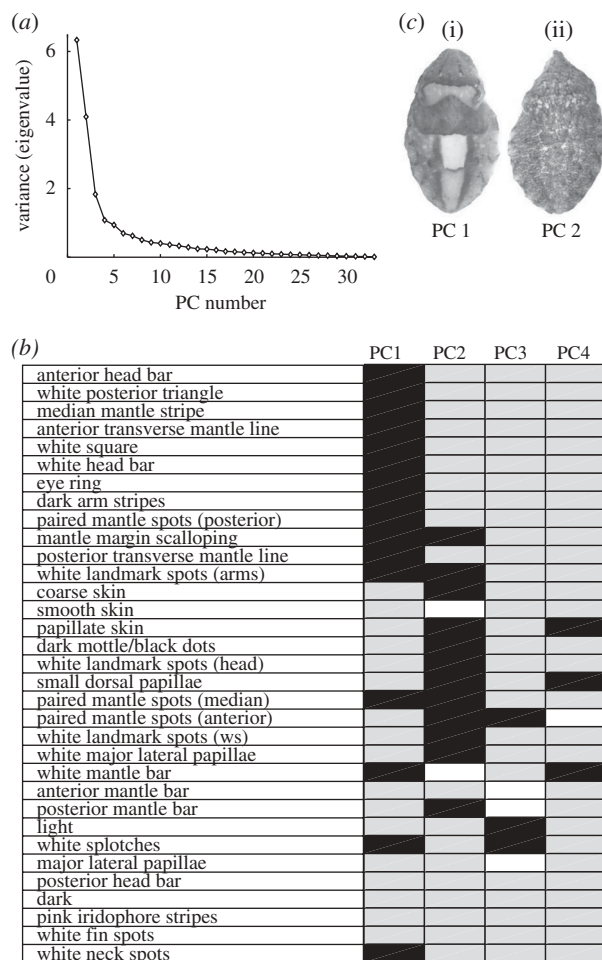


Figure 2. (a) Scree plot of variance accounted for by all PCs, showing that only the first four are meaningful; (b) body pattern components (based on those described by Hanlon & Messenger 1988) with highly positive or highly negative associations (loadings) with PCs 1–4. A threshold of 0.4 has been applied to clearly highlight those components providing an important contribution to each PC; (c) body patterns representative of strong (i) PC 1 and (ii) PC 2, which are similar to the disruptive and mottle body patterns. PCs 3 and 4 do not relate to recognizable body patterns (see text) and cannot be easily illustrated as they co-occur with PC 1 and 2 attributes. Black shade, +0.40 to +1.00; grey shade, –0.39 to +0.39; white, –0.40 to –1.00.

during and after the movement. Images of animals were cut out from the background to avoid bias during grading. Each image was graded manually for the expression of 33 chromatic and textural body pattern components on a four-point scale with 0 = not expressed and 3 = strongly expressed (Kelman *et al.* 2007; Zylinski *et al.* 2009). These were based on the components described by Hanlon & Messenger (1988, 1996) with some adaptations. For example, the chromatic component described by Hanlon & Messenger (1988) as ‘paired mantle spots’ was expanded to separately score anterior, median and posterior paired mantle spots (figure 2b) as the strength of expression of these dark spots can be independently varied (Kelman *et al.* 2008). Similarly, we introduced categories of ‘light’ and ‘dark’, as there were occasions where the overall brightness of a body pattern appeared comparatively lighter or darker than the ‘usual’ brightness level regardless of the components expressed. All body pattern responses for all stages were entered into a

principal component analysis (PCA). Resulting coefficients were used to test for differences between body patterns used.

### 3. RESULTS

#### (a) PCA

We graded 33 body components of cuttlefish before, during and after movement on two backgrounds of check sizes (small or large) chosen to promote either mottle- or disruptive-type responses. Twenty-seven movement episodes were recorded on the small check stimulus and 23 on large checks. Four principal components (PCs) were retained under the Kaiser criterion of retaining those PCs with a variance greater than 1 (Jolliffe 1986) (figure 2a). These accounted for over 65 per cent of the variance contained in the original dataset, with PC 1 accounting for 32 per cent and PC 2 for 21 per cent, respectively. PCs 3 and 4 accounted for 9 per cent and 5 per cent of the variance within the original dataset, respectively.

PC 1 corresponded to the so-called disruptive body pattern and PC 2 to the mottle body pattern (figure 2b,c; Hanlon & Messenger 1988, 1996). As previously observed, backgrounds composed of ‘large’ checks (more than 70% of the area of the white square (WS) component) characteristically resulted in a high PC 1 static responses, while ‘small’ checks (less than 70% of WS component) resulted in a high PC 2 static responses (Kelman *et al.* 2007, 2008; Zylinski *et al.* in press). PCs 3 and 4 do not correspond to a recognizable body pattern (figure 2b) and this is discussed below.

#### (b) Body pattern use

We used the PCA coefficients obtained by scoring individual body pattern components of 10 animals to compare body pattern use when static to when moving on two sizes of checkerboard background. Comparing the PC scores of settled body patterns used prior to movement with those used when the animals resettled after episodes of movement showed no significant differences on any PCs, regardless of the stimulus size or starting body pattern (figure 3a; ANOVA: small checks  $F_{1,36} = 0.02$  for PC 1,  $<0.01$  for PCs 2 and 3 and 0.57 for PC 4;  $p > 0.1$  in all cases. Large checks  $F_{1,42} = 0.08$ , 0.04, 0.06, 0.41 for PCs 1–4, respectively;  $p > 0.1$  in all cases).

Animals moving on the small check stimulus showed no significant differences in the body patterns used compared with those used pre- and post-movement for PCs 1, 2 and 4 (figure 3a; ANOVA  $F_{2,54} = 0.61$ , 0.02, 0.39 for PCs 1, 2 and 4, respectively,  $p = > 0.1$  in all cases). This equates to the maintenance of a very similar body pattern during movement to that used when settled (figure 3b(i)). However, a significant difference was found for PC 3 responses ( $F_{2,54} = 5.76$ ,  $p = 0.005$ ), with PC 3 characteristics reduced during movement (figure 3a). On the large check stimulus, significant differences were found in PCs 1 and 3 for moving animals compared with those used pre- and post-movement (PC 1:  $F_{2,63} = 31.69$ ,  $p \ll 0.01$ ; PC 3:  $F_{2,63} = 12.41$ ,  $p \ll 0.01$ ). This is due to a significant reduction in PC 1 characteristics (i.e. disruptive components were significantly reduced) and increase in PC 3 characteristics (figure 3b(ii)). No significant differences were found in PC 2 or 4 for animals moving on the large check stimuli



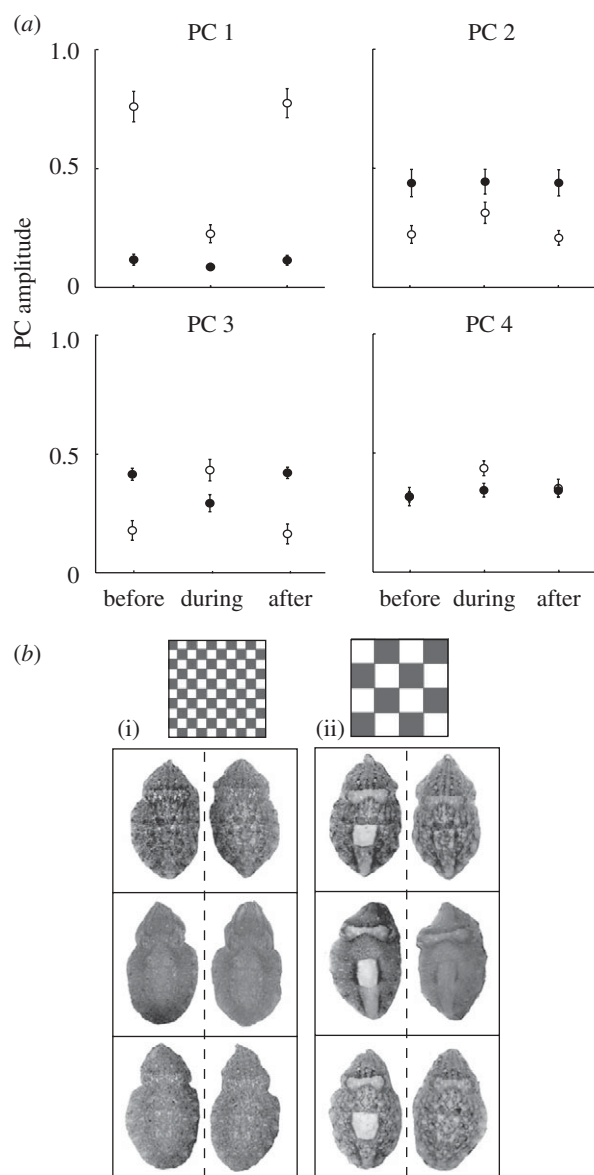


Figure 3. (a) PC amplitudes  $\pm$  s.d., for responses before, during and after movement for PCs 1–4 on small and large checkerboard stimuli (rescaled between 0 and 1). Closed circles, small checks; open circles, large checks. (b) Examples of body pattern responses before (left) and during (right) movement in each box (post-movement examples are not shown as these were not significantly different from before movement in either group). Three examples of different individuals are shown in each row for the two background types: (i) small checks from mottle patterns; (ii) large checks resulting in a static pattern containing high-contrast disruptive components.

(PC 2:  $F_{2,54} = 1.20$ ,  $p = 0.31$ ; PC 4:  $F_{2,54} = 2.87$ ,  $p = 0.0741$ ; figure 3a). This significant decrease in PC 1 attributes, but a small increase in PC 2 attributes on large checks, suggests that animals tend to reduce the intensity of disruptive components without a corresponding increase in mottle components. Previous work has shown that combined low PC 1 and PC 2 scores are indicative of uniform body patterns (expression of few or no chromatic components) (Hanlon & Messenger 1988; Zylinski *et al.* 2009), so animals tended to reduce the intensity of components associated with PC 1 and move towards a uniform pattern when moving on this stimulus.

As the expression of PC 4 did not change significantly during movement on either stimulus, and accounts for only 5 per cent of the variance in the data, we will not consider it further. However, PC 3 is of more interest as its expression is significantly different during movement for both stimuli, but in opposite directions: on small checks, the expression of associated components are significantly reduced during movement, while for large checks they are significantly increased (figure 3a). Several of the chromatic components with high positive weightings for PC 3 are generally associated with the mottle pattern, namely ‘anterior paired mantle spots’ and ‘dark mottle/black dots’. Several other components contributing positively to PC 3 are light but small-scale components such as ‘white splotches’ and ‘light’.

#### 4. DISCUSSION

Figure 1 illustrates a range of possible scenarios for body pattern use by a moving cuttlefish. The experimental results show that two of these scenarios are used; the body pattern used during movement is context dependent and may be visually distinct from that used when the animal is stationary relative to the background on which it rests (figure 3). If the static body pattern used prior to and following movement contains large, high-contrast disruptive components, then animals significantly alter their camouflage pattern during movement, predominantly by reducing the intensity of expression of these disruptive components. However, if animals use a static body pattern containing few and/or small-scale light and dark components (mottle), then this is retained while moving. We found no evidence here of novel high-contrast patterns being used during movement (strategy (d) in figure 1).

If we presume that cuttlefish ‘choose’ their body patterns to maintain optimum camouflage in a given visual environment, then our results suggest that low contrast and/or small-scale patterns offer the best protection from predators during movement, even when the optimal static camouflage strategy for that visual environment is to use larger scale high-contrast disruptive components. An alternative explanation is that physiological (optical/neurological) limitations constrain the speed at which the animal can process sensory input. This would result in visual blur and the background being perceived as homogeneous/lower contrast during movement, causing the cuttlefish to adopt a sub-optimal strategy.

Little literature exists on this subject; however, observations of the reef cornetfish (*Fistularia commersonii*) suggest that this fish expresses a disruptive band pattern when stationary, but rapidly changes to a uniform silvery coloration when in motion (Thomson *et al.* 2000, in Rosenthal 2007). Teleost body patterns are not under the same rapid visual control as those of cephalopods, and so this evidence supports a functional role to reducing high-contrast components rather than a physiological limitation. A study of pattern use in response to orientated visual backgrounds (stripes) by the tropical cuttlefish *Sepia pharaonis* found that orientation had no effect on the patterns displayed (Shohet *et al.* 2006). Consistent with our results, the authors proposed that a body pattern without stripes would minimize relative motion signals, as motion between the stripes on an animal’s back and the background would be highly visible.

It has been suggested that *Octopus cyanea* uses polyphenism via camouflage, conspicuousness and mimicry to maintain 'apparent rarity' of any single phenotype when movement is necessary in coral reef habitats (Hanlon *et al.* 1999). In the present study, it might follow that an individual animal could benefit from using a different body pattern during movement, thus confusing potential predators via coloration changes on a short-term temporal scale. A second possibility relates to more traditional search image theories (Tinbergen 1960; Bond & Kamil 2002), whereby frequent changes in appearance will prevent predators from recognizing an object as prey based on reoccurring visual features. For the tactic of polyphenism to fully explain our results, we would expect to see alternative patterns being used during movement irrespective of the static pattern used before movement. That these results show these changes occurring only for high-contrast static patterns suggest that an alternative explanation is needed.

Given the strong visual cues provided by high-contrast stimuli, particularly during movement, it seems intuitively logical that an animal capable of reducing potentially conspicuous markings should act to do so. However, Stevens *et al.* (2008) showed that targets that match the background (in this case for luminance) during movement suffered the lowest capture rate of all target types, suggesting that background matching is the optimal strategy. As high-contrast, edgy body Disruptive components are only used by *S. officinalis* on high-contrast backgrounds containing edgy objects, we might assume that these markings are optimal in terms of luminance and spatial matching for this visual environment, and therefore that it might be detrimental to reduce the extent of background matching in view of Stevens *et al.*'s results. However, the significant increase in PC 3, associated with a small number of small-scale light and dark chromatic components, during movement on large checks may be an indication of animals attempting to maintain the same overall luminance while reducing large-scale high-contrast chromatic components such as the 'white square' and 'white mantle bar' (figure 2).

The tendency to reduce high-contrast components may reflect the physical properties of the visual environment in which *S. officinalis* and its predators are found. For example, benthic coastal regions of the UK, where cuttlefish are commonly observed, are subject to tidal currents and wave-driven swells that can cause scene motion even in relatively deep waters. Personal observations (S. Zylinski) suggest that such environmental motion often results in the movement of seaweeds, small substrate particles and biological matter, all of which tend to reflect light at low intensities. Conversely, edgy areas of high contrast tend to be associated with larger objects such as pebbles and shells (figure 4), which are less susceptible to being moved by the surrounding water (Troschianko *et al.* 2009). The Gestalt laws of perceptual organization show that image regions are grouped by common fate; image components that move together tend to be grouped together (Bruce & Green 1990). Therefore, the visual system of a potential predator is less likely to be sensitive to the movement of small-scale, low-intensity stimuli, such that a mottle body pattern will blend into background noise, both spatially and temporally. However, disruptive

components resemble background objects in which movement is uncommon, so may act as a rare/novel stimulus and therefore attract attention when in motion.

Until recently, the tendency in the camouflage literature has been to label all body patterns that contain high-contrast elements that touch the body outline as 'disruptive', under the implied assumption is that such markings convey what Cott (1940) described as 'maximum disruptive contrast' (Cuthill *et al.* 2005; Stevens *et al.* 2006). High-contrast patterns are often used by animals that frequently move (e.g. stripes on zebra and many species of fish) and may in fact have a more common function in motion dazzle. Furthermore, high-contrast markings may be compatible/incorporated with body patterns with functions such as sexual signalling, aposematism and thermoregulation (Stuart-Fox & Moussalli 2009). In *S. officinalis*, high-contrast patterns are also used in the kinetic display known as 'passing cloud', where bands of dark chromatophores are passed rapidly over a pale body surface (Hanlon & Messenger 1996). Rarely observed in the laboratory, knowledge of both the conditions that predispose the animal to use passing cloud and its precise function remains elusive. It is possible, however, that these dynamic patterns hinder accurate targeting by predators in mid-water.

The context-dependent strategy shown here by *S. officinalis* is in keeping with other behaviours, such as threat responses where the signal used is determined by the type and severity of the threat (Langridge *et al.* 2007). Similarly, when seizing, prey animals often undergo rapid pattern changes (Adamo *et al.* 2006), which appear to be dependent on prey type and/or handling difficulty (S. Zylinski 2006, unpublished data). We therefore assume that such signals are tuned to the visual sensitivities of different viewers, and body patterns used during movement might be similarly tuned. A key difference between the experiments of Stevens *et al.* (2008) and those presented here is that in the former study the prey were all relatively conspicuous; here the cuttlefish start from a situation of being well camouflaged and move on their own accord. This is relevant because if motion dazzle markings are detrimental to conventional camouflage, then animals might only possess them if they already have conspicuous markings resulting from other selection pressures or signalling functions (Caro 2009).

Whether an individual perceives that it has been detected or not might be crucial to the strategy employed by animals that can change their appearance rapidly (Langridge *et al.* 2007). In the absence of threat, the best strategy could be to retain/produce low-contrast camouflage markings that are less likely to be detected. Conversely, if the animal has been detected already, then it may then be better to adopt dazzle markings because although it can no longer prevent detection, it can still reduce the chance of capture as it moves from the threat. It remains to be resolved whether moving cuttlefish use markings that can prevent both detection/recognition (i.e. camouflage) and targeting (i.e. motion dazzle). This might be achieved through comparing body patterns used by cuttlefish induced to move by a simulated predator without eliciting a secondary defence response to those when they move of their own accord, as in this study.

Here we tested the use of body patterns for animals moving over an artificial periodic stimuli in the absence

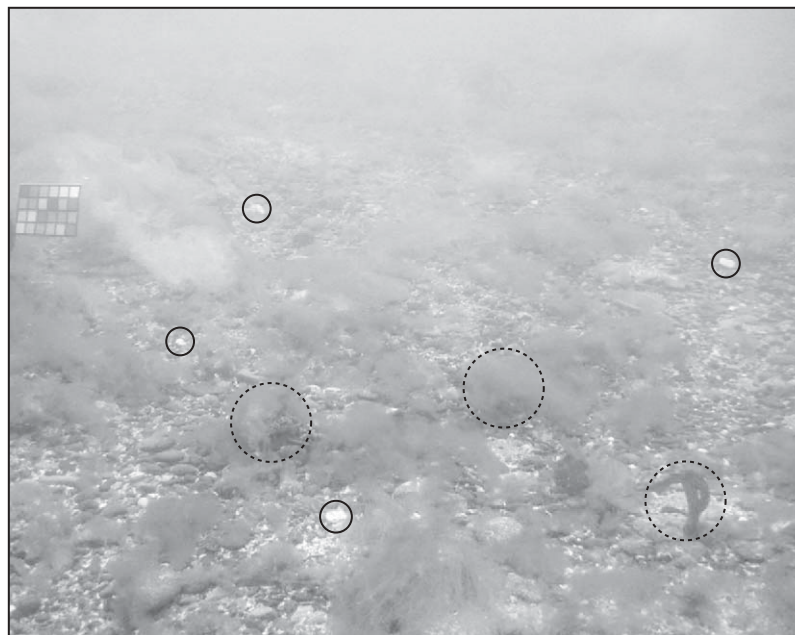


Figure 4. An underwater scene in an area where both juvenile and adult *S. officinalis* were observed (S. Zylinski, south coast UK, 4 m water depth, May), demonstrating that high contrasting areas of high reflectance are generally associated with discrete objects such as pebbles and shells (some of which are circled with small circles) which are not easily moved by typical water-induced motion. Conversely, seaweeds and biomatter (large broken circles), which are subject to movement in currents and swell, tend to be of low reflectance and of low contrast within the overall scene.

of any perceived threat or motivational stimulus. This resulted in a relatively small dataset as, once settled on a substrate, cuttlefish typically spend long periods (many hours) stationary (a behaviour presumably used to maintain camouflage and avoiding motion cues). By taking a single frame at the midpoint of movement, we have not attempted to analyse any sequential changes during an episode of movement, which may have resulted in loss of information of any multiple changes taking place (e.g. polyphenism described above), although observations suggest body patterns are relatively constant over the movement episode. Further studies are required to assess in more depth how adaptive camouflage is altered sequentially, during movement over larger areas (a relatively small arena was used here), over non-periodic and/or natural stimuli (including homogeneous backgrounds promoting the third main described cuttlefish body pattern, uniform (Hanlon & Messenger 1988; Hanlon 2007)), and in the presence of perceived threat.

The static body patterns of cuttlefish have been well studied in recent years, providing an excellent groundwork for experiments into body pattern use during movement (Barbosa *et al.* 2007, 2008; Chiao *et al.* 2007; Kelman *et al.* 2008; Mäthger *et al.* 2008). We have a good (but by no means complete) understanding of which visual parameters are salient in the use of different body patterns and which low-level mechanisms might be employed in detecting these. Given their capacity for rapid adaptive camouflage, cuttlefish have the potential to inform much of our understanding of how body patterns can be optimized during movement. Here we provide a first demonstration of this, showing that there may be no single solution to minimizing the effects of movement, which is reflected in the range of behaviours and body patterns employed by motile animals across the animal kingdom.

We thank the staff at Brighton SeaLife for help with animal care, and Martin Stevens and an anonymous referee for useful comments on the manuscript. S.Z. was funded by a BBSRC CASE award with QinetiQ.

## REFERENCES

- Adamo, S. A., Ehgoetz, K., Sangster, C. & Whitehorne, I. 2006 Signaling to the enemy? Body pattern expression and its response to external cues during hunting in the cuttlefish *Sepia officinalis*. *Biol. Bull.* **210**, 192–200. (doi:10.2307/4134557)
- Barbosa, A., Mathger, L. M., Chubb, C., Chiao, C.-C., Florio, C. & Hanlon, R. T. 2007 Disruptive coloration in cuttlefish: a visual perception mechanism that regulates ontogenetic adjustment of skin patterning. *J. Exp. Biol.* **210**, 1139–1147. (doi:10.1242/jeb.02741)
- Barbosa, A., Mäthger, L. M., Buresch, K. C., Kelly, J., Chubb, C., Chiao, C.-C. & Hanlon, R. T. 2008 Cuttlefish camouflage: the effects of substrate contrast and size in evoking uniform, mottle or disruptive body patterns. *Vision Res.* **48**, 1242–1253. (doi:10.1016/j.visres.2008.02.011)
- Behrens, R. R. 1999 The role of artists in ship camouflage during World War I. *Leonardo* **22**, 53–59. (doi:10.1162/002409499553000)
- Bond, A. B. & Kamil, A. C. 2002 Visual predators select for crypticity and polymorphism in virtual prey. *Nature* **415**, 609–613. (doi:10.1038/415609a)
- Bruce, V. & Green, P. R. 1990 *Visual perception: physiology, psychology and ecology*. 2nd edn. Hove, UK: LEA.
- Caro, T. 2009 Contrasting coloration in terrestrial mammals. *Phil. Trans. R. Soc. B* **364**, 537–548. (doi:10.1098/rstb.2008.0221)
- Chiao, C.-C. & Hanlon, R. T. 2001 Cuttlefish camouflage: visual perception of size, contrast and number of white squares on artificial checkerboard substrata initiates disruptive coloration. *J. Exp. Biol.* **204**, 2119–2125.



- Chiao, C.-C., Chubb, C. & Hanlon, R. T. 2007 Interactive effects of size, contrast, intensity and configuration of background objects in evoking disruptive camouflage in cuttlefish. *Vision Res.* **47**, 2223–2235. (doi:10.1016/j.visres.2007.05.001)
- Cott, H. B. 1940 *Adaptive colouration in animals*. London, UK: Methuen.
- Cuthill, I. C., Stevens, M., Sheppard, J., Maddocks, T., Parraga, C. A. & Troscianko, T. S. 2005 Disruptive coloration and background pattern matching. *Nature* **434**, 72–74. (doi:10.1038/nature03312)
- Frost, B. J. 1993 Subcortical analysis of visual motion: relative motion, figure-ground discrimination and self-induced optic flow. In *Visual motion and its role in the stabilisation of gaze* (eds F. A. Miles & J. Wallman). Amsterdam, The Netherlands: Elsevier.
- Hanlon, R. 2007 Cephalopod dynamic camouflage. *Curr. Biol.* **17**, 1–5. (doi:10.1016/j.cub.2007.03.034)
- Hanlon, R. T. & Messenger, J. B. 1988 Adaptive coloration in young cuttlefish (*Sepia officinalis* L.)—the morphology and development of body patterns and their relation to behaviour. *Phil. Trans. R. Soc. Lond. B* **320**, 437–487. (doi:10.1098/rstb.1988.0087)
- Hanlon, R. T. & Messenger, J. B. 1996 *Cephalopod behaviour*. Cambridge, UK: Cambridge University Press.
- Hanlon, R. T., Forsythe, J. W. & Joneschild, D. E. 1999 Crypsis, conspicuousness, mimicry and polyphenism as antipredator defences of foraging octopuses on Indo-Pacific coral reefs, with a method of quantifying crypsis from video tapes. *Biol. J. Linn. Soc.* **66**, 1–22. (doi:10.1111/j.1095-8312.1999.tb01914.x)
- Hanlon, R. T., Chiao, C.-C., Mäthger, L. M., Barbosa, A., Buresch, K. C. & Chubb, C. 2009 Cephalopod dynamic camouflage: bridging the continuum between background matching and disruptive coloration. *Phil. Trans. R. Soc. B* **364**, 429–437. (doi:10.1098/rstb.2008.0270)
- Jolliffe, I. T. 1986 *Principal component analysis*. New York, NY: Springer-Verlag.
- Julesz, B. 1971 *Foundations of cyclopean perception*. Chicago, IL: University of Chicago Press.
- Kelman, E. J., Baddeley, R. J., Shohet, A. J. & Osorio, D. 2007 Perception of visual texture and the expression of disruptive camouflage by the cuttlefish *Sepia officinalis*. *Proc. R. Soc. B* **274**, 1369–1375. (doi:10.1098/rspb.2007.0240)
- Kelman, E. J., Osorio, D. & Baddeley, R. 2008 Review on sensory neuroethology of cuttlefish camouflage and visual object recognition. *J. Exp. Biol.* **211**, 1757–1763. (doi:10.1242/jeb.015149)
- Langridge, K., Broom, M. & Osorio, D. 2007 Selective signalling by cuttlefish to predators. *Curr. Biol.* **17**, R1044–R1045. (doi:10.1016/j.cub.2007.10.028)
- Mäthger, L. M., Chiao, C.-C., Barbosa, A. & Hanlon, R. T. 2008 Color matching on natural substrates in cuttlefish *Sepia officinalis*. *J. Comp. Physiol. A* **194**, 577–585. (doi:10.1007/s00359-008-0332-4)
- Rosenthal, G. G. 2007 Spatiotemporal dimensions of visual signals in animal communication. *Annu. Rev. Ecol. Evol. Syst.* **38**, 155–178. (doi:10.1146/annurev.ecolsys.38.091206.095745)
- Ruxton, G. D., Sherratt, T. N. & Speed, M. P. 2004 *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry*. Oxford, UK: Oxford University Press.
- Shohet, A. J., Baddeley, R. J., Anderson, J. C., Kelman, E. J. & Osorio, D. 2006 Cuttlefish responses to visual orientation, water flow and a model of motion camouflage. *J. Exp. Biol.* **209**, 4717–4723. (doi:10.1242/jeb.02580)
- Smith, A. T. & Snowden, R. J. 1994 Motion detection: an overview. In *Visual detection of motion* (eds A. T. Smith & R. J. Snowden), pp. 3–13. London, UK: Academic Press.
- Srinivasan, M. V., Lehrer, M. & Horridge, G. A. 1990 Visual figure-ground discrimination in the honeybee: the role of motion parallax at boundaries. *Proc. R. Soc. Lond. B* **238**, 331–350. (doi:10.1098/rspb.1990.0003)
- Stevens, M. & Merilaita, S. 2009a Animal camouflage: current issues and new perspectives. *Phil. Trans. R. Soc. B* **364**, 423–427. (doi:10.1098/rstb.2008.0217)
- Stevens, M. & Merilaita, S. 2009b Defining disruptive coloration and distinguishing its functions. *Phil. Trans. R. Soc. B* **364**, 439–448. (doi:10.1098/rstb.2008.0216)
- Stevens, M., Cuthill, I. C., Windsor, A. M. M. & Walker, H. J. 2006 Disruptive contrast in animal camouflage. *Proc. R. Soc. B* **273**, 2433–2438. (doi:10.1098/rspb.2006.3614)
- Stevens, M., Yule, D. H. & Ruxton, G. D. 2008 Dazzle coloration and prey movement. *Proc. R. Soc. B* **275**, 2639–2643. (doi:10.1098/rspb.2008.0877)
- Stuart-Fox, D. & Moussalli, A. 2009 Camouflage, communication and thermoregulation: lessons from colour changing organisms. *Phil. Trans. R. Soc. B* **364**, 463–470. (doi:10.1098/rstb.2008.0254)
- Thayer, G. H. 1909 *Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pattern: being a summary of Abbott H. Thayer's discoveries*. New York, UK: Macmillan.
- Thomson, D. A., Findlay, L. T., Kerstitch, A. N., Ehrlich, P. R. & Van Dyke, C. M. 2000 *Reef fishes of the Sea of Cortez: the rocky shore fishes of the Gulf of California*. Austin, TX: University of Texas Press.
- Tinbergen, N. 1960 The natural control of insects in pine woods: Vol. I. Factors influencing the intensity of predation by songbirds. *Arch. Neerlandaises de Zoologie* **13**, 265–343.
- Troscianko, T., Benton, C. P., Lovell, P. G., Tolhurst, D. J. & Pizlo, Z. 2009 Camouflage and visual perception. *Phil. Trans. R. Soc. B* **364**, 449–461. (doi:10.1098/rstb.2008.0218)
- Zylinski, S., Osorio, D. & Shohet, A. 2009 Perception of edges and visual texture in the camouflage of the common cuttlefish *Sepia officinalis*. *Phil. Trans. R. Soc. B* **364**, 439–448. (doi:10.1098/rstb.2008.0264)
- Zylinski, S., Osorio, D. & Shohet, A. In press. Edge detection and texture classification by cuttlefish. *J. Vis.*