The role of habitat heterogeneity on signal evolution in predator–prey interactions, with implications for the evolution of crypsis and aposematism

Marcio R. Pie
Departamento de Zoologia, Universidade Federal do Paraná, C.P. 19020, 81531–980, Curitiba, PR, Brazil.
* Corresponding author: pie@ufpr.br

Abstract
Little is known about mechanisms promoting the diversity of antipredation strategies found in nature. In this study I explore how habitat heterogeneity may have profound effects on predator–prey communication. Habitat heterogeneity inevitably increases background noise in communication systems. Therefore, as habitat heterogeneity increases, an organism must produce more signal in order to convey the same amount of information (signal–to–noise ratio; S/N). Therefore, all else equal, strategies maximizing S/N (e.g. aposematism, sexually–selected traits) should become more exacerbated as habitat heterogeneity increases, whereas strategies minimizing S/N (e.g. crypsis) should show the opposite trend. A test of this hypothesis is provided based on information on detection-avoidance strategies of Ghanaian preying mantids. If this hypothesis is widely applicable, it can provide a parsimonious explanation for the origin of aposematism, given that the same organisms can become more cryptic or aposematic simply by shifting their habitats and the corresponding levels of background noise.

Key–words Waldo effect, camouflage, antipredation, sexual selection, sensory drive.
From the brightly coloured monarch butterfly to the exquisite crypsis found in stick insects, the bewildering diversity of antipredation strategies have not only intrigued naturalists for centuries, but also were a main theme during the development of the theory of evolution by natural selection. The primary function of antipredation strategies such as crypsis and aposematism are fairly obvious, yet degree of elaboration of these strategies vary considerably among species (Ruxton et al. 2004; Stevens and Merilaita 2011). For instance, strategies to evade detection from predators can vary from a general overall green coloration to a highly elaborate imitation of a leaf, including counterfeit veins and signs of herbivory (Ruxton et al. 2004). Although mechanisms such as differential predation pressures or anatomical constraints might play an important role in explaining variation in the degree of elaboration of antipredation strategies, in this study I explore a simple, parsimonious explanation that could nevertheless involve considerable explanatory power. I suggested elsewhere (Pie 2005) that the sensory drive model developed by Endler (1992; 1993) could be applied in the context of prey–predator interactions. One of the implications of this model is that much of the variation in prey–predator strategies may be described in terms of signal–to–noise ratios (S/N): organisms may evolve strategies that either to minimize S/N or to maximize it (Endler 1978; Endler 1993). For heuristic purposes, S/N can be decoupled into signal and noise components. Usually the organism has more control over the former, since environmental noise is independent of the presence of the organism. On the other hand, the noise component may vary according to differences in habitat heterogeneity: simpler environments provide less background noise than highly heterogeneous environments. If we assume that noise increases with habitat heterogeneity, for the same amount of signal, S/N should decrease with habitat heterogeneity (Fig. 1). Consequently, animals in highly
heterogeneous environments must invest more signal than animals in simpler environments to convey the same amount of information. Given that these assumptions are likely to be highly applicable in many contexts, the resulting trade-off should have profound consequences for signal design and evolution.

Let us first consider the influence of habitat heterogeneity on a strategy that maximizes S/N such as aposematism. A very simple environment (e.g. desert) provides little background noise. Thus even a small amount of signal is sufficient for an aposematic animal to be conspicuous. Alternatively, a complex environment such as a rainforest provides an enormous amount of noise; a visual signal of an aposematic animal may easily be missed among the variety of other signals and light environments. Therefore, to be as conspicuous as its desert counterpart, a forest animal should provide more signal to generate the same S/N. The same arguments could simply be reversed in relation to strategies that minimize S/N. For instance, deserts provide little noise, forcing cryptic organisms to use elaborate strategies to attain a low S/N ratio. This same level of S/N could be attained more easily by a forest animal, given the high level of background noise. An effective way of conveying this principle could be to refer to it as the “Waldo effect”, after the famous cartoon book by Martin Handford (1997). The drawing representing Waldo is the same in all situations (the same amount of signal), but his detection by the reader varies according to the background situation (varying amounts of noise, providing different S/N). It is noteworthy that heterogeneity depends on the sensory system: deserts may be highly homogeneous in relation to visual signals and light environments, but may be highly heterogeneous in wind currents, which can have a strong influence on the evolution of olfactory and/or sound cues (e.g. Legnagne et al. 1999. See also Ruxton 2009). Also, the nature of the heterogeneity in a given habitat
depends largely on its scale. If habitat heterogeneity is spatially coarse–grained, S/N may be low or high depending upon which patch the animal signals in. Conversely, if the spatial heterogeneity is fine–grained, the visual background is essentially homogeneous (Endler 1988).

To the best of my knowledge, this simple model has never been tested explicitly. However, there is some empirical evidence supporting its predictions. Marchetti (1993) found a negative correlation between the presence of bright patches in the plumage of *Phylloscopus* warblers and brightness of their respective habitat. These bright patches have been shown to function in intraspecific territoriality (Marchetti 1993) and in prey–flush foraging (Jablonski 1996; 1999). Either way, the brightness of the habitat is clearly associated with habitat heterogeneity (open/closed habitats). Also, there is experimental evidence for a role of background noise on prey detection (e.g. Dimitrova and Merilaita 2010; 2012). As a first approach to test this hypothesis I collated data on the relative frequency of different kinds of crypsis in different environments using published records of praying mantids. Robinson (1969; 1981) discriminates two kinds of crypsis: eucrypsis and special protective resemblance. The term eucrypsis denotes simple devices such as homochromy, countershading and disruptive coloration, whereas special protective resemblance involves more elaborate strategies such as flower–, bark–, leaf– and stick–mimicry. (Although there has been a strong controversy over the validity of different classifications of cryptic signals (see Robinson 1981 and additional papers on the same issue), for the current purposes I will assume that Robinson’s classification is appropriate.) Given two habitats that differ in heterogeneity such as a savannah and a rainforest, we would expect that S/N minimizing strategies should be less elaborate in the rainforest and more elaborate in the savannah. In other words: eucrypsis should be more common in the complex
environment (forest), whereas special protective resemblance should be more common in the simpler environment (savannah). Using reviews in Edmunds (1972; 1976) I was able to examine information on 40 mantid species. Although not strictly a random sample, the original purposes of the author should not bias these results in any specific direction. As predicted, among the savannah mantids, 15 out of 18 cryptic species had special protective resemblance (83.3%), in contrast to 10 out of 22 species from the forest (45.4%; p=0.015, Fisher’s exact test). Also, another interesting pattern arose from this analysis. In addition to crypsis, many mantid species have startle displays (a S/N maximizing strategy) as a backup strategy. Interestingly, although not systematically quantified, Edmunds’s descriptions suggest that startle displays were generally more dramatic among forest species, frequently including sounds in addition to the visual signals.

The framework explored in the present study has interesting implications for a long-standing conundrum in evolutionary biology: the origin of aposematism. The evolution of this antipredation strategy has been difficult to explain because rare conspicuous mutants should experience a higher cost of discovery by predators relative to the cryptic majority, while at frequencies that would be exceedingly low to lead to predator aversion learning. A variety of mechanisms have been proposed to explain the early stages of aposematism, such as predator dietary conservatism (Thomas et al. 2003, Speed 2001), gregariousness (Mappes and Alatalo 1997), density–dependent phenotypic plasticity (Sword 2002), kin selection (Malcolm 1986), and variation in selective pressures over space and time (Mappes et al. 2005). However, many of these hypotheses either lack the generality expected for such a taxonomically and ecologically widespread phenomenon, or simply push the explanation one step back (ex. why should predators innately avoid brightly coloured
prey?). On the other hand, the dramatic changes in conspicuousness of different species according to the background is highly familiar during field work, such as the sudden "disappearance" of clear–winged ithomiine butterflies as soon as they leave a clearing and enter a patch of forest. The existence of such distinct levels of S/N in neighbouring habitats could lead to the establishment of an "enemy–free space" (Jeffries and Lawton 1984), such that a species can be simultaneously cryptic in visually noisy background and conspicuous in a neighbouring simple background, thus circumventing many of the limitations of previous hypotheses.

The conclusions drawn here should not be restricted to predator–prey interactions. Analogous effects should be evident in other systems where S/N is minimized or maximized, such as sexual selection (e.g. Price 1996). Also, the use of more precise measures of signal and noise (Endler 1990) should provide quantitative tests of this hypothesis, which could be a prolific area for future research.

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References


Fig. 1. An illustration of the principle presented in the present study. The "X" in both figures represents the same amount of signal, yet it is more easily detected in the figure on the right given the lower level of background noise.