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SQUID SAY IT WITH SKIN: A GRAPHIC MODEL FOR SKIN DISPLAYS IN CARIBBEAN REEF SQUID (*SEPIOTEUTHIS SEPIOIDEA*)

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ABSTRACT

The aim of this paper is to describe the construction and use of a graphic model to express 'squiddish', visual skin displays in reef squid *Sepioteuthis sepioidea*. It was created and refined as a result of a field study off the Caribbean island, Bonaire, to systematize the repertoire of this species' patterns for an ethogram. Squid communication is composed of visual units and components on their body and postures. The color components and reflective units can be turned on and off and are grouped together for complex inter- and intraspecific communication. Like squid skin patterns, our graphic model is composed of components. It was created in Adobe PhotoShop® and consists of a dorsal and a lateral view of a squid. These two shapes can be filled with components for displays and changes of posture by turning combinations of multiple layers in the PhotoShop program on and off. Components are divided into basic background colors and areas of the body on which they overlay distinct patterns. This model demonstrates an assortment of intraspecific displays of *S. sepioidea,* including variations in patterns between males and females and across different age groups, as well as interspecific displays such as camouflage patterns. It will be made publicly available via CephBase (www.cephbase.utmb.edu) to help researchers catalog the full range of displays of *S. sepioidea* and can also establish consistent terminology for the displays and their components of these squid.

INTRODUCTION

We have created a model to illustrate and store graphic information on displays of a living cephalopod. It developed out of the main question of a field project, whether social Caribbean reef squid, *Sepioteuthis sepioidea*, communicate with their skin (Mather *et al.* in prep.). Moynihan and Rodaniche (1982) were the first to recognize and describe the amazing variety of body patterns that *S. sepioidea* produces. But after outlining the components that the skin display system might use, they conducted no further research. We felt that to answer questions about the squid communication system, what was needed first of all was a detailed description of patterns, displays and postures as well as their components to systematize the repertoire as part of the species' ethogram (Griebel *et al.* 2002). The emphasis here is on the construction and use of the model, the data supporting it, the pattern repertoire, will be published elsewhere.

It has been suggested that these highly flexible skin displays have evolved primarily for camouflage and predator-avoidance purposes (Packard 1972), matching the receiver characteristics of the vertebrate eye. As squid themselves are color-blind (Messenger 1991) intraspecific signals would be conveyed more in terms of contrast than color. The flexibility of the chromatophore system and its speed of change lend themself ideally to communication purposes, therefore it is not surprising that cephalopods evolved intraspecific communication signals with this system.

As cephalopod skin display systems fascinate

scientists, there have been many publications describing them, which were approached in different ways. Hanlon & Messenger (1988) carried out an extremely detailed assessment of skin components and patterns in *Sepia officinalis* using photography. A similar approach was chosen for the study on *Octopus burryi* (Hanlon & Hixon 1980) and a more general study on field identification on cephalopods in the Caribbean Sea (Hanlon 1988). On the other hand, drawings were used to show and list components of patterns in *Octopus vulgaris* (Packard & Sanders 1971) and *S. sepioidea* (Moynihan & Rodaniche 1982). Probably the most detailed most technically advanced graphic catalog of behavior so far is the ethogram of *Loligo pealei* (Hanlon *et al.* 1999). The approach chosen for the present model is also graphic, but more flexible, as digital methods are used.

S. sepioidea belongs to the "social" loliginids and is thus likely to have more sophisticated communication abilities than solitary cephalopods (Hanlon & Messenger 1996). These squid are obligate daytime schoolers, preferring to school with individuals of similar sizes, in groups of 20 individuals on average (Boom *et al.* 2001). They also live in a complex environment, coral reefs, which could evoke a rich pattern repertoire (Hanlon & Messenger 1996). Squid displays are composed of visual skin pattern components and postures (Hanlon & Messenger 1996). These components can be turned on and off and are grouped for complex inter- and intraspecific communication. To accomplish this, squid have a chromatophore system that is directly controlled by the brain (Messenger 2001) and they can change color and position in 30 msec. In addition to this, they use iridophores and leucophores to differentially reflect light (Hanlon & Messenger 1996).

Our model was created in a similar way to the actual squid skin displays, with a background color overlain by components and units to create a graphic display. It works by clicking together combinations of layers in the Adobe PhotoShop® program and demonstrates an assortment of intraspecific displays of *S. sepioidea,* including variations in patterns between males and females and across different age groups, as well as interspecific displays such as camouflage patterns.

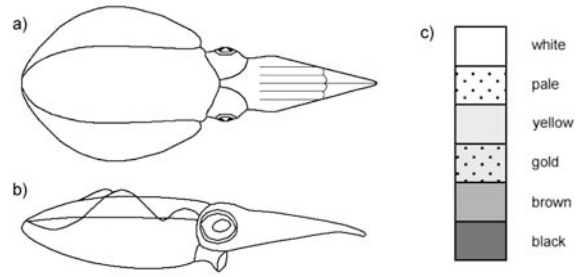

Fig. 1 The model consists of a dorsal (**a**) and a lateral (**b**) view of a squid (*S. sepioidea*). These shapes can be filled with basic background colors (**c**)

MATERIAL AND METHODS

The background for this graphic model was a five-year observational study of *S. sepioidea* carried out on the Caribbean island of Bonaire. Total observation time was approximately 880 hours. It was carried out in the months May and June from 1998 to 2002. The main times for field observation were the early morning (0700 to 1000) and late afternoon (1500 to 1800) because the squid are most active during these times. At night only limited observation was carried out as squid behavior was disrupted by divers' lights.

Data were collected by snorkelers who recorded notes on underwater slates and filed them shortly thereafter. For additional documentation to these observations squid were photographed with Sea&Sea, Nikonos and CoolPix cameras and filmed with a Sony Handycam in an underwater housing. Fourteen hours of footage (hdtv format) was made available to us in 2001 by a professional camera team making a film of our squid research ('Tentacles' by Randy Haight and Danny Mauro).

Squid skin patterns and displays were sketched and then drawn directly on the computer. Adobe PhotoShop® was used to create the graphic model as it has the very useful feature of 'layers' which work like the overlay technique with overhead transparencies. To avoid misunderstanding it is necessary to mention that the layers in Adobe PhotoShop® are not arranged like the layers of different cell types in the cephalopod skin. However, the arrangement of the model is similar to the arrangement of specific background colors which are overlain by units and components adding up to patterns and displays.

RESULTS

Our model consists of a dorsal and lateral view of a squid (Fig. 1 a, b). These two shapes can be filled with the background colorations *White, Pale, Yellow, Gold, Brown* and *Black* (Fig. 1 c). We illustrated the model in black and white and used shades of gray as adequate for the colors *Yellow*, *Brown* and *Black*.

The body coloration *Pale* in squid is a special case since the body is nearly translucent, the beak and internal organs can be seen through the tissue and there is a distinct difference from the opaque, reflective body coloration *White*. In the model, *Pale* is shown as a pattern of small black dots on white. In squid skin displays reflective units and color components overlay the background color. Figure 2 shows the outlines of the most common units and components in their most intense expression in the dorsal view of a squid. Reflective units are visible when not covered by expanded chromatophores; examples for these are *Blue-green Eyebrows*, the *Mid-dorsal Line* and *Mantle* and *Fin Dots*. Components are patterns shown on certain parts of the body by chromatophore expansion and can be divided into stripes, bars, dots, and splotches (Mather *et al.* in prep.). Stripes extend maximally along the longitudinal body axis. Bars have a greater extent perpendicular to the longitudinal body axis than parallel to it. Dots have a relatively regular outline with approximately equal extents in both dimensions, and splotches have the same relative extents as dots but with irregular outlines (e.g. in *Zebra* and *Mottle* patterns). This description of the different types of units and components shows that this level of detail is highly complex and therefore underlines the need for a nomenclature for all components and their combinations.

For the model every unit and component was drawn unilaterally on a single layer in the Adobe PhotoShop® program (Fig. 3), in a similar way to squid skin displays as components overlay a background color. 110 layers can be made visible by a mouse click and thus can be grouped together to construct a display.

Three Chronic Patterns and nine Acute Displays make up the repertoire of *S. sepioidea*'s communication system (Mather *et al.* in prep.). Chronic patterns are visible longer than a few minutes and are found equally at all stages of the lifespan and in

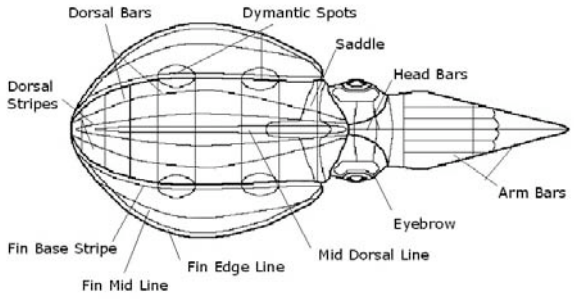

Fig. 2 The most common components of squid skin displays and their names

both sexes. Acute displays last up to a few minutes, though often only seconds, and can be specific to certain life stages and sexes. Some of these patterns and displays will be discussed here to explain the construction and use of the model.

The Basic Color Patterns (Fig. 4a, b, c) are dependent on the level of ambient light (Griebel *et al.* 2002). At dawn and dusk squid show *Basic Pale*, during the day *Basic Brown* and as an in-between stage *Basic Intermediate*. *Basic Pale* consists of a pale background color and the reflective units (*Blue-green Eyebrows*, *Mid-dorsal Line*). The *Beak* is visible through the tissue at the base of the arms. Figure 4a shows all of these components in single layers. They are stacked virtually on top of each other and form a picture of the pattern *Basic Pale.* In Figure 4b the same process is shown for the pattern *Basic Intermediate* in which only the arms and fins are *Pale*. The reflective *Blue-green Eyebrows* are still visible, while brown components (*Dorsal Stripes, Arm Bar* and *Head Bar*) come into the picture. On the edge of the mantle a lighter brown is used as fill-color. *Basic Brown* (Fig. 4c) has a uniform *Brown* background on which the reflective units *Mid-dorsal Line* and *Mantle Dots* can be seen. In contrast to Boal and Gonzalez's (1998) claim that captive *S. lessoniana* do not show sexual dimorphism, it was possible for us to distinguish between adult male and female *S. sepioidea* in the field. The males show distinct *Fin Dots* on *Brown* background and the females have a gradual transition from *Brown* to *Pale* towards the edge of their fins. We used the individual dot pattern of *Fin* and *Mantle Dots* for identification and were able to track most adult individuals in several groups in an area along 500 m of shore line over periods of weeks.

The nine Acute Displays and their meaning are

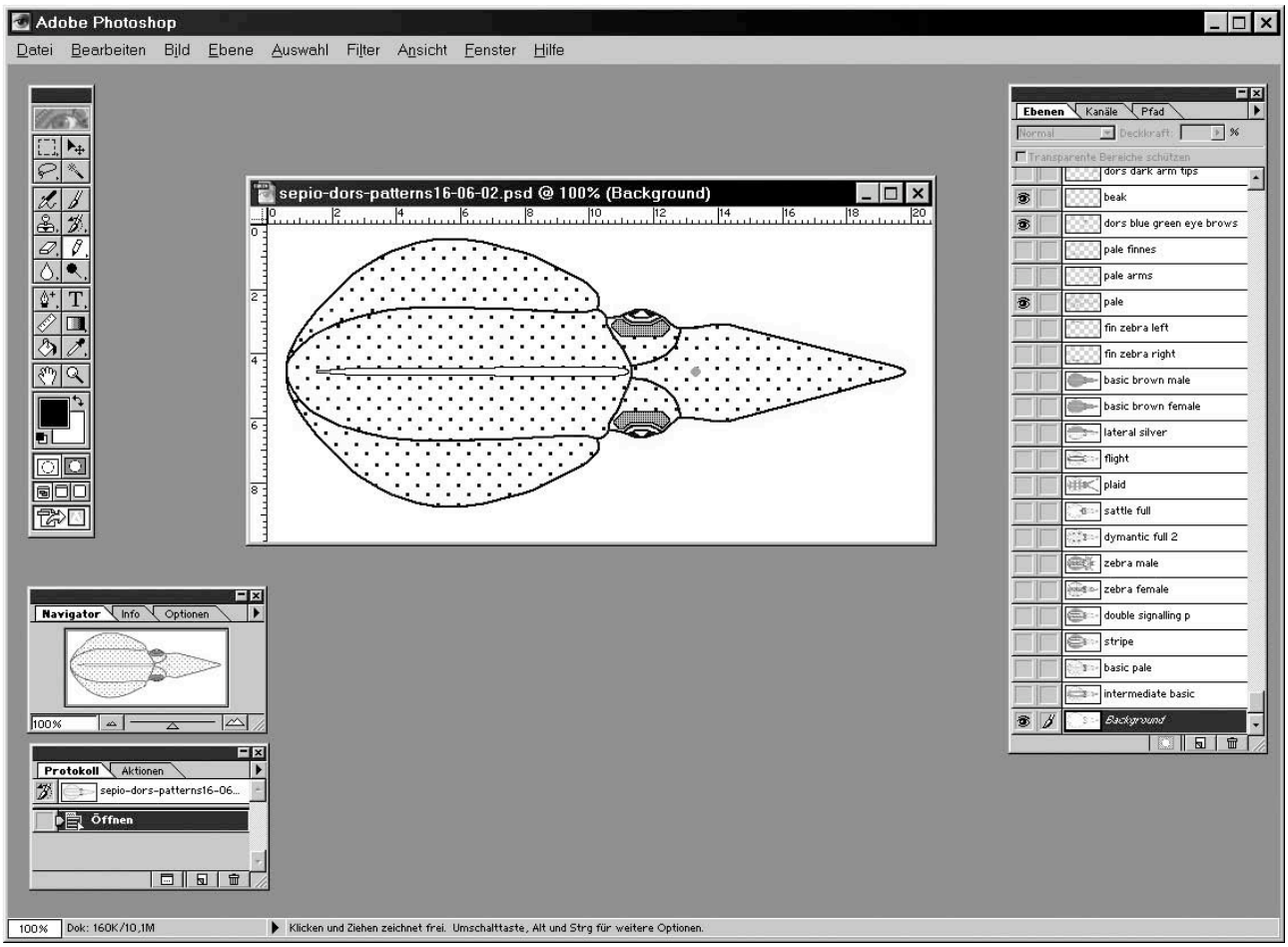

Fig. 3 Adobe PhotoShop® screen shot. On the right side of the picture the layer menu in which the different layers can be made visible is opened

described in Mather *et al.* (in prep.). Some displays have not only color components but also accompanying arm postures (Mather *et al.* in prep.). The original dorsal and lateral views of a squid used for the model have the posture *Standard* but Fig. 5a and b show some examples of displays with other arm postures. Similar to units and components, each posture is also drawn on an individual layer and can be made visible by clicking on it in the layer menu.

S. sepioidea have the amazing ability to signal displays unilaterally to a specific receiver (see Moynihan & Rodaniche 1982 for lateral silver) and they are even able to send two different messages to different receivers on either side of their body at the same time. We call this phenomenon *Double Signaling*. It was a challenge to design a model which can do such things too, but since all units and components in the model are drawn unilaterally on individual layers it is possible to show such display combinations on a single picture by grouping only the unilateral components. A common D*ouble Signal* (Fig. 5d) displayed by males in courtship is the combination of *Stripe* (Fig. 5c), towards the female, and *Zebra* (Fig. 5b), towards a challenging male.

Another important feature of squid skin displays is intensity. The male *Zebra* display, for example, consists of a variety of components - *Zebra* on arms, mantle and fins, and angle of *Spread* of the accompanying arm posture (Mather 2001). The message is more intense when more components are shown. In addition to this, a lighter background color also means more intensity. In the model all background colors can be changed immediately and only certain zebra components can be grouped together to show those intensity gradations.

DISCUSSION

Our model was created to demonstrate intraspecific displays of *S. sepioidea* systematically, including variations in patterns between males and females and

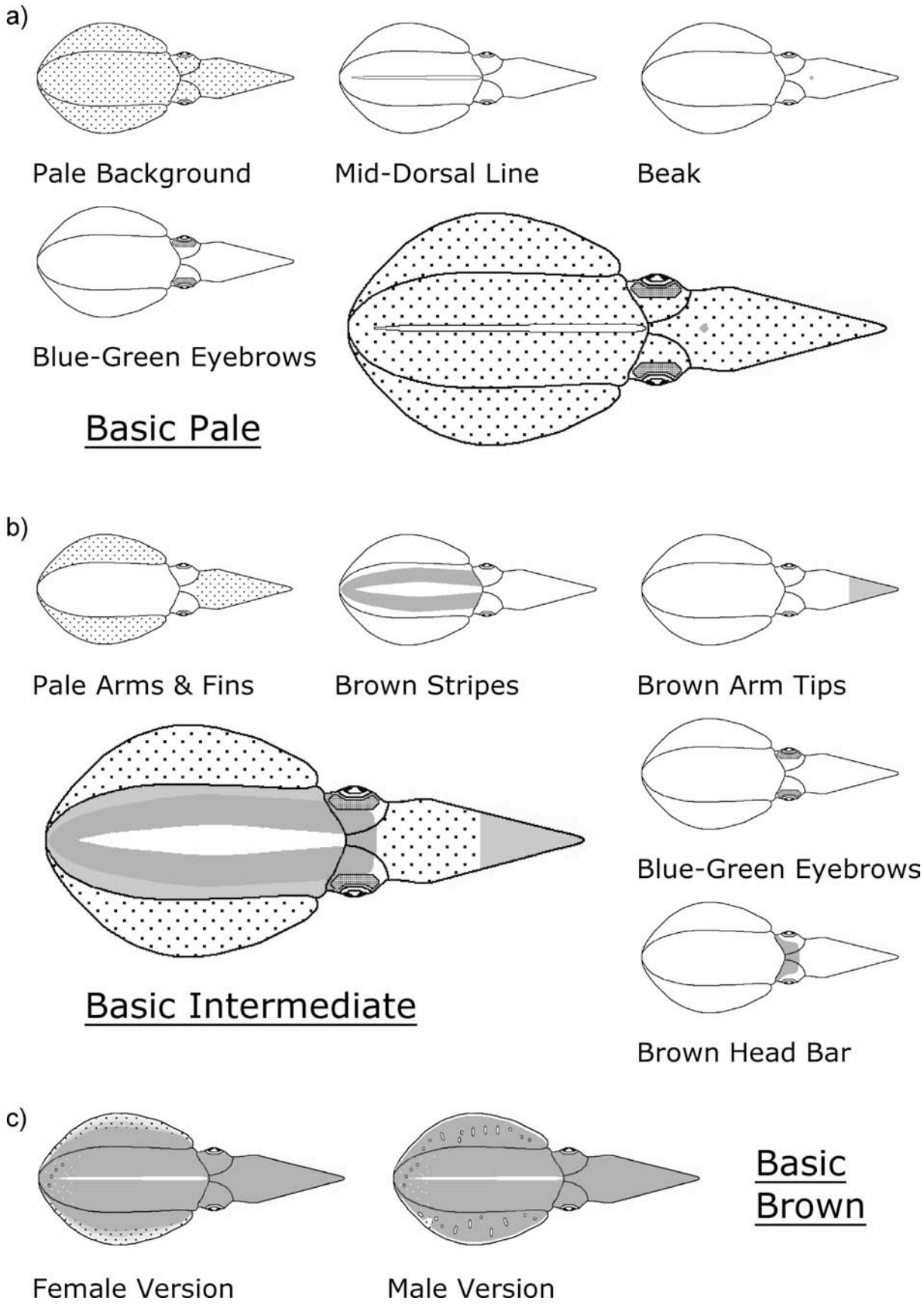

Fig. 4 Basic color patterns. (**a**) *Basic Pale* consists of a pale background, the reflective units *Blue-green Eyebrows* and *Mid-dorsal Line* and the *Beak* showing through the tissue at the base of the arms. These layers stacked on top of each other make up a picture of *Basic Pale*. (**b**) Basic Intermediate has pale arms and fins. *Blue-green Eyebrows* and brown components (*dorsal stripes, arm bar* and *head bar*) are visible. A lighter brown fill-color is used for the edge of the mantle. (**c**) In *Basic Brown* it is possible to distinguish between males and females

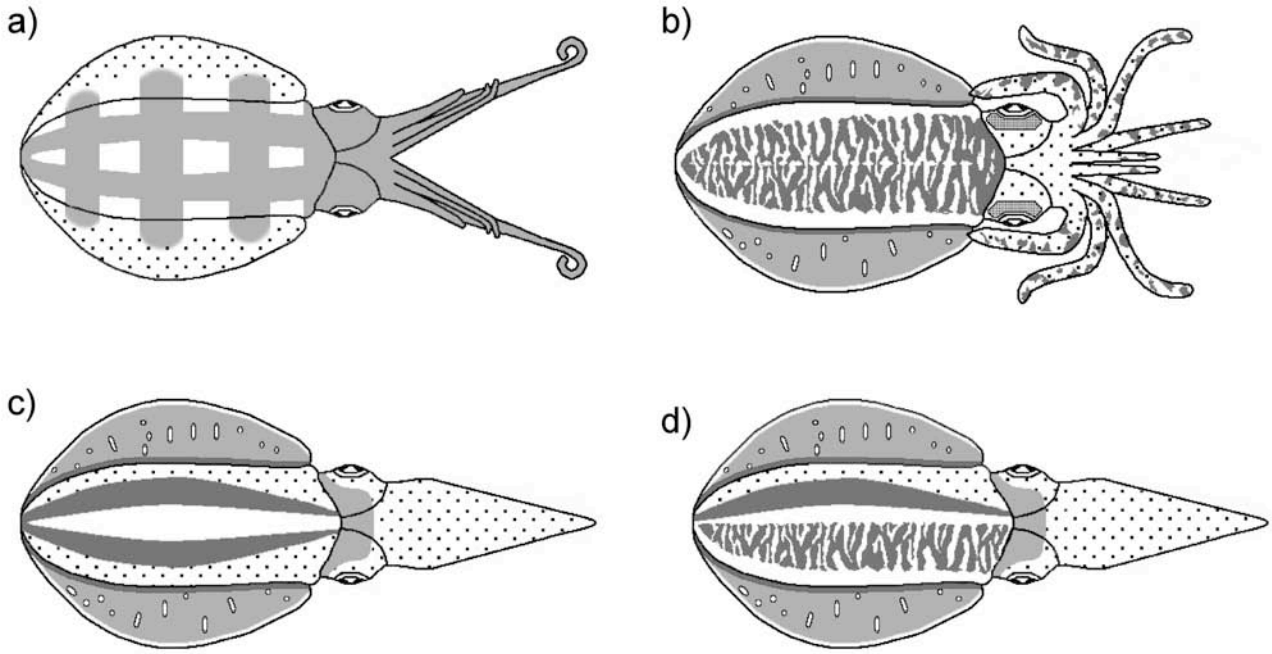

Fig. 5 Examples for acute displays. (**a**) *Plaid* is a display used mostly by juvenile squid for camouflage purposes. It is made up of brown *Stripes* and *Bars* on the mantle and is accompanied by a posture called *Full-V*. (**b**) *Zebra* is used in male-male agonistic interactions. The arm posture *Spread* intesifies the message of this display. (**c**) *Stripe* is a male courtship signal towards the female. (**d**) *Double Signaling* is the amazing ability of squid to send two different messages to different receivers at the same time. Here a combination of *Zebra* (towards a male) and *Stripe* (towards a female) is shown

across different age groups, as well as interspecific displays such as camouflage patterns. It was created in Adobe PhotoShop® and consists of a dorsal and a lateral view of a squid. These two shapes can be filled with components for displays by turning combinations of multiple layers in the PhotoShop program on and off. Components are divided into basic background colors, areas on the body where distinct patterns are overlain and postures. Many other studies show skin display repertoires of different cephalopod species and list the components they are made of by using photography and graphics (Hanlon *et al.* 1999, Hanlon & Messenger 1988, Moynihan & Rodaniche 1982, Packard & Sanders 1971). They all have published detailed descriptions of patterns but none of them are interactive. As *S. sepioidea* has a very complicated communication system in terms of variety of patterns, intensity grading and unilaterality of messages, we felt that it would be necessary to have a more flexible graphical model to show what is really going on.

This model will be made available for common use via CephBase (www.cephbase.utmb.edu) (Wood *et al.* 2003) and/or The Cephalopod Page (www.dal.ca/~ceph/TCP/). It is meant to be a catalog for inter- and intraspecific patterns and displays of *S. sepioidea,* and provides a nomenclature on the level of patterns and displays as well as units and components. It will help researchers catalog the full range of displays of *S. sepioidea* and can also establish consistent terminology for the components and displays of this squid species. This tool can be easily modified or added to as changes and new patterns are observed. It can also be used to compare the patterns and displays of the Bonaire population of *S. sepioidea* to other populations maybe to find 'local dialects'. Finally it might be possible to compare the displays of *S. sepioidea* and components they are made of to the ones of other cephalopod species, to perhaps find implications about evolutionary trends in development and meanings of these signals.

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REFERENCES

Boal JG, Gonzalez SA (1998) Social behaviour of individual oval squids (Cephalopoda, Teuthoidea, Loliginidae, *Sepioteuthis lessoniana*) within a captive school. Ethology 104: 161-178

Boom S, Byrne RA, Mather JA (2001) Schooling behavior of the Caribbean reef squid *Sepioteuthis sepioidea* in Bonaire. Adv Ethol 36: 88

Griebel U, Byrne RA, Mather JA (2002) Squid skin flicks. Animal Behavior Society Meeting 2002, Bloomington, Illinois

Hanlon RT (1988) Behavioral and body patterning characters useful in taxonomy and field identification of cephalopods. Malacologia 29(1): 247-264

Hanlon RT, Hixon RF (1980) Body patterning and field observations of *Octopus burryi*, 1950. Bull Mar Sci 30(4): 749-755

Hanlon RT, Maxwell MR, Shashar N, Loew ER, Boyle KL (1999) An ethogram of body patterning in the medically and commercially valuable squid *Loligo pealei* off Cape Cod, Massachusetts. Biol Bull 197: 49-62

Hanlon RT, Messenger JB (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

Hanlon RT, Messenger JB (1996) Cephalopod behaviour. Cambridge University Press, New York

Mather JA (2001) Do squid lie with Zebra? Comparison of male-male displays in agonistic situations. World Congress of Malacology 2001, Vienna, Austria

Messenger JB (1991) Photoreception and vision in Molluscs. In: Evolution of the Eye and Visual System, MacMillan, London

Messenger JB (2001) Cephalopod chromatophores: neurobiology and natural history. Bio Rev 76: 473-528

Moynihan M, Rodaniche AF (1982) The behaviour and natural history of the Carribean reef squid *Sepioteuthis sepioidea*. Adv Ethol 25: 1-151

Packard A (1972) Cephalopods and fish: the limits of convergence. Bio Rev 47: 241-307

Packard A, Sanders GD (1971) Body patterns of *Octopus vulgaris* and maturation of the response to disturbance. Anim Behav 19: 780-790

Wood JB, Byrne RA, Monks N (2003) Coleoid cephalopods through time, space and cyberspace; using CephBase to examine behavior and selection. In: Warnke K, Keupp H, Boletzky Sv (eds) Coleoid cephalopods through time. Berliner Paläobiol Abh 3: 261-266

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