Selective signalling by cuttlefish to predators

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Rather than simply escaping, prey animals often attempt to deter an attack by signalling to an approaching predator, but this is a risky strategy if it allows time for the predator to draw closer (especially when the signal is a bluff) [1,2]. Because prey are vulnerable to multiple predators, the hunting techniques of which vary widely, it could well be beneficial for a prey animal to discriminate predators and to signal only to those that are likely to be deterred. Higher vertebrates make alarm calls that can identify the type of predator to the signaller's conspecifics [3,4], and a recent study shows that squirrels direct an infrared deterrent signal specifically at infrared-sensitive pit-vipers and not at other snakes [5]. We show here that naïve juvenile cuttlefish (*Sepia officinalis* L.) use a visual signal selectively during encounters with different predatory species. We analysed sequences of defensive behaviours produced by cuttlefish, to control for effects of relative threat level (or 'response urgency' [4]). This showed that a high contrast 'eyespot' signal, known as the deimatic display [6], was used before flight against visually oriented teleost fish, but not crabs and dogfish, which are chemosensory predators [7,8].

We recorded interactions between naïve juvenile cuttlefish and three predatory species in large tanks that provided a naturalistic setting. Predators were free to move around the tank, approaching or receding from the cuttlefish, but the subjects were separated by a transparent screen, so that interactions were purely visual. Cuttlefish encountered juvenile sea bass (*Dicentrarchus labrax*), juvenile dogfish (*Scyliorhinus canicula*) and crabs (*Necora puber*). These species are all potential predators of juvenile cuttlefish [9,10], and were chosen to represent the commonest 'threatening' taxa. All predators were roughly the same size (20–30 cm in length). See the Supplemental data available on-line with this issue for experimental details.

Coleoid cephalopods, including cuttlefish, have a unique neurally controlled system for generating skin patterns, which evolved primarily for visual defence [6]. In addition to camouflage patterns, cuttlefish produce conspicuous signals, including the 'deimatic display' (Figure 1), which are thought to startle or intimidate an approaching predator [6]. Eyespot displays and other forms of 'deimatic' behaviour are well-known anti-predator devices found in many animal groups [1].

We found that, as a predator approaches, starting from an initial camouflage pattern, cuttlefish produce the deimatic display and three other threat responses: 'intensify' (the appearance or intensification of a disruptive body pattern); 'all-dark' (uniform dark grey coloration); and flight. All these behaviours are acute (lasting seconds) and occur as a direct response to the predatory stimulus.

We found that the deimatic display is highly predator-specific: in none of the 24 encounters with crabs or 48 encounters with dogfish did a cuttlefish use this display, but it was shown in all but four of the 48 encounters with sea bass. This result could not be explained by proximity to the predator, as all predators routinely approached the cuttlefish to within 2–4 cm (one mantle length [6]). However, this apparent predator-specificity might also be an artefact of the overall threat level perceived by the cuttlefish. To control for the strength of threat posed by each stimulus, we recorded sequences of responses to an approaching predator (Figure 2). In these approach sequences, transitions between the five defined behavioural states occurred exclusively in a strict order of increasing intensity (above the diagonal in the matrix shown in Figure 2A). Precisely the reverse pattern applied for decreasing threat level as the predator receded. By observing the progression of cuttlefish behavioural state changes, we were able accurately to assess whether a threat is approaching or receding. Intensify was the lowest level response, which commonly escalated to all-dark coloration. The deimatic display occurred only when the threat had escalated further, and flight was the final response in any sequence. The responses did not all invariably occur within a given encounter; but if present, they were expressed in this order. There were significant differences in the sequence of responses to each of the three types of predator (Figure 2B): crabs and dogfish most commonly elicited immediate flight, or an all-dark response followed by flight, while the deimatic display never

Figure 1. The deimatic display.

A juvenile cuttlefish exhibits a deimatic display in response to the close approach of a small juvenile sea bass. The display involves both pattern (black and white with dark 'eyespots' and contour) and postural (flattening and fin spreading) components.

A

Crabs

From: / To:	2	3	4	5
1 Sitting cryptic	0.28	0.20		0.52
2 Intensify		0.85		0.15
3 All dark				1.00
4 Deimatic				
5 Flight				

Dogfish

From: / To:	2	3	4	5
1 Sitting cryptic	0.34	0.57		0.08
2 Intensify		0.68		0.32
3 All dark				1.00
4 Deimatic				
5 Flight				

Sea bass

From: / To:	2	3	4	5
1 Sitting cryptic	0.15	0.04	0.79	0.02
2 Intensify		0.02	0.98	
3 All dark			1.00	
4 Deimatic				1.00
5 Flight				

B

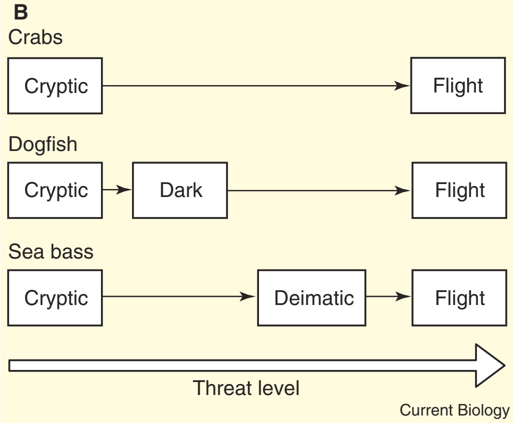

Figure 2. Sequential organisation of threat responses in juvenile cuttlefish during encounters with three different predatory species.

(A) Transition matrices illustrating the probability of transitions between behavioural states as the threat level escalated during encounters with crabs (number of sequences: n = 99), dogfish (n = 151) and sea bass (n = 424). First-order Markov models were applied to each matrix, and transitions between states are consistent with independence, and thus plausibly Markov (likelihood ratio tests: crabs $\chi^2 = 0.23$, d.f. = 1, $p > 0.05$; dogfish $\chi^2 = 0.86$, d.f. = 1, $p > 0.05$; sea bass $\chi^2 = 3.13$, d.f. = 1, $p > 0.05$). (B) Assuming independence, transition probabilities can be used to construct the most probable complete sequences of behaviour (from cryptic to flight) exhibited by young cuttlefish on approach by each predatory species. Differences between species are highly significant (contingency table analysis: $\chi^2 = 591.9$, d.f. = 6, $p < 0.001$). See Supplemental data for further details.

preceded flight. Conversely, sea bass most commonly elicited deimatic display before flight.

Our experimental observations support the hypothesis that young cuttlefish use the deimatic display selectively, as an alternative to immediate flight, in response to teleost fish. Teleosts (including sea bass) are visual hunters [11], whereas dogfish and crabs rely primarily on chemoreception (dogfish also use electroreception) [7,8]. A visual predator is more likely to perceive a visual signal, and hence to make the desired response (hesitation, retreat, abortion of the attack). Deceptive signals, such as eyespots, that exaggerate or falsely advertise prey's retaliatory or escape abilities are particularly risky, since predators that cannot perceive (or choose to ignore) the signal may approach more closely during this display (weakening the effectiveness of subsequent flight), and the prey may attract the attention of other predators [1,2]. The soft-bodied and vulnerable cuttlefish may reduce the risks of their deceptive signal by preferentially employing it against visually oriented species, which are most likely to perceive the signal and respond appropriately. Future studies could investigate this hypothesis by analysing the responses of aquatic predators to cuttlefish deimatic displays.

Supplemental data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/17/24/R1044/DC1

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