Interactions between background matching and motion during visual detection can explain why cryptic animals keep still

Christos C. Ioannou* and Jens Krause

Institute of Integrative and Comparative Biology, University of Leeds, Leeds LS2 9JT, UK
*Author and address for correspondence: Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA (cioannou@princeton.edu).

A widespread example of coevolution between behaviour and morphology is that crypsis is associated with motionlessness. Surprisingly, however, the adaptive function of this association has never been investigated experimentally. We tested whether the risk of being detected by a predator is affected by crypsis, movement or an interaction between these two traits. We show that, to avoid being detected and attacked by three-spined sticklebacks (*Gasterosteus aculeatus* L.), chironomid larvae need both to match their background and to keep still. Additionally, relatively more active individuals were targeted from cryptic prey groups, but not from conspicuous ones. Therefore, rather than crypsis and keeping still both contributing to reducing detection, the two traits are synergistic in reducing detection rates. This interdependence has implications for the coevolution of background matching and motion, and also between anti-predator traits and predators' visual systems.

1. INTRODUCTION

Although crypsis is a common morphological adaptation to avoid detection by predators or prey (Ruxton *et al.* 2004; Caro 2005*a*,*b*), its effectiveness is sensitive to behaviour. A long-recognized and striking observation across the animal kingdom is that cryptic animals keep still (Poulton 1890; Cott 1940; Heatwole 1968; Zhang & Richardson 2007): ambush and sit-and-wait predators tend to be cryptic (Thery *et al.* 2005), prey 'freeze' upon detecting a distant predator (Broom & Ruxton 2005; Eilam 2005) and some species show paired changes in movement and background matching based on when they are most at risk of predation (Feltmate *et al.* 1992; Hanlon *et al.* 2007). Cryptic individuals can even keep still to avoid detection by dominant conspecifics (Takahashi *et al.* 2001). These examples all suggest that background matching is ineffective at reducing the risk of detection when animals are in motion. Compared with this large body of anecdotal evidence, however, there is a lack of rigorous data investigating the selective advantage of

this strategy. The most convincing evidence comes from a recent phylogenetically controlled comparative study, which demonstrated that the young of artiodactyls were more likely to hide rather than to follow their mothers in species with spotted young (Stoner *et al.* 2003). We present the first controlled experiment investigating a possible interaction between cryptic visual appearance and keeping still on the probability of being detected by a predator, and discuss the implications of these results for both predator and prey evolution.

2. MATERIAL AND METHODS

Forty three-spined sticklebacks (from the Great Eau river estuary, UK, 53°25′07″ N; 0°11′25″ E) were fed and habituated overnight in the test arena (figure 1) before being restricted to the non-testing area. A single fish was placed under a refuge at the end of the channel. The fish was observed using an overhead camera and monitored as it emerged from the refuge, swam down the channel and crossed the line of sight to the prey (chironomid larvae). Once the prey was attacked or the fish left the plastic disc area, the fish was removed and not reused. Removed fish were replaced with untested fish at the end of each day.

The first experiment examined the separate and combined effects of background matching and keeping still on the probability of detecting prey. Three chironomid larvae (mean length $\pm$ s.d. = 12.5 ± 1.0 mm) were presented in a sealed Petri dish (35 mm diameter, 13 mm height) as prey. Two factors relating to the appearance and behaviour of prey, each with two levels, were manipulated to make up the four treatments: conspicuous moving; conspicuous still; cryptic moving; and cryptic still. A 57 mm diameter plastic disc attached to the Petri dish coloured either white or red provided a conspicuous or cryptic background, respectively, for the prey. Two dishes of each colour were left in the feeding area overnight to habituate the fish (40.1 ± 2.5 mm). Prey were killed in 70 per cent alcohol for 1 hour (still prey) or kept alive in aged tap water (moving prey). To minimize odour cues, all prey were rinsed in aged tap water before use and the dishes were sealed before placing in the feeding area. Trials were carried out until there were 18 trials where prey were encountered (the fish swam above the disc area) for each treatment, recording whether or not an attack was made. Trials were ended if an encounter was not made within 15 min after first crossing the line of sight, and aborted if the fish took longer than 5 min to leave the refuge. A complete random block ordered the treatments, i.e. four consecutive trials constituted a block, with all four treatments appearing in each block in a random sequence. A fully factorial binomial generalized linear model (GLM; using R v. 2.4.1) was used to determine the effect of background and/or movement on the probability prey were detected and attacked.

In experiment two, the benefit of keeping still relative to other prey was determined. Nine live chironomids (14.8 ± 2.7 mm) were presented to the fish (39.5 ± 2.6 mm) in an open Petri dish (85×13 mm) on a conspicuous or cryptic background (92 mm diameter). Thirty trials were carried out where the prey were encountered for each of the two backgrounds, although prey were attacked and the target prey unambiguously identified from the videos in 29 trials with conspicuous prey and 23 trials with cryptic prey. The movement of prey was recorded using a camcorder, classifying each prey into four increasing levels of activity: (i) no movement, (ii) some movement, (iii) wave movement (a continuous wave travelling down the bloodworm), and (iv) swimming (the wavelength was greater than the length of the bloodworm). The activity of the prey targeted by the fish was ranked relative to the rest of the group (1, most active).

3. RESULTS

The prey needed to be both cryptic and motionless to avoid being attacked by the fish, i.e. there was a significant interaction between movement and crypsis in the probability of attack (figure 2*a*, GLM, background $\times$ movement: $\text{LRT}_{1,68} = 5.92$, $p < 0.05$). When prey were both cryptic and still, they were almost never detected, with the fish often swimming directly over them without making an attack. This result was not sensitive to the relatively small area within which the fish was defined to have encountered the prey.
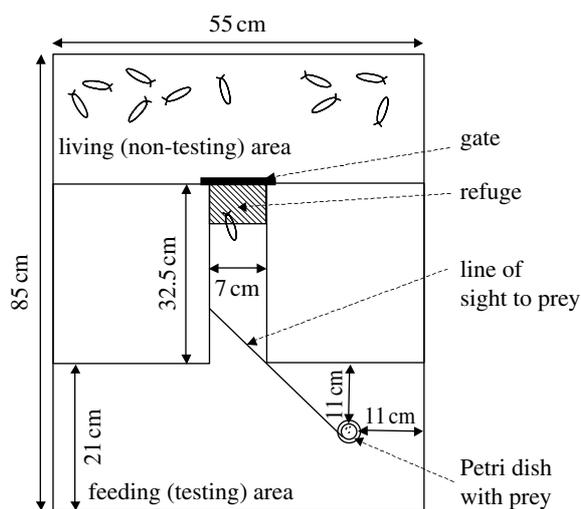
Figure 1. The experimental arena (not to scale) used to present prey, chironomid larvae, to searching sticklebacks. By habituating the fish in the tank overnight before restricting them to the non-testing area, they readily attacked prey once detected. A fish is shown leaving the refuge; at this point, it is naive to the presence of prey. Water depth is 13 cm throughout the arena.
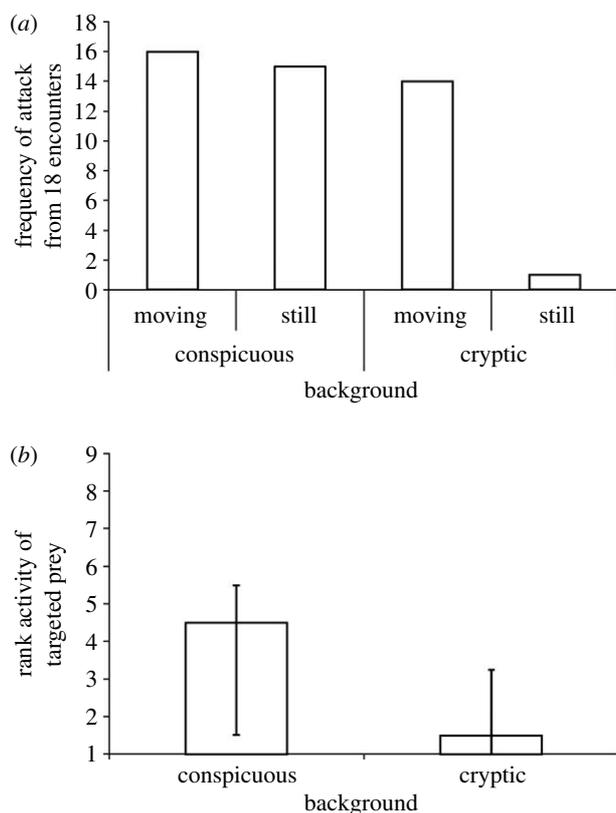

Figure 2. The interaction between chironomid movement and background matching on detection by three-spined sticklebacks. (a) The frequency of attacking the larvae after encounter as a function of prey crypsis and movement. (b) Median rank activity (with inter-quartile ranges) of the targeted prey from cryptic and conspicuous groups of nine prey. A rank of 1 is the most active prey in the group, 9 is the least active prey in the group.

When an encounter was redefined as being within a line of sight to the prey, which included additional trials where a small-scale encounter did not take place, the interaction remained significant (GLM,

background×movement: $LRT_{1,82} = 10.69$, $p = 0.001$). The importance of movement to the detection of cryptic prey was confirmed in the second experiment, as the fish attacked significantly more active individuals from cryptic prey compared with a randomly selecting predator (in none of 1000 virtual runs of the experiment where a 'predator' selected prey randomly was the median rank of the target greater than that observed in the real experiment, i.e. $p < 0.001$). By contrast, the fish selected prey randomly from conspicuous groups regardless of prey activity ($p = 0.803$). Movement only had an effect on target selection, therefore, when the prey were cryptic. Correspondingly, the activity rank of the target was significantly higher on a cryptic background (figure 2b, Mann–Whitney test, $Z = -2.82$, $n = 29$ (conspicuous) and 23 (cryptic), $p < 0.005$).

4. DISCUSSION

That cryptic animals keep still could be explained by the two traits both reducing the probability of detection independently of one another, with the effects being multiplicative. However, we demonstrate that this is not the case: crypsis and a lack of movement are both required, synergistically reducing the probability of detection. The survival advantage to still, cryptic prey was both absolute (reducing the probability of being detected) and relative to other prey within the visual field of the predator. We can rule out that the fish might have perceived the prey as dead and unpalatable as they readily attacked motionless prey on a conspicuous background.

Our study is limited to visual detection. How motion interacts with background matching in other sensory modalities (such as odour: Akino *et al.* 2004, and noise: Briskie *et al.* 1999) remains unknown, and is likely to be sensitive to the physics governing the cue and the properties of the receiver system. For example, if diffusion of an odour cue is accelerated by motion, the increased local concentration of odour may reveal the presence of an animal otherwise cryptic relative to the olfactory background. The issue is further complicated as in a number of non-visual sensory modalities, detection and location are separate phases (Ruxton 2009).

An interaction between crypsis and keeping still is consistent with anatomical, physiological and psychophysical studies on primates (principally humans), which show that although some components of a visual image are processed separately (Wu *et al.* 2004), contrast sensitivity and motion are both processed by the same apparatus (the magnocellular geniculate pathway: Livingstone & Hubel 1988). With the generality of being cryptic and motionless as a strategy to avoid detection, our results suggest that the interaction between motion and contrast sensitivity is far more common than just in the primate species studied to date. It also seems that cryptic prey can exploit the neurological architecture of predators by keeping still. In fact, the magnocellular pathway may have evolved directly in response to this morphobehavioural strategy, as the pathway is highly sensitive to motion even with low contrast (i.e. cryptic) images (Livingstone & Hubel 1987). In a similar manner,

the fine colour differentiation demonstrated by *Gallus* chicks (Osorio *et al.* 1999) has been suggested to be an adaptation to distinguish between aposematic prey and their imperfect Batesian mimics (Speed 2000).

The inter-reliance of crypsis with a lack of movement would lead to the morphological trait of background matching coevolving with a change in behaviour to reduce movement, as seen in other examples of coevolution between morphology and behaviour (Brodie 1989). Moreover, assessing the cost of effective crypsis must also include the opportunity costs of keeping still. The evolution of crypsis will be constrained where a reduction in movement is too costly, and other adaptations to avoid predation, such as aposematism or group living, will be favoured (Merilaita & Tullberg 2005). This may explain why shoaling is more common in juvenile fish than adults (Shaw 1978) as their relatively higher metabolic rate excludes keeping still as a response to predation risk. Nevertheless, cryptic animals from a wide range of taxa keep still, and our results demonstrate that being cryptic and keeping still, but only when associated, is a highly effective strategy to reduce detection by predators.

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