Symmetrical crypsis and asymmetrical signalling in the cuttlefish *Sepia officinalis*

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The salience of bilateral symmetry to humans has led to the suggestion that camouflage may be enhanced in asymmetrical patterns. However, the importance of bilateral symmetry in visual signals (and overall morphology) may constrain the evolution of asymmetrical camouflage, resulting in the bilaterally symmetrical cryptic patterns that we see throughout the animal kingdom. This study investigates the cuttlefish (*Sepia officinalis*), which can control the degree of symmetry in its coloration. Ten juvenile *S. officinalis* were filmed in two behavioural contexts (cryptic and threatened) to test the prediction that cryptic patterns will be expressed more asymmetrically than an anti-predator signal known as the 'deimatic display'. Cryptic body patterns, particularly those with a disruptive function, were found to exhibit a high degree of bilateral symmetry. By contrast, the components of the deimatic display were often expressed asymmetrically. These results are contrary to the predicted use of symmetry in defensive coloration, indicating that the role of symmetry in both crypsis and visual signalling is not as straightforward as previously suggested.

Keywords: symmetry; adaptive coloration; crypsis; cephalopod; *Sepia officinalis*; deimatic display

1. INTRODUCTION

It has been hypothesized that pattern asymmetry may impair the ability of a predator to detect and recognize cryptic prey due to the decreased regularity of the colour pattern (Robinson 1969; Curio 1976; Kirkpatrick & Rosenthal 1994; Osorio 1994; Forsman & Merilaita 1999, 2003; Evans *et al.* 2000). This is almost certainly the case for the human visual system, for which symmetrical shapes and patterns embedded in a complex background are easier to detect and identify than those exhibiting asymmetry (Julesz 1971; Szilagyi & Baird 1977; Barlow & Reeves 1979; Rock 1983). Similar experiments with non-human animals are yet to be described. However, symmetry perception has been demonstrated in several vertebrate groups including primates (Rensch 1957, 1958; Anderson *et al.* 2005), dolphins (von Fersen *et al.* 1992) and birds (Rensch 1957, 1958; Delius & Habers 1978; Menne & Curio 1978). These animals appear to respond to the quality of symmetry in a similar way to humans, often showing innate preferences for symmetric over asymmetric stimuli. Artificial neural network models have demonstrated that sensitivity to, and a bias towards, symmetry could arise in the vertebrate visual system as a by-product of the image recognition process (Enquist & Arak 1994; Osorio 1996).

If symmetry perception was an intrinsic property of vertebrate visual systems, the potential ability to utilize symmetry as a cue in prey-background segregation would be widespread (Kirkpatrick & Rosenthal 1994). Prey animals may, therefore, have experienced selection for asymmetric cryptic patterns, because their predators would find this asymmetry harder to detect and recognize against a random background (Robinson 1969; Curio 1976; Kirkpatrick & Rosenthal 1994; Osorio 1994; Forsman & Merilaita 1999, 2003; Evans *et al.* 2000).

By contrast, we would expect visual signals to be symmetrical, since the fitness benefit to the signaller depends on the ease with which the signal can be detected and identified by the receiver. Support for this prediction comes from empirical studies with both honeybees (Horridge 1996) and pigeons (Delius & Habers 1978), which have revealed that these animals, like humans (Attneave 1954, 1955; Bruce & Morgan 1975), find symmetrical shapes and patterns easier to detect, learn and remember than those with asymmetries.

Furthermore, experimental evidence from studies with domestic chicks and warningly coloured paper 'butterflies' has demonstrated that the efficacy of visual warning signals can be reduced by asymmetry (Forsman & Merilaita 1999; Forsman & Herrstrom 2004).

The importance of symmetry in signalling is further suggested by the prevalence of symmetrical patterns and ornaments in the courtship displays of a variety of taxa (Kirkpatrick & Rosenthal 1994). Mate choice experiments with birds (Møller 1992, 1993; Swaddle & Cuthill 1994a,b), fish (Sheridan & Pomiankowski 1997; Morris & Casey 1998; but see Merry & Morris 2001), insects (Thornhill 1992; Radesäter & Halldórsdóttir 1993) and humans (Grammer & Thornhill 1994; Thornhill & Gangestad 1994) have demonstrated the ability of females not only to detect symmetry, but also to actively choose symmetric over asymmetric displays.

Thus the selection pressures for cryptic and signalling patterns are in direct conflict, and the advantages of bilateral symmetry for both signalling coloration and gross morphology may outweigh any benefits that asymmetry could convey upon crypsis. This is thought to be the main reason for the surprising prevalence of animals with bilaterally symmetrical cryptic patterns: natural and

sexual selection impose constraints on the evolution of pronounced asymmetry (Robinson 1969; Osorio 1994; Forsman & Merilaita 1999, 2003).

In order to determine whether selection for symmetry was relaxed in cryptic patterns, Forsman & Merilaita (2003) measured the intra-individual difference in asymmetry between the cryptic forewings and the signalling hindwings of several moth species. Their results showed no difference in the level of asymmetry of cryptic versus signalling pattern elements; both were largely symmetrical. Because of the way in which moth wing patterns are produced, the authors suggest that developmental or genetic constraints may be responsible for the lack of asymmetry in cryptic pattern elements. My study attempts to overcome the issue of pattern constraints by investigating the body patterns of the cuttlefish, which can control the degree of symmetry in its coloration.

Within the skin of modern coleoid cephalopods (cuttlefish, squid and octopus) are thousands of pigment-filled sacs known as chromatophores, which are responsible for coloration and are unique in the animal kingdom because they are under neuromuscular control directly from the brain (for a review of cephalopod chromatophores, see Messenger 2001). The chromatophores are ultimately driven by the eyes, and the whole system is bilateral: each eye projects to its optic lobe, which in turn projects to its lateral basal lobe, which sends efferent tracts to the chromatophore lobes on the same side (Boycott 1961). Nervous control allows pattern components to be graded in intensity, and also allows expression of components to differ on the two sides of the body, often resulting in unilateral expression. The result is a diverse array of complex body patterns that can vary in bilateral symmetry and can be used very effectively for both crypsis and signalling (Hanlon & Messenger 1996). There is no conflict between the requirements of a successful cryptic pattern versus an effective signal, because the design of each is independent of the other.

This study examines the degree of bilateral symmetry in the body patterns of the common cuttlefish (*Sepia officinalis*) in two contexts: (1) concealed on the substrate, and (2) displaying a highly conserved anti-predator signal known as the 'deimatic display' (Moynihan 1975; Hanlon & Messenger 1996). I aimed to test the prediction that cryptic patterns will exhibit asymmetry, whereas signalling patterns such as the deimatic display will be expressed symmetrically.

2. MATERIAL AND METHODS

The common cuttlefish (*Sepia officinalis* Linneaus 1758) is a shallow-water species that has been studied in some detail with regard to both the body patterns it produces (Holmes 1940; Boycott 1958; Hanlon & Messenger 1988) and the neural processes behind pattern production (Boycott 1961).

Ten juvenile *S. officinalis* (mean mantle length 75 mm) were housed at the University of Sussex laboratory in the Sea Life Centre, Brighton, between January and March 2004. Animals were kept together in a large holding tank, and were transferred individually to a smaller glass aquarium for filming. The filming tank (900×750 mm, water depth 150 mm) had a large mirror positioned above at an angle of 45° to allow recording with a horizontally placed camera. A curtain to minimize disturbance surrounded both the tank

and the mirror; filming was done through a small viewing window, into which the camera lens fitted precisely.

Cuttlefish were given a minimum of 2 h to acclimatize to the filming tank. Thirty minutes prior to filming (upon the cessation of any stress-related behaviour, such as erratic swimming), the focal animal was placed within a circular plastic 'arena' (40 cm in diameter and 30 cm in height; walls were opaque) to restrict it to a certain substrate. Recording in the arena did not begin until the focal animal had settled on the substrate for at least 10 min.

All 10 cuttlefish were used in each set of observations. After filming, individuals were returned to a separate region of the holding tank to avoid pseudoreplication. Both the holding tank and filming aquarium were evenly illuminated with diffuse overhead lighting, and were maintained at 19 °C, 12L : 12D diurnal cycle. All observations took place between 0900 and 1700.

S. officinalis were recorded in two different behavioural contexts: cryptic and threatened (showing the deimatic pattern).

(a) *Cryptic patterns*

All 10 cuttlefish were recorded resting on a variety of substrates, including sand, mud, gravel, stones and shells, used singly and in various combinations, to elicit as many different cryptic patterns as possible. A series of digital photographs (Nikon Coolpix 5400) of varied magnification were taken of each animal/background combination. A total of 256 images were captured overall, with a minimum of 20 per individual.

The observations carried out above involved placing the cuttlefish on a substrate that was essentially uniform, so that both eyes were viewing the same background. Because the system controlling patterning is bilateral, it is possible that cuttlefish cryptic patterns may exhibit a higher degree of asymmetry if each eye receives different visual input. To examine this possibility, a second series of cryptic cuttlefish observations were carried out with the same 10 individuals as before.

Several studies have demonstrated the importance of both the degree of contrast in the background and the size of the substrate in producing bold pattern elements associated with 'mottle' and 'disruptive' patterns in *Sepia* (Hanlon & Messenger 1988; Chiao & Hanlon 2001; Chiao *et al*. 2005). The focal animal was therefore recorded on two different backgrounds: a homogeneous low contrast substrate, which consistently resulted in the expression of a 'uniformly stippled' body pattern, and a highly contrasting substrate that would consistently elicit a bolder pattern ('mottle' or 'disruptive'). These backgrounds were presented separately, at least 1 h apart, and several digital images of the cryptic pattern were recorded after the animal had settled. The two substrates were then placed side by side, and a shallow trough was made at the boundary between them to encourage the cuttlefish to settle in that position, with one eye looking at each substrate (previous observations had shown that the animals will often settle in a small hollow in the substrate if one is present). The animal was photographed as soon as it settled, and then every minute for 5 min to ensure that the pattern did not change over time.

All 10 individuals were recorded in this way on two occasions, but three individuals were excluded from the analysis due to their unwillingness to settle in the desired position. In total, 14 examples were included in the analysis: seven

chromatic components

light

- (1) white posterior triangle
- (2) white square
- (3) white mantle bar
- (4) white lateral stripe
- (5) white fin spots
- (6) white fin line
- (7) white neck spots
- (8) iridescent ventral mantle
- (9) white zebra bands
- (10) white landmark spots
- (11) white splotches
- (12) white major lateral papillae
- (13) white head bar
- (14) white arm triangle
- (15) pink iridophore arm stripes
- (16) white arm spots (males only)

dark

- (17) anterior transverse mantle line
- (18) posterior transverse mantle line
- (19) anterior mantle bar
- (20) posterior mantle bar
- (21) paired mantle spots
- (22) median mantle stripe
- (23) mantle margin stripe
- (24) mantle margin scalloping
- (25) dark fin line
- (26) black zebra bands
- (27) mottle
- (28) latero-ventral patches
- (29) anterior head bar
- (30) posterior head bar
- (31) pupil
- (32) eye ring
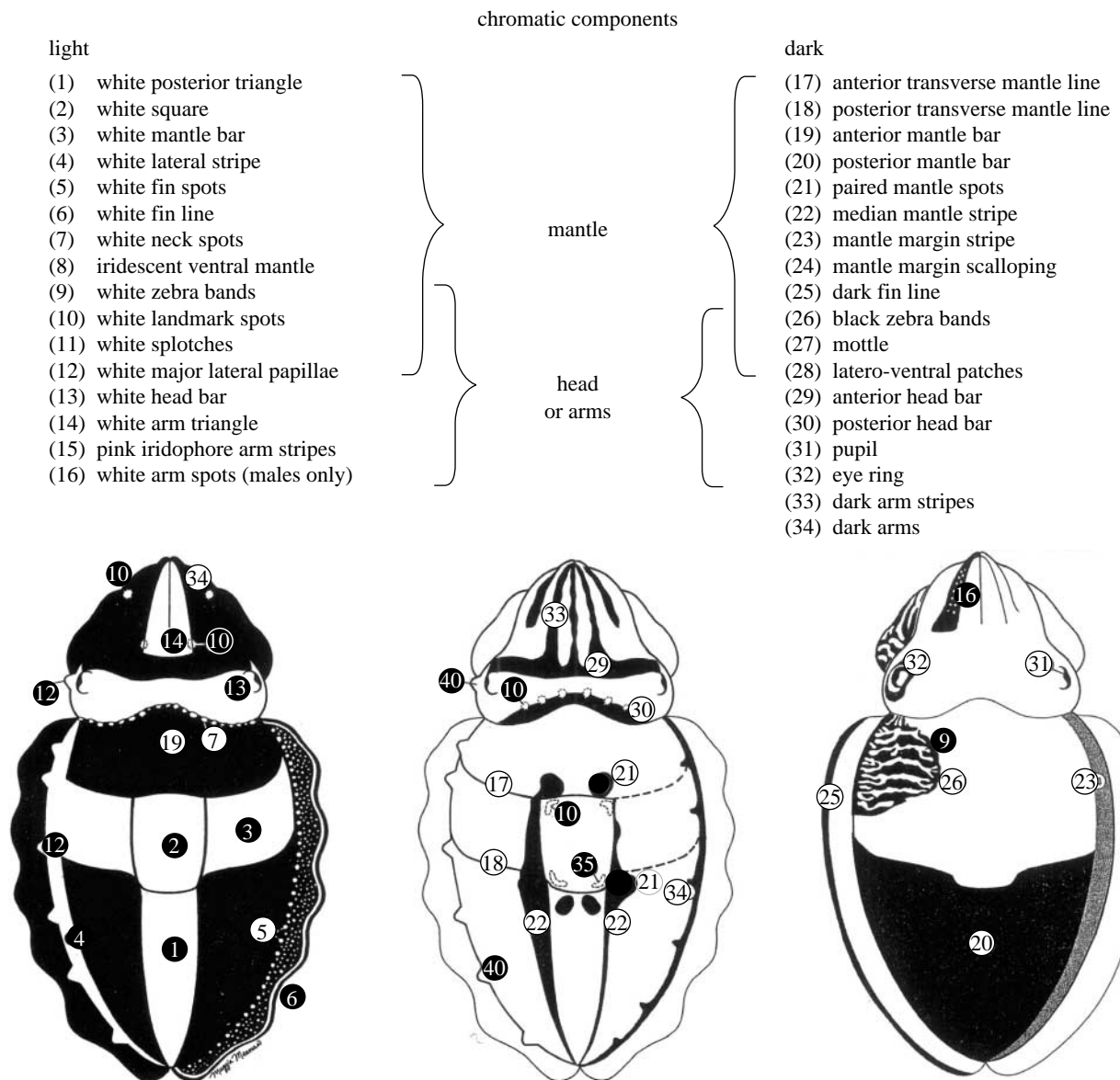- (33) dark arm stripes
- (34) dark arms

mantle

head
or arms

Figure 1. The chromatic components found in the body patterns of the common cuttlefish *Sepia officinalis*. Reproduced from Hanlon & Messenger (1988).

individuals recorded twice on a low contrast background, a high contrast background, and on the border between the two.

(b) *Deimatic patterns*

A white plastic square (50 mm^2) attached to a long metal rod was used as a novel stimulus to evoke the 'deimatic display', an anti-predator signal shown to threatening stimuli (Moynihan 1975; Hanlon & Messenger 1988, 1996).

When the focal animal had settled on the substrate, the rod was introduced into the water within the arena, via a hole in the curtain. Filming (Canon XL-1) would begin just before the rod was introduced, and would continue for one minute (or until the cuttlefish ceased responding) while the threatening stimulus was moved towards and around the cuttlefish. All 10 cuttlefish were only presented with the rod twice, and these presentations were on different days, since cuttlefish habituate rapidly to models (Hanlon & Messenger 1988; Crook *et al.* 2002). One individual reacted abnormally to the second presentation of the stimulus; this response has been excluded from the analysis.

All 19 presentations were analysed in the following way: video images were assessed for symmetry every ten frames (2/3 of a second) for 20 s, from when the cuttlefish first responded to the stimulus, resulting in 30 analysed frames per presentation. This time frame was chosen because most individuals ceased responding to the stimulus after around 20–30 s. However, on several occasions the animals responded for less than 20 s, giving a minimum of 12 frames. A total of 542 frames were analysed overall.

(c) *Assessment of symmetry*

All coleoid body patterns are composed primarily of 'chromatic components': groups of chromatophores with common innervation, occurring in a fixed position in the skin (the same position on both sides of the midline) and depending upon selective neural excitation for their appearance (Packard & Sanders 1971; Packard & Hochberg 1977; Hanlon & Messenger 1996; Messenger 2001).

In order to assess the symmetry of cuttlefish body patterns, 100 still images were randomly selected from the cryptic patterns (10 images taken from each of 10 individuals, chosen at random according to the number of the picture). All 542

frames of the deimatic pattern were analysed since this pattern comprises only a few components.

The individual chromatic pattern components in these images, classified according to Hanlon & Messenger (1988) (see figure 1), were then scored for symmetry based on the intensity of expression of the component on each side of the animal, as follows:

High asymmetry—component is only visible on one side of the focal animal.

Low asymmetry—component visible on both sides of the animal, but expressed with different intensity.

Symmetrical—component present, and expressed with equal intensity on both sides.

For statistical analysis, data in the 'high asymmetry' and 'low asymmetry' categories were combined to produce a single asymmetry category.

3. RESULTS

(a) Cryptic patterns

A variety of different cryptic body patterns were recorded, and had a high degree of bilateral symmetry; the plane of symmetry was most easily detected in the disruptive patterns (figure 2). Close inspection of the chromatic pattern components revealed that they were usually expressed with equal intensity on both sides of the body in undisturbed, cryptic *S. officinalis* (table 1), resulting in a body pattern with an axis of symmetry down the midline.

Despite the high degree of symmetry in cryptic patterns it is apparent from table 1 that some, if not all, components can be expressed asymmetrically. Where asymmetry of component expression was observed, the difference in intensity was small (i.e. low asymmetry), and usually involved one of the 'dark' components seen in deimatic patterning, such as the 'paired mantle spots' and 'median mantle stripe'.

Several 'light' components were occasionally expressed asymmetrically, including the 'white landmark spots' and the 'white square'. Unilateral expression of the white square was not observed, but differences in intensity of the two halves of the square were seen occasionally, and resulted in a gradation of tone and brightness across the surface of the square (figure 3).

Asymmetrical expression of components was recorded in a total of 17/100 images. Thus, it was more common for the entire body pattern to be symmetrical, but if asymmetrical expression occurs, it often involves more than one component.

Cuttlefish resting on the border between two different substrates (14 examples), and therefore seeing a different background with each eye, still produced bilaterally symmetrical cryptic body patterns, with the same components on each half of the body being expressed with equal intensity (figure 4).

(b) Deimatic patterns

The bilateral symmetry of the deimatic pattern was extremely variable both among and within individuals, and ranged from symmetrical (figure 5a) to highly asymmetrical unilateral expression (figure 5b). The chromatic components that make up this pattern were frequently expressed at different intensities on each half of the body, both on the head and on the mantle (table 2).
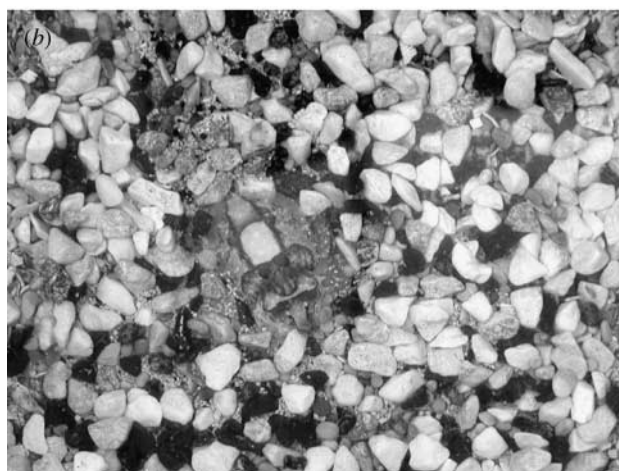

Figure 2. Cryptic patterns of *S. officinalis*. (*a*) The chromatic components in this strong disruptive pattern are expressed equally on either side of the midline, resulting in a bilaterally symmetrical cryptic pattern. (*b*) From a distance the effectiveness of the disruptive pattern in concealment becomes apparent, despite the identifiable plane of symmetry.

The following features of the stimulus influenced the symmetry of the deimatic pattern: position in the visual field of the focal animal, distance from the focal animal, speed of movement towards the animal and novelty. High strength stimuli (i.e. fast-moving, close approaches of the rod) resulted in symmetrical patterning, irrespective of the position of the stimulus in the visual field of the focal animal. A weak stimulus elicited symmetrical expression of components if it could be seen by both eyes. Weak visual input on one side only resulted in unilateral expression of components on the ipsilateral side of the body; if the intensity of the stimulus was increased (i.e. by moving it rapidly) component expression began on the contralateral side. A higher degree of asymmetrical expression was often seen in the second presentations because the animals recognized the stimulus and treated it as a low level threat, often ceasing to respond at all after 10–20 s.

(c) Cryptic versus deimatic patterns

The chromatic components of cryptic patterns were expressed symmetrically more frequently than those components of the deimatic pattern (tables 1 and 2).

Table 1. The chromatic components observed in 100 still images of cryptic *Sepia officinalis*, and the frequency of symmetrical and asymmetrical expression of each component.

chromatic component	total frequency	frequency of component in each symmetry category			% symmetrical expression
		high asymmetry	low asymmetry	symmetrical	
(1) white posterior triangle	24	0	1	23	95.8
(2) white square	30	0	6	24	80
(3) white mantle bar	15	0	2	13	86.7
(5) white fin spots	36	1	0	35	97.2
(7) white neck spots	36	0	2	34	94.4
(10) white landmark spots	65	1	4	60	92.3
(11) white splotches	33	1	3	29	87.9
(12) white major lateral papillae	48	0	2	46	95.8
(13) white head bar	31	0	0	31	100
(14) white arm triangle	12	0	0	12	100
(15) pink iridophore arm stripes	12	0	1	11	91.7
(17) anterior transverse mantle line	48	0	5	43	93.5
(18) posterior transverse mantle line	31	0	5	26	83.9
(19) anterior mantle bar	29	0	1	28	96.6
(20) posterior mantle bar	9	0	1	8	88.9
(21) paired mantle spots	64	0	9	55	85.9
(22) median mantle stripe	38	1	10	27	71.1
(23) mantle margin stripe	17	0	2	15	88.2
(27) mottle	35	0	5	30	85.7
(29) anterior head bar	48	0	0	48	100
(30) posterior head bar	19	0	0	19	100
(33) dark arm stripes	19	0	0	19	100
(34) dark arms	5	0	0	5	100
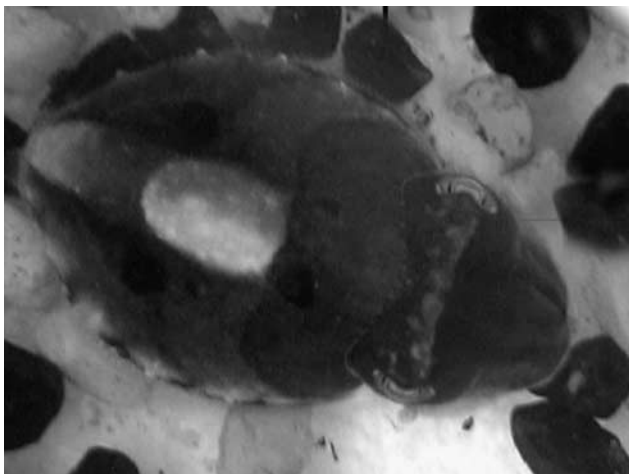
Figure 3. Asymmetrical expression of the white square can create the illusion of relief.

Figure 4. Although each eye is viewing a different substrate, the resulting 'mottle' body pattern is bilaterally symmetrical.

For example, components 1, 13, 19 and 29 (see figure 1) are commonly found in cryptic patterns and were expressed symmetrically in 95–100% of observations, whereas components 31 and 32 of the deimatic pattern were symmetrical in only 25–27% of observations.

Unilateral expression of components (high asymmetry) is also much more common in the deimatic patterns, being recorded on only a few occasions in the cryptic images (tables 1 and 2).

Several components were recorded in both cryptic and deimatic patterns, the most common being the paired mantle spots (component 21). There was a significant difference in the frequency of symmetrical versus asymmetrical expression of the mantle spots between cryptic and deimatic patterns ($\chi^2 = 64.1$,
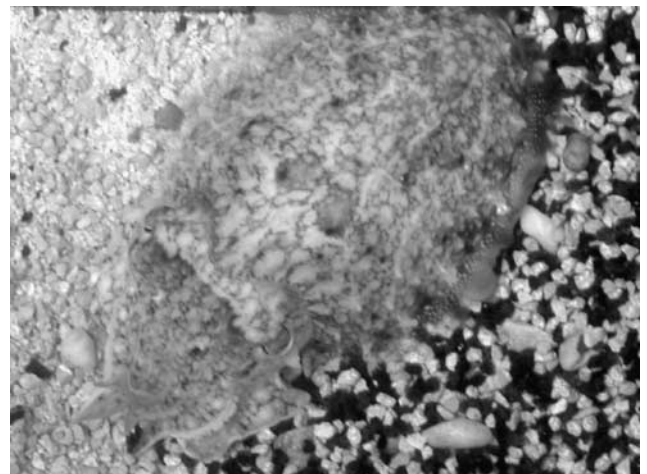
d.f. $= 1$, $p < 0.001$), with cryptic patterns showing symmetrical expression and deimatic patterns exhibiting asymmetry. The posterior transverse mantle line (component 18) is not commonly associated with deimatic patterning; however, it was found in a small percentage of deimatic images (table 2), where it was expressed asymmetrically significantly more often than during crypsis ($\chi^2 = 20.3$, d.f. $= 1$, $p < 0.001$). The only other component observed frequently enough in both types of pattern to allow statistical comparison was component 27 (mottle). The frequency of asymmetrical expression of the mottle was higher in deimatic patterns than in cryptic patterns, although this difference was not as pronounced as for the previous components ($\chi^2 = 3.9$, d.f. $= 1$, $p = 0.05$).
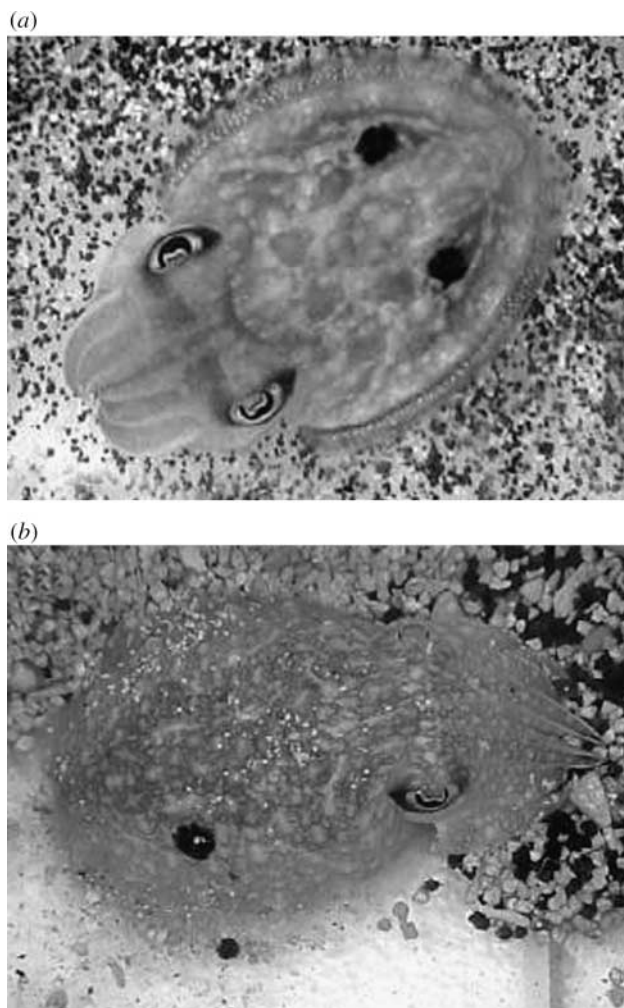
(a)

(b)

Figure 5. Variation in the symmetry of the deimatic display. (a) Symmetrical expression of both the dark eye components and the eyespots. The dark line around the edge of the fin is not expressed in juveniles; the mantle is also paler in adult animals. (b) Unilateral expression of the dark eye components and the eyespot. The threatening stimulus was located 5 cm from the cuttlefish on the side of component expression.

4. DISCUSSION

Despite unparalleled flexibility in pattern production, *S. officinalis* usually produced cryptic body patterns with a high degree of bilateral symmetry. The deimatic display, in particular, was often expressed asymmetrically, which is contrary to the predicted use of symmetry in colour patterns involved in predator–prey interactions.

It is possible that cuttlefish produce symmetrical cryptic patterns due to mechanistic constraints: the bilateral nature of the nervous system controlling patterning means that the two sides of the body may only be patterned differently (i.e. asymmetrically) when the visual input from each eye is different. However, there are several lines of evidence against this explanation. Hanlon & Messenger (1988) showed that unilaterally blinded cuttlefish could still produce full and appropriate cryptic patterns, demonstrating that one eye is sufficient to coordinate a whole body pattern. My study has revealed that cuttlefish on the border between two different substrates still exhibit a high degree of bilateral symmetry, despite each eye receiving different visual input, suggesting that binocular rivalry does not create asymmetric

expression during crypsis. Finally, the white square component is often expressed asymmetrically, even on a homogeneous background when the rest of the body pattern is symmetrical and the animal has not been disturbed. Asymmetric expression of the square produces a gradation of tone across the component, creating the illusion of relief and making the square appear to stand out from the rest of the body (Cott 1940; Hanlon & Messenger 1988, 1996). The shading of the white square demonstrates a more subtle way in which asymmetry can play a role in crypsis.

In the absence of an explanation invoking constraints on asymmetry, why are the cryptic patterns of *S. officinalis* symmetrical, and how does this reflect on the ability of their predators to detect symmetry? Despite the striking bilateral symmetry of cryptic patterns, particularly those with a disruptive function, cuttlefish are incredibly difficult to find in their natural environment. Hanlon & Messenger (1988) describe over 40 field observations of the teleost predator *Serranus cabrilla* swimming within centimetres of motionless cuttlefish (*S. officinalis*) and failing to detect their presence. They further report that the cryptic patterns shown by *S. officinalis* were the same as those seen in the laboratory. Thus, they would presumably have exhibited bilateral symmetry.

Cumulatively, these observations may suggest that the vertebrate predators with which cuttlefish coevolved did not (or were not able to) use symmetry as a cue in prey recognition, and therefore cryptic patterns have not experienced selection for asymmetry (i.e. the proposed hypothesis is incorrect). However, the human visual system undoubtedly possesses mechanisms of symmetry detection, and yet we also have great difficulty locating cryptic cuttlefish (Holmes 1940; Boycott 1958; Hanlon & Messenger 1988, 1996, personal observation). The most likely reason is that, despite the high degree of symmetry in the body pattern, the axis of symmetry (i.e. the midline of the cuttlefish) is orientated randomly from the perspective of the observer. The ability of the human visual system to detect bilaterally symmetrical patterns is markedly reduced when the axis of symmetry is not vertical, or when it has not been defined (Julesz 1971; Barlow & Reeves 1979; Wagemans *et al.* 1992; Wenderoth 1994; Evans *et al.* 2000). If marine predators are indeed able to perceive symmetry, these axis orientation effects could explain why symmetrically patterned but randomly orientated prey animals have not experienced selection for asymmetry.

Alternatively, the role of symmetry in camouflage may not be as straightforward as we might first assume. There are different ways in which colour and pattern make for concealment (Cott 1940), and symmetry may be utilized in different ways depending on how the method of crypsis has its desired effect. In the case of disruptive patterns, symmetry may actually aid concealment. Disruptive coloration attempts to hinder recognition by drawing the eye away from the overall form of the animal, and diverting attention to a conspicuous but otherwise meaningless area of the pattern (Cott 1940; Edmunds 1974). The bold patches of contrasting tone around the midline of the cuttlefish function to draw attention away from the recognizable outline; they may be more effective at catching the eye if they exhibit bilateral symmetry. This could be true of other cryptic animals with symmetrical

Table 2. The chromatic components observed in 542 video images of the deimatic display, and the frequency of symmetrical and asymmetrical expression of each component.

chromatic component	total frequency	frequency of component in each symmetry category			% symmetrical expression
		high asymmetry	low asymmetry	symmetrical	
(18) Posterior transverse mantle line	25	6	13	6	24
(21) Paired mantle spots	480	118	200	162	33.8
(23) Mantle margin stripe	215	59	84	72	33.5
(25) Dark fin line	123	26	51	46	37.4
(27) Mottle	225	18	51	156	69.3
(31) Pupil	347	83	170	94	27.1
(32) Eye ring	333	99	150	84	25.2
(33) Dark arm stripes	114	0	17	97	85.1

disruptive patterns; symmetry may facilitate detection of part of the pattern but not recognition of the whole animal.

The signalling patterns of the cuttlefish appear to utilize symmetry in an equally unexpected fashion. The deimatic display shown by *S. officinalis* to potential predators is strikingly symmetrical when expressed fully. Swaddle (1999) identifies several features of visual signals that amplify symmetry detection: the use of simple, conspicuous elements around the midline, a border around the edge, a vertical axis of bilateral symmetry, and orientation of that axis towards the receiver. The complete deimatic display comprises all of these features, suggesting that symmetry is important to the efficacy of this signal, and thus supporting the prediction that anti-predator displays will evolve towards a symmetrical design. However, the components of this display may also be expressed asymmetrically, depending on the position of the stimulus in the visual field and the degree of threat that it poses to the cuttlefish.

Asymmetrical expression may often be beneficial to individual cuttlefish when they are concealed on the substrate. A small fish or invertebrate likely presents a weak stimulus, which may result in a low intensity, asymmetrical pattern. This pattern may be enough to scare away a small intruder, while allowing the cuttlefish to maintain crypsis on the contralateral side of the body. A large threat, in the form of a big, fast-moving fish will result in the production of a full, symmetrical pattern, which will be detected quickly by the predator and may result in termination of the attack. Unfortunately, there are no recorded observations of the effect of the cuttlefish deimatic display on a potential predator, let alone manipulations of the symmetry of deimatic pattern components.

It is possible that symmetry is not so important to this particular type of display because it incorporates a 'startle' component. Asymmetry may even be a way of minimizing predator habituation, since this display is most likely a bluff (Hanlon & Messenger 1996). This could be the case for startle displays that use bright colours, such as those of some mantids and stick insects (Edmunds 1974). But for those deimatic displays that incorporate eye-like schemata, the eyespots are a key stimulus in producing an unlearned avoidance response in the receiver (Cott 1940; Edmunds 1974; Vallin *et al.* 2005). Vertebrate predators react most strongly to these

stimuli when they are paired and similar (Blest 1957; Scaife 1976; Jones 1980; Coss 1978a,b), possibly because they mimic the frontal aspect of a potentially threatening animal. Thus, selection will favour displays with bilaterally symmetrical ocelli.

It is noteworthy in the cuttlefish that even unilateral deimatic patterns, though extremely asymmetrical at the level of the whole animal, are actually symmetrical from the perspective of a small fish approaching on one side, since the dark eyespot creates a plane of left–right symmetry with the dark eye components. Selection for symmetry may even act more strongly on the eyespots than on the deimatic pattern as a whole, which would explain why eyespot symmetry is preserved during lateral displays.

In conclusion, the role of symmetry in adaptive coloration may be more complex than previously suggested. The results of this study are not consistent with the idea that symmetrical cryptic patterns are the result of constraints on the evolution of asymmetry. Symmetry may not be an essential attribute of certain types of visual signal: cuttlefish often display their deimatic pattern unilaterally, suggesting that the overall symmetry of this pattern is not so important as the symmetry of the key stimuli, two eye-like shapes. The fact that cuttlefish successfully utilize symmetrical body patterns to evade detection/recognition suggests that symmetry is not simply a failing of camouflage; empirical studies that can determine whether asymmetry holds any selective advantages over symmetry are needed to resolve this issue. Such studies should take into account the precise mechanism by which cryptic patterns bring about concealment, since disruptive pattern components that function by attracting attention may benefit from a symmetrical design.

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