



26 From the brightly coloured monarch butterfly to the exquisite crypsis found in  
27 stick insects, the bewildering diversity of antipredation strategies have not only  
28 intrigued naturalists for centuries, but also were a main theme during the development  
29 of the theory of evolution by natural selection. The primary function of antipredation  
30 strategies such as crypsis and aposematism are fairly obvious, yet degree of  
31 elaboration of these strategies vary considerably among species (Ruxton *et al.* 2004;  
32 Stevens and Merilaita 2011). For instance, strategies to evade detection from  
33 predators can vary from a general overall green coloration to a highly elaborate  
34 imitation of a leaf, including counterfeit veins and signs of herbivory (Ruxton *et al.*  
35 2004). Although mechanisms such as differential predation pressures or anatomical  
36 constraints might play an important role in explaining variation in the degree of  
37 elaboration of antipredation strategies, in this study I explore a simple, parsimonious  
38 explanation that could nevertheless involve considerable explanatory power. I  
39 suggested elsewhere (Pie 2005) that the sensory drive model developed by Endler  
40 (1992; 1993) could be applied in the context of prey–predator interactions. One of the  
41 implications of this model is that much of the variation in prey–predator strategies  
42 may be described in terms of signal–to–noise ratios (S/N): organisms may evolve  
43 strategies that either to minimize S/N or to maximize it (Endler 1978; Endler 1993).  
44 For heuristic purposes, S/N can be decoupled into signal and noise components.  
45 Usually the organism has more control over the former, since environmental noise is  
46 independent of the presence of the organism. On the other hand, the noise component  
47 may vary according to differences in habitat heterogeneity: simpler environments  
48 provide less background noise than highly heterogeneous environments. If we assume  
49 that noise increases with habitat heterogeneity, for the same amount of signal, S/N  
50 should decrease with habitat heterogeneity (Fig. 1). Consequently, animals in highly

51 heterogeneous environments must invest more signal than animals in simpler  
52 environments to convey the same amount of information. Given that these  
53 assumptions are likely to be highly applicable in many contexts, the resulting trade-  
54 off should have profound consequences for signal design and evolution.

55 Let us first consider the influence of habitat heterogeneity on a strategy that  
56 maximizes S/N such as aposematism. A very simple environment (e.g. desert)  
57 provides little background noise. Thus even a small amount of signal is sufficient for  
58 an aposematic animal to be conspicuous. Alternatively, a complex environment such  
59 as a rainforest provides an enormous amount of noise; a visual signal of an  
60 aposematic animal may easily be missed among the variety of other signals and light  
61 environments. Therefore, to be as conspicuous as its desert counterpart, a forest  
62 animal should provide more signal to generate the same S/N. The same arguments  
63 could simply be reversed in relation to strategies that minimize S/N. For instance,  
64 deserts provide little noise, forcing cryptic organisms to use elaborate strategies to  
65 attain a low S/N ratio. This same level of S/N could be attained more easily by a  
66 forest animal, given the high level of background noise. An effective way of  
67 conveying this principle could be to refer to it as the “Waldo effect”, after the famous  
68 cartoon book by Martin Handford (1997). The drawing representing Waldo is the  
69 same in all situations (the same amount of signal), but his detection by the reader  
70 varies according to the background situation (varying amounts of noise, providing  
71 different S/N). It is noteworthy that heterogeneity depends on the sensory system:  
72 deserts may be highly homogeneous in relation to visual signals and light  
73 environments, but may be highly heterogeneous in wind currents, which can have a  
74 strong influence on the evolution of olfactory and/or sound cues (e.g. Legnagne *et al.*  
75 1999. See also Ruxton 2009). Also, the nature of the heterogeneity in a given habitat

76 depends largely on its scale. If habitat heterogeneity is spatially coarse-grained, S/N  
77 may be low or high depending upon which patch the animal signals in. Conversely, if  
78 the spatial heterogeneity is fine-grained, the visual background is essentially  
79 homogeneous (Endler 1988).

80 To the best of my knowledge, this simple model has never been tested explicitly.  
81 However, there is some empirical evidence supporting its predictions. Marchetti  
82 (1993) found a negative correlation between the presence of bright patches in the  
83 plumage of *Phylloscopus* warblers and brightness of their respective habitat. These  
84 bright patches have been shown to function in intraspecific territoriality (Marchetti  
85 1993) and in prey-flush foraging (Jablonski 1996; 1999). Either way, the brightness  
86 of the habitat is clearly associated with habitat heterogeneity (open/closed habitats).  
87 Also, there is experimental evidence for a role of background noise on prey detection  
88 (e.g. Dimitrova and Merilaita 2010; 2012). As a first approach to test this hypothesis I  
89 collated data on the relative frequency of different kinds of crypsis in different  
90 environments using published records of praying mantids. Robinson (1969; 1981)  
91 discriminates two kinds of crypsis: eucrypsis and special protective resemblance. The  
92 term eucrypsis denotes simple devices such as homochromy, countershading and  
93 disruptive coloration, whereas special protective resemblance involves more elaborate  
94 strategies such as flower-, bark-, leaf- and stick-mimicry. (Although there has been a  
95 strong controversy over the validity of different classifications of cryptic signals (see  
96 Robinson 1981 and additional papers on the same issue), for the current purposes I  
97 will assume that Robinson's classification is appropriate.) Given two habitats that  
98 differ in heterogeneity such as a savannah and a rainforest, we would expect that S/N  
99 minimizing strategies should be less elaborate in the rainforest and more elaborate in  
100 the savannah. In other words: eucrypsis should be more common in the complex

101 environment (forest), whereas special protective resemblance should be more  
102 common in the simpler environment (savannah). Using reviews in Edmunds (1972;  
103 1976) I was able to examine information on 40 mantid species. Although not strictly a  
104 random sample, the original purposes of the author should not bias these results in any  
105 specific direction. As predicted, among the savannah mantids, 15 out of 18 cryptic  
106 species had special protective resemblance (83.3%), in contrast to 10 out of 22 species  
107 from the forest (45.4%;  $p=0.015$ , Fisher's exact test). Also, another interesting pattern  
108 arose from this analysis. In addition to crypsis, many mantid species have startle  
109 displays (a S/N maximizing strategy) as a backup strategy. Interestingly, although not  
110 systematically quantified, Edmunds's descriptions suggest that startle displays were  
111 generally more dramatic among forest species, frequently including sounds in addition  
112 to the visual signals.

113 The framework explored in the present study has interesting implications for a  
114 long-standing conundrum in evolutionary biology: the origin of aposematism. The  
115 evolution of this antipredation strategy has been difficult to explain because rare  
116 conspicuous mutants should experience a higher cost of discovery by predators  
117 relative to the cryptic majority, while at frequencies that would be exceedingly low to  
118 lead to predator aversion learning. A variety of mechanisms have been proposed to  
119 explain the early stages of aposematism, such as predator dietary conservatism  
120 (Thomas *et al.* 2003, Speed 2001), gregariousness (Mappes and Alatalo 1997),  
121 density-dependent phenotypic plasticity (Sword 2002), kin selection (Malcolm 1986),  
122 and variation in selective pressures over space and time (Mappes *et al.* 2005).  
123 However, many of these hypotheses either lack the generality expected for such a  
124 taxonomically and ecologically widespread phenomenon, or simply push the  
125 explanation one step back (ex. why should predators innately avoid brightly coloured

126 prey?). On the other hand, the dramatic changes in conspicuousness of different  
127 species according to the background is highly familiar during field work, such as the  
128 sudden "disappearance" of clear-winged ithomiine butterflies as soon as they leave a  
129 clearing and enter a patch of forest. The existence of such distinct levels of S/N in  
130 neighbouring habitats could lead to the establishment of an "enemy-free space"  
131 (Jeffries and Lawton 1984), such that a species can be simultaneously cryptic in  
132 visually noisy background and conspicuous in a neighbouring simple background,  
133 thus circumventing many of the limitations of previous hypotheses.

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

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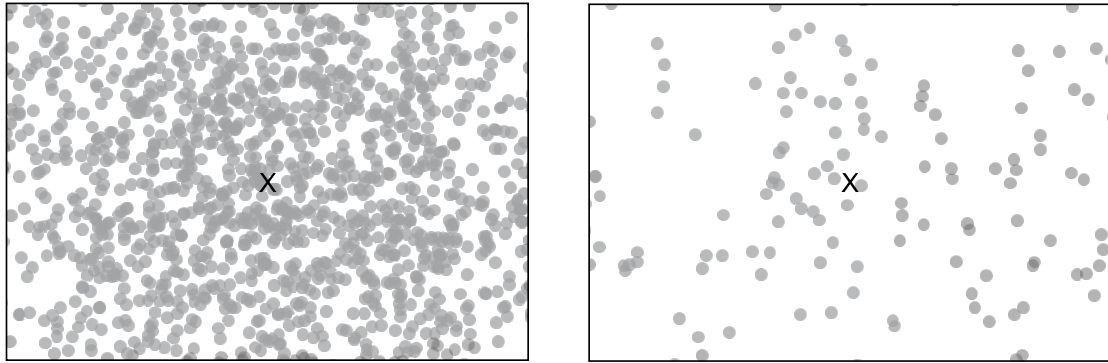
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211 Fig. 1. An illustration of the principle presented in the present study. The "X" in both  
212 figures represents the same amount of signal, yet it is more easily detected in the  
213 figure on the right given the lower level of background noise.