Natural History Miscellany

Adaptable Night Camouflage by Cuttlefish

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ABSTRACT: Cephalopods are well known for their diverse, quick-changing camouflage in a wide range of shallow habitats worldwide. However, there is no documentation that cephalopods use their diverse camouflage repertoire at night. We used a remotely operated vehicle equipped with a video camera and a red light to conduct 16 transects on the communal spawning grounds of the giant Australian cuttlefish *Sepia apama* situated on a temperate rock reef in southern Australia. Cuttlefish ceased sexual signaling and reproductive behavior at dusk and then settled to the bottom and quickly adapted their body patterns to produce camouflage that was tailored to different backgrounds. During the day, only 3% of cuttlefish were camouflaged on the spawning ground, but at night 86% (71 of 83 cuttlefish) were camouflaged in variations of three body pattern types: uniform ($n = 5$), mottled ($n = 33$), or disruptive ($n = 34$) coloration. The implication is that nocturnal visual predators provide the selective pressure for rapid, changeable camouflage patterning tuned to different visual backgrounds at night.

Keywords: crypsis, concealment, disruptive coloration, coincident disruptive coloration, cephalopod, *Sepia apama*.

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The use of camouflage as an antipredator tactic is widespread among animal taxa (Thayer 1909; Cott 1940; Edmunds 1974; Endler 1986; Ruxton et al. 2004). Most accounts of camouflage in the literature are based on daytime or crepuscular observations, partly because of the observers' diurnal habits and the technical difficulties of recording photographic or video behavioral data at night. Yet a great deal of predation occurs at night, and many animals have keen night vision (Land and Nilsson 2002). Thus, it would be expected that some camouflage patterns have evolved in response to visual night predators. Although camouflage patterns are known to be shown at night in various marine fish and invertebrates (e.g., Randall and Randall 1960; Böhlke and Chaplin 1968; Hendler 1984), a literature search of all taxa (land and sea) revealed no demonstrations of nighttime camouflage patterns that were tailored to different visual backgrounds. The scarcity of studies on visual predator-prey interactions at night constitutes a major gap in sensory and behavioral ecology.

Cephalopods are known to be masters of changeable, adaptive coloration (e.g., Packard 1972; Hanlon and Messenger 1996). Camouflage is highly developed in this taxon, yet all studies thus far have concentrated on camouflage in daylight or crepuscular periods (Hanlon and Messenger 1996; Hanlon et al. 1999). Cuttlefish are known to show three general classes of camouflage body patterns—uniform, mottled, and disruptive—and each pattern is tailored to different backgrounds (Hanlon and Messenger 1988; Chiao and Hanlon 2001; Chiao et al. 2005). To our knowledge, no one has shown clearly that any cephalopod uses camouflage body patterns under full darkness nor whether the patterns are coordinated with different visual backgrounds. To do so requires that the observer use noninvasive lighting so that the cephalopod does not react to the light. Here we report direct evidence that giant Australian cuttlefish *Sepia apama* in a spawning aggregation cease sexual signaling behaviors and become sessile and camouflaged during the night. Predators of *S. apama* include marine mammals (fur seals, bottlenose dol-
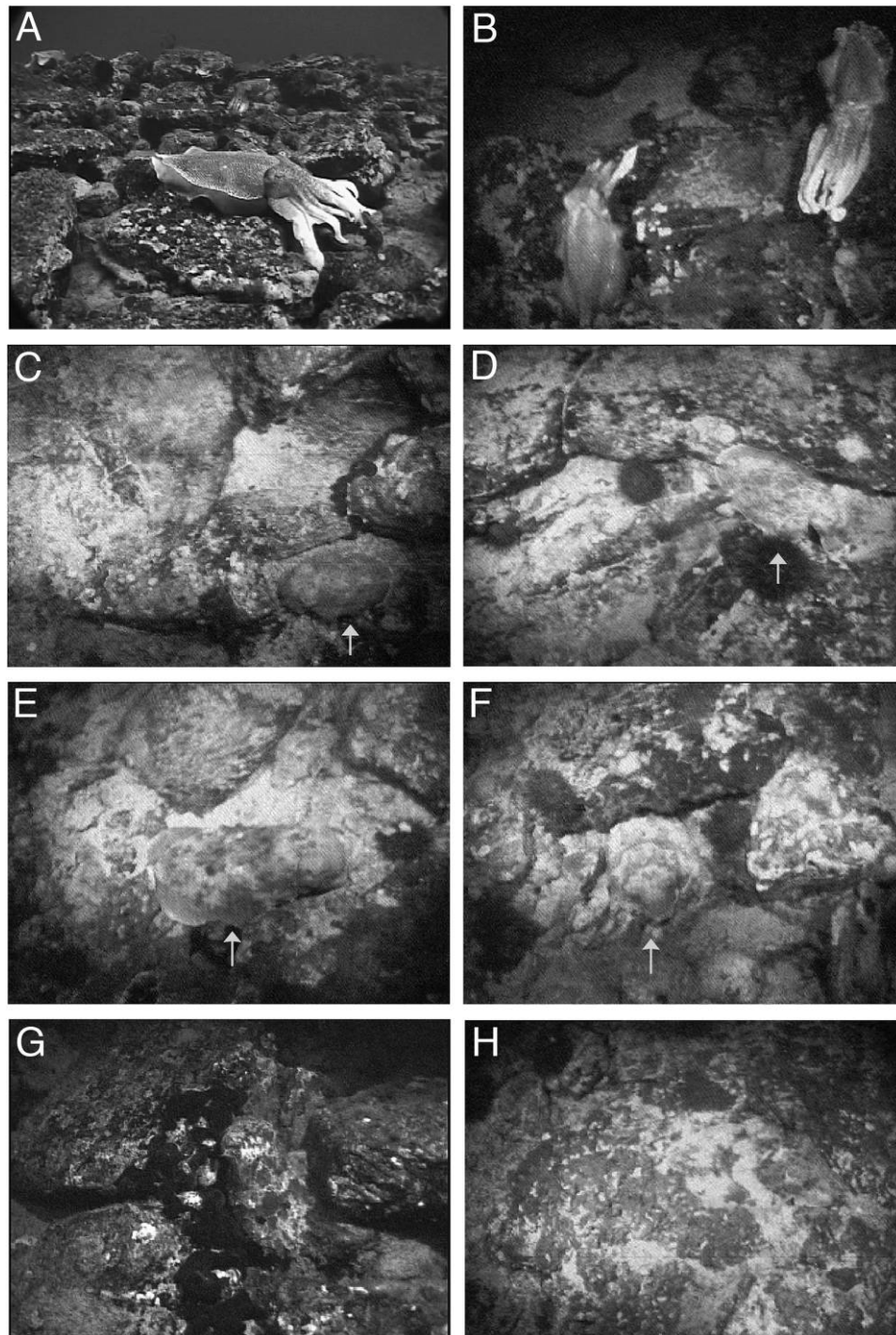
Figure 1: Cuttlefish (*Sepia apama*) in conspicuous coloration (*A*, *B*) or camouflaged at night (*C–H*). Water depths range from 2 to 5 m. *A*, Overall habitat structure shown during the day, characterized by large rocks interspersed with smaller rocks and dark patches of algae. Large male cuttlefish (ca. 40-cm mantle length) in conspicuous agonistic signaling (note bright white arms used in male-male agonistic bouts). *B*, Two large males in early night displaying conspicuous white arms in an agonistic bout. No camouflage is being shown. *C*, Cuttlefish (*arrow*) in a uniform body pattern with very light mottling beginning to be expressed. This animal is an example of deceptive resemblance to a rock. *D*, Cuttlefish (*arrow*) in a light mottled camouflage body pattern. This animal is wedged into a shallow rock crevice. *E*, Cuttlefish (*arrow*) in a mottled pattern. Note that the dark splotches of the mottling are the same approximate size as the dark patches on the adjacent rocks and sand. *F*, Cuttlefish (*arrow*) in a weak disruptive pattern. The posterior end of the animal is under the rock ledge. *G*, Cuttlefish (*center*, *right*) in a mixed pattern: moderately disruptive and dark mottling. Note the spiky texture produced by the papillae on the body. *H*, Cuttlefish (*center*) in an extraordinarily effective disruptive camouflage pattern, with several examples of coincident disruptive coloration. (See fig. 4.)

phins) and several teleost fishes (families Sciaenidae, Sparidae, and Carangidae).

Material and Methods

Sixteen visual surveys (i.e., 100-m linear transects) were conducted between May 31 and June 6, 2003, eight in daytime (1530–1700 hours) and eight at night (1800–2100 hours), at Black Point, South Australia (32°59.5′S, 137°43.1′E), near the town of Whyalla. To obtain objective surveys, we deployed a very small ROV (remotely operated vehicle; model 1505 Little Benthic Vehicle, 53 cm long, SeaBotix) from a 6-m outboard dive boat, and both drifted with the current approximately 50 m from shore in 2–4 m of water. For night observations, the video light was covered with a red filter (Rosco Light Red 26, with peak λ_{max} at 88% transmission of 680 nm; peak wavelength transmitted at 50% is 606 nm). Since the peak sensitivity of the animals' sole visual pigment is 492 nm, their sensitivities to wavelengths that together constitute red are very low (Brown and Brown 1958; Mathger et al. 2006). This dim red light served two purposes: the cuttlefish did not react to it, and the ROV camera could record video in the red spectrum for subsequent pattern analyses. The ROV videotapes were played back slowly for analysis, and individual frames were extracted into Photoshop software to produce figure 1. (Please see the appendix for more details about the ROV and the methodology.)

Three scuba dives were conducted at dusk and three at dawn to verify the behavioral changeovers at those times, although video was not used. The new moon occurred on May 31, and thus our observations were made under a waning (May 28 and 30) or waxing (June 4) moon crescent on the order of 0%–17% illumination and clear sky. Sunrise and sunset during this austral fall period were approximately 0715 and 1720 hours, respectively (see the U.S. Naval Observatory's [USNO] Web page for a day's sun and moon data at http://aa.usno.navy.mil/data/docs/RS_OneDay.html). The end of civil twilight was 1750 hours. Civil twilight is defined on the USNO's Web page as lasting until the center of the sun is geometrically 6° below the horizon. This is the limit beyond which illumination under good weather conditions is insufficient for terrestrial objects to be distinguished clearly. We consider dusk scuba dives to include the period between 1720 and 1750 hours, as light levels fall rapidly; dawn dives included the period between 0645 and 0715 hours. Thus, the eight ROV transects run between 1800 and 2100 hours underwater were considered night trials, not crepuscular trials.

For these trials, we define camouflage in a descriptive manner and rely on figure 1 to convey the general degree to which the animals were blending into the visual background. Uniform, mottled, and disruptive camouflage patterns are described below in their respective sections. In all cases, camouflaged cuttlefish were motionless.

Results

During the eight daytime ROV transects, only 3% of the cuttlefish were camouflaged (i.e., six of 247 cuttlefish). In contrast, 86% of cuttlefish (i.e., 71 of 83) were camouflaged during the eight night transects (fig. 2).

Transition Behaviors at Dusk and Dawn

During dusk, there was a dramatic shift in the animals' behavior from continual movement and conspicuous sexual signaling (fig. 1A) to lack of movement and camouflage (fig. 1C–1H). Only rarely were animals seen actively signaling after sunset (e.g., fig. 1B); at least in a few cases, these were mating pairs that had been together in late afternoon. The night scuba dives on May 28, 2003, confirmed these trends: at 1930 hours, three scuba teams counted 133 camouflaged cuttlefish and 12 noncamouflaged cuttlefish, which is 91% camouflaged versus 9% active and signaling.

Conversely, in very early morning (i.e., before and during civil twilight, which began about 0645 hours and extended to sunrise at about 0715 hours), three scuba teams observed only camouflaged cuttlefish (i.e., 100%), although specific counts were not made. Curiously, there was a delay in the onset of social behaviors. That is, these camouflaged cuttlefish slowly began to move about at about 0700 hours—well after first light (about 0630–0645 hours). The first male-male bouts and male-female interactions were seen at 0730—a full hour after first light. By about 0745, dozens of signaling cuttlefish could be seen everywhere, and the full spectrum of conspicuous sexual selection behaviors was occurring.
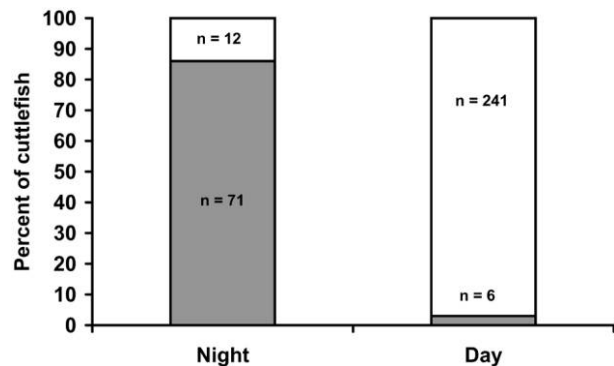

Figure 2: Percentages of camouflaged (*shaded area*) versus noncamouflaged cuttlefish during night and day.

Uniform Camouflage Patterns

Uniform patterns are characterized by being uniformly light or dark on all of the body (Hanlon and Messenger 1988). We observed only light uniform patterns. Figure 1*C* shows a cuttlefish in a uniform body pattern that has a hint of very light, small-scale mottling. From the perspective of the ROV—about 1 m above the animal—this animal resembles a large rock. This is known as "deceptive resemblance" to inanimate objects such as rocks or algae (Cott 1940).

Camouflaged uniform patterns were rare in our night transects; only four of the 71 camouflaged cuttlefish were uniform (fig. 3). Conversely, cuttlefish engaged in sexual signaling during the day were most often in conspicuous (i.e., not camouflaged) uniform body patterns as they moved about the rock reef.

Mottled Camouflage Patterns

Mottled patterns are characterized by small-scale dark and light splotches distributed over the body (Hanlon and Messenger 1988). Overall, 33 of the 71 camouflaged cuttlefish were classified as having primarily a mottled pattern (fig. 3). Several variations were observed. Figure 1*D* shows a light, relatively large-scale mottled pattern. The key feature here is that the individual dark splotches on the body are of similar size to dark splotches in the adjacent background. This enables "general background resemblance" to the background (sensu Cott 1940). Figure 1*E* shows a typical mottled pattern that, compared to figure 1*D*, is overall darker. Mottled patterns tend to show variation in the size or brightness of the light and dark splotches over all of the body. Thus, we characterized some variations as very light small-scale mottle, dark small-scale mottle, or light large-scale mottle; the last was most common, being noted in 14 of the 33 cases (e.g., fig. 1*D*).

Another variation of mottling was a camouflage body pattern in which the mottling was the primary visual effect but some components of disruptive coloration were expressed weakly. These 10 patterns (of 33 mottles) were referred to as "mottle/weak disruptive," indicating that mottled was the primary visual appearance, but the bold transverse markings of disruptive coloration (see "Disruptive Camouflage Patterns") were expressed weakly.

In general, the visual background features that were adjacent to the mottled cuttlefish were relatively small-scale rocks and dark algae that were not very different in size from the mottled components expressed in the skin of the cuttlefish. Large-scale mottles tended to be shown on backgrounds that had larger dark splotches. In cases where the camouflage body pattern had disruptive com-
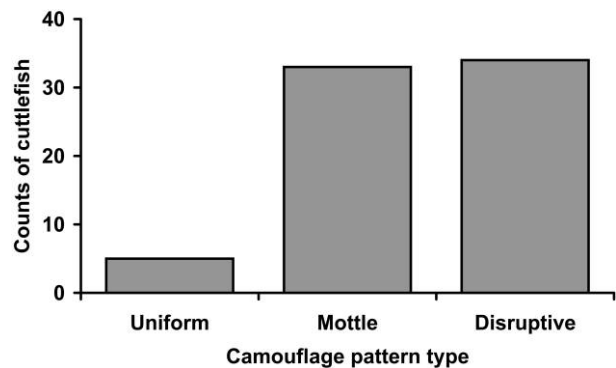

Figure 3: Three camouflage pattern types observed in 71 *Sepia apama* at night.

ponents, the backgrounds tended to have quite large-scale splotches of light and dark.

Disruptive Camouflage Patterns

Disruptive body patterns are characterized by large transverse and longitudinal light and dark components that tend to visually disrupt the body outline of the cuttlefish (Cott 1940; Hanlon and Messenger 1988). Overall, 34 of the 71 camouflaged cuttlefish were classified as having primarily a disruptive pattern (fig. 3). Of these, 10 animals were noted as having a significant amount of mottling mixed in the pattern. Figure 1*F* shows a cuttlefish in a weak disruptive pattern. The term "weak" denotes the low contrast between the light and dark disruptive components in the skin. Note in figure 1*F* that part of the animal's mantle is under the rock, and the exposed two-thirds of the body does not look like a cuttlefish. Figure 1*G* illustrates a cuttlefish with a moderately disruptive pattern characterized principally by a bold, dark transverse bar across the middle of the mantle; the head region also has a transverse "white head bar" (terminology from Hanlon and Messenger 1988). This animal has a large amount of mottling in its skin pattern as well and illustrates a typical pattern in which disruptive coloration and mottling are mixed together in a single pattern.

Some common variations included weak, moderate, or strong disruptive patterns; these were distinguished mostly by the contrast levels between the light and dark components within the patterns. Mottling was mixed in one-third of the patterns, but this occurred generally in the weak and moderate disruptive patterns, not in the strong patterns.

In general, the visual background features that were adjacent to the cuttlefish were relatively large-scale rocks and dark algae that were not very different in size from

the sizes of the disruptive components expressed in the skin of the cuttlefish. When the camouflage body patterns had components of mottling, the backgrounds tended to have slightly smaller-scale splotches of light and dark.

Coincident Disruptive Coloration

Coincident disruptive coloration (Cott 1940) appears to be occurring in figure 1*H*, in which this cuttlefish is nearly impossible to detect because of the disruptive body pattern that obscures the body outline. Cott (1940) explains that "while disruptive patterns appear to break up what is really a continuous surface, coincident patterns seem to unite what are actually discontinuous surfaces" (p. 70). Although Cott mostly describes how body parts in amphibians and insects are coincidentally joined together for "an optical construction of what is not present," he also describes how animal body parts can coincide with background objects and patterns (see Cott 1940 for fuller descriptions).

Three coincidences occur in figure 1*H*, and these are illustrated in figure 4. Most striking is the white mantle bar that coincides well (in brightness, size, and scale) with a bar-shaped white patch in the adjacent substrate, so the white mantle bar of the cuttlefish coincidentally joins visually with the light sandy patch adjacent to it (fig. 4*b*). Second, the dark patches on the right rear mantle coincide with the dark algae in the substrate (fig. 4*a*). Third, the entire head of the cuttlefish (fig. 4*c*) is dark, yet this dark head is comparable in shape and brightness to other dark objects in the immediate surroundings and thus becomes a random sample of those background objects.

Quick Daytime Shift to Camouflage When Dolphins Swam Overhead

On May 30, 2003, at 0930 hours, a small pod of dolphins swam over the ROV, and the video showed the cuttlefish within view immediately drop to the substrate, cease moving, and put on a camouflaged body pattern. Within minutes, the cuttlefish emerged and began the conspicuous signaling associated with sexual selection. K. Hall, in previous years' studies, has seen the same defensive reaction when large stingrays or kingfish swam over the spawning aggregation during daytime.

Discussion

The unique spawning grounds at Whyalla, South Australia, have been well studied recently, yet emphasis thus far has been on the sexual selection processes that occur in this large annual aggregation (Norman et al. 1999; Hall and Hanlon 2002; Naud et al. 2004, 2005; Hanlon et al. 2005). The density of cuttlefish in the aggregation is very high
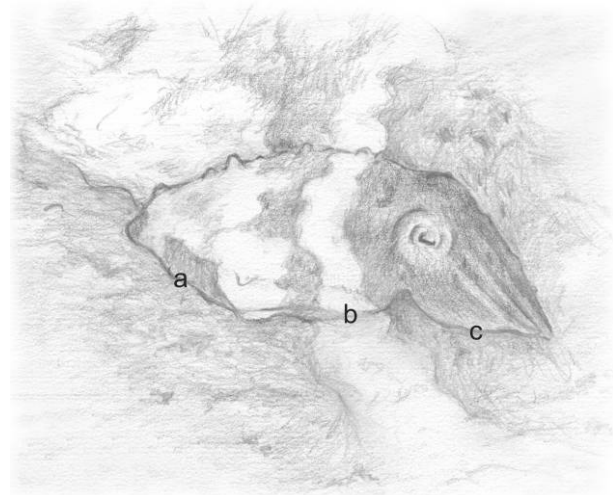

Figure 4: Drawing rendered from figure 1*H*. Three examples (*a–c*) of coincident disruptive coloration.

(up to 105 individuals per 100 m^2; Hall and Hanlon 2002), and it was not clear whether most of the cuttlefish were leaving the spawning grounds during the night (Aitken et al. 2005) or they continued their sexual behavior and signaling after dusk. In this study, we initially conducted night surveys to determine whether sexual behavior and signaling were continuing into the night. We were surprised at the quick transition from conspicuous signaling to quiescent camouflage in the animals that we had been following with focal animal sampling (Naud et al. 2004, 2005). Overall, on the standardized 100-m-long ROV night transects of this study, we observed 71 camouflaged cuttlefish (86% of the total observed; fig. 2) whose body patterns were distributed as 5% uniform, 47% mottled, and 48% disruptive coloration (fig. 3).

Visual Background Diversity

The distribution of body pattern types is probably related to the rocky habitat of the communal spawning grounds near Whyalla. There is little rocky habitat in northern Spencer Gulf (Gostin et al. 1984; Edyvane and Baker 1996), and the cuttlefish migrate there partly because they have to attach their large white eggs to the undersides of large flat rocks (Hall and Hanlon 2002). Cuttlefish come from various parts of Spencer Gulf, whose substrates are known to vary but include a good deal of open sand and mud. Thus, for the earlier phases of the 1-year life cycle, the cuttlefish are probably using a higher proportion of uniform patterns to achieve camouflage; this is known for *Sepia officinalis*, which often sits on or is partially buried in sand in uniform patterns (Hanlon and Messenger 1988).

A recent telemetry study of *Sepia apama* (Aitken et al. 2005) indicates that, except on the spawning grounds, cuttlefish adults spend more than 95% of their daily cycle resting. Thus, camouflage is playing a role nearly every hour of every day and night. *Sepia apama* is endemic to Australian waters, with a distribution reported to extend across temperate southern Australia from southern Queensland to Point Cloates in Western Australia, including northern Tasmania (Lu 1998). Thus, the species must adapt its camouflage to a wide range of habitats.

Camouflage Pattern Diversity: Nocturnal Vision Implications

In this article, we observed a variety of uniform, mottled, and disruptive patterns each night (fig. 1). The fact that we observed multiple pattern types—each effective in different microhabitats—indicates that visual camouflage is an important antipredator behavior in this dark environment. This is noteworthy because it signifies that the animals are fine-tuning their changeable camouflage patterns in concert with the different visual surroundings of each microhabitat, just as in the daytime (e.g., Hanlon and Messenger 1988; Chiao and Hanlon 2001; Chiao et al. 2005). If predation were not significant at night, then animals might show either no camouflage or only one camouflage pattern. Two suggestions emerge from these findings. First, the cuttlefish visual system must be efficient under dark conditions because visual input controls the camouflage pattern that the animal produces in its skin (Chiao and Hanlon 2001; Chiao et al. 2005). Cuttlefish vision is excellent, and it is thought that cuttlefish see well at night, although specific experimental results are not available (Messenger 1991; Muntz 1999). Second, predator vision at night is likely to be excellent too; thus the cuttlefish are using multiple pattern types—and fine grades of each—to achieve crypsis. It is generally accepted that the camouflage patterns in cephalopods have coevolved with predator vision (Packard 1972; Hanlon and Messenger 1996), a concept that holds for much of the visual predator-prey world (e.g., Endler and Basolo 1998).

Cephalopod camouflage has been summarized by Hanlon and Messenger (1996), who pointed out that the primary defense of soft-bodied cephalopods is camouflage (or crypsis), which is achieved via six mechanisms: general background resemblance, disruptive coloration, deceptive resemblance, countershading, rarity through rapid neural polyphenism, and cryptic behavior and vigilance. The skin patterning repertoires of shallow-water cephalopods (cuttlefish, squid, octopus) are extremely diverse (Hanlon and Messenger 1996; see also Hanlon 1982; Moynihan and Rodaniche 1982; Forsythe and Hanlon 1988), yet, as pointed out for the cuttlefish *S. officinalis* (Hanlon and Messenger 1988), the numerous variations of camouflage patterns fall into the categories of uniform/stippled, mottled, and disruptive. Uniform and mottled patterns work by the mechanism of general background resemblance. In this study, the mottled skin components of cuttlefish were similar in size to dark and light background features, which is to be expected in order to accomplish general background resemblance (Cott 1940; Endler 1984; Hanlon and Messenger 1988; Merilaita et al. 2001). Disruptive coloration operates by breaking up the outline of the animal; it was seen commonly in this study, and coincident disruptive coloration (a special subset of disruptive coloration; Cott 1940) was seen in a few cuttlefish (figs. 1*H*, 4 illustrate its effectiveness). The complex mechanisms of disruptive coloration are dealt with by other writers, a few of whom disagree about the mechanisms and functions of disruptive coloration (Cott 1940; Merilaita et al. 2001; Merilaita 2003; Ruxton et al. 2004; Cuthill et al. 2005; Merilaita and Lind 2005).

The large number of hybrid patterns that included mottled and disruptive coloration was noteworthy. Overall, 20 of the 67 patterns (30%) classified as mottled or disruptive had a mix of components: 10 of 33 mottles had a mix of disruptive components, and 10 of 34 disruptive patterns had a mix of mottled components. This probably indicates the fine-tuning of camouflage body patterns to certain features of the visual background. Chiao and colleagues (Chiao and Hanlon 2001; Chiao et al. 2005) have shown that specific cues in the visual background elicit disruptive coloration, and many patterns evoked with artificial backgrounds in the laboratory (Chiao and Hanlon 2001; Chiao et al. 2005; R. T. Hanlon, personal communication, 2006) also evoke mixes of mottled and disruptive coloration. Octopuses in the field and laboratory also show patterns with mixes of mottled and disruptive coloration (e.g., Packard and Hochberg 1977; Forsythe and Hanlon 1988; Hanlon and Messenger 1996; Hanlon et al. 1999). This is an active aspect of current research, and further discussion here would be premature.

Are the night camouflage patterns observed here the same as day camouflage patterns? We do not have data for a comparison. We have anecdotal video from previous years showing some animals camouflaged on the spawning grounds, and these cuttlefish are in mottled, disruptive, or mixed coloration similar to what we observed in our night video. Unfortunately, the quality of the night video is poor due to technical difficulties we had with this ROV and the small generator we were using, so detailed analysis of the patterns (i.e., at the skin level) are not possible. We plan to study the camouflage patterns during daytime. Notwithstanding our general lack of knowledge of nighttime camouflage patterns, there is a suggestion that shallow-water cephalopods that are known to be strongly nocturnal

have somewhat smaller repertoires of body patterning (fig. 3.9 in Hanlon and Messenger 1996). However, even these species have changeable camouflage, and it would be instructive to study their nocturnal pattern changes in comparison to diurnally active cephalopods in similar habitats.

Potential Cuttlefish Predators: Diurnal, Crepuscular, and Nocturnal

No definitive information exists on crepuscular or nocturnal predation of cephalopods. In terms of visual ecology, the behavioral shift from conspicuous body patterns to camouflage body patterns by cuttlefish could possibly correspond to their crepuscular or nocturnal predators' Purkinje shift, as with guppies (Lythgoe 1979), but this awaits future investigation.

Fur seals *Arctocephalus australis* are known predators of *S. apama*, and these seals hunt at night in some locations (e.g., Gales and Pemberton 1993; Klages 1996; Thompson et al. 2003). However, there are no published records of predation on *S. apama* at or near the spawning grounds or of any night predation on cuttlefish. Potential predators in the vicinity of the spawning grounds include Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), mulloway (*Argyrosomus japonicus*, family Sciaenidae), large stingrays, snappers (*Pagrus auratus*, family Sparidae), and yellowtail kingfish (*Seriola lalandi*, family Carangidae). Snappers and mulloway are reputed to be active predators at night. During the day, bottlenose dolphins have been recorded on video to actively feed on giant cuttlefish in the vicinity of the spawning grounds (J. Aldenhoven, personal communication, 2005), and moribund cuttlefish have been consumed by Port Jackson sharks *Heterodontus portusjacksoni* (T. Bramley, personal communication, 2005).

Do Other Animals Change Their Patterns at Night?

Even fishes that are not known for color change often have patterns that are used exclusively at night while they are inactive. Coral reef fishes are particularly well known for this, and many of those patterns are considered disruptive and mottled (Randall and Randall 1960; Böhlke and Chaplin 1968). Many fishes have fixed saddle patterns that are thought to aid disruptive coloration (e.g., Armbruster and Page 1996). Aquatic animals as different as needlefish (Sazima and Uieda 1979) and brittlestars (Hendler 1984) change color pattern at night. Many animals perform some variety of nocturnal change (Verrill 1897), although curiously, this phenomenon—so seemingly vital in the daily lives of animals—has received scant attention.

APPENDIX

Methodology and ROV

The ROV (remotely operated vehicle) proved to be a valuable tool that allowed more objective data acquisition under difficult night diving conditions. It was fairly practical to mark 100-m transects with a global positioning system (GPS) on the surface vessel and to swing around and not repeat the same transect. Repeating the exact transect, however, would have been quite difficult with the GPS unit we had on this very small vessel. With appropriate geo-referencing equipment, it could be possible to rather exactly duplicate transects. However, night operations obscure visual landmarks near shore, currents are running in this area, and there is wave action, all of which influence the ability to duplicate transects with any degree of confidence.

The red filter worked effectively, as judged by the nonreactions of the cuttlefish. One drawback was that this particular Little Benthic Vehicle was not equipped with a higher-resolution camera (ours was a leased unit, and other units with high resolution were not available). Thus, the image quality was restrictive in terms of doing better body pattern descriptions or performing image analyses to background patterns. On the positive side, by "flying" the ROV about a meter over the bottom, we obtained images in which the cuttlefish filled approximately one-fifth to one-tenth of the frame, which provides good perspective for assessing camouflage. Future work with higher-resolution cameras would be the major improvement that we recommend.

The restricted view of the camera lens of the ROV and the rather dim red light restricted the field of view on each transect, and this was a main reason why we observed only 83 cuttlefish at night versus 247 cuttlefish during the day

(using the same number of transects). Furthermore, cuttlefish aggregate in groups of eight to 15 during the reproductive behaviors that occur on this spawning ground (Hall and Hanlon 2002; Naud et al. 2004), and the ROV passed over many of these during the day. As noted by Forsythe et al. (2004), the ROV can provide reliable, quantitative, and safer data than scuba under some conditions.

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