



## When it's good to signal badness: using objective measures of discriminability to test the value of being distinctive



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The hypothesis that prey organisms can reduce the risk of predation by overtly signalling their unprofitability, or aposematism, has a long history in behavioural and evolutionary biology. To fully understand this longstanding idea, we need to measure and manipulate traits of aposematic prey, such as their distinctiveness from other prey, from the perspective of the potential predator. Specifically, we need measurements that are not anthropomorphic and that are based on the principles of discrimination developed by psychophysicists. This paper utilizes an experimentally tractable measure of discriminability based on signal detection theory as originally studied by psychophysicists. In addition, we develop and experimentally test a model to characterize the predator avoidance advantages derived from being distinct from other prey. By experimentally varying discriminability (and thus distinctiveness) we find that increased discriminability does confer a predator avoidance advantage, but the extent of this effect depends on the unprofitability of prey and the relative frequency of unprofitable prey.

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As any student of introductory biology knows, many unpalatable, dangerous or unprofitable prey animals produce conspicuous signals that appear to warn potential predators to stay away. The hypothesis of aposematism has an unimpeachable pedigree in evolutionary biology. Historians trace its origins to an exchange between Alfred Russel Wallace and Charles Darwin (see [Ruxton, Sherratt, & Speed, 2004](#), for a historical review). In the time since Wallace and Darwin, the problem of aposematic signalling has continued to attract the attention of behavioural and evolutionary biologists (e.g. [Arenas, Walter, & Stevens, 2015](#); [Barnett, Bateson, & Rowe, 2014](#); [Barnett, Scott-Samuel, & Cuthill, 2016](#); [Guilford, 1988](#); [Leimar, Enquist, & Sillen-Tullberg, 1986](#); [Mappes, Marples, & Endler, 2005](#); [Speed & Ruxton, 2005](#)). These modern students of aposematism have focused, for example, on the problem of how predators learn to avoid unprofitable prey (e.g. [Gittleman, Harvey, & Greenwood, 1980](#); [Roper & Wistow, 1986](#)), or on the question of how prey gregariousness influences the evolution of aposematism (e.g. [Gamberale & Tullberg, 1998](#); [Rowland, Ruxton, & Skelhorn, 2013](#)).

A primary goal of aposematism research is identifying the benefits prey obtain by conspicuously signalling to predators, benefits such as improved predator learning or memory (reviewed in [Ruxton et al., 2004](#)). Such benefits are necessary to counterbalance the potential costs of alerting predators to one's presence. These benefits can generally be divided into two categories: those benefits derived from conspicuously contrasting with the background (e.g. [Gittleman & Harvey, 1980](#); [Ham, Ihalainen, Lindström, & Mappes, 2006](#); [Roper & Redston, 1987](#)) or those derived from contrasting with other prey items, termed 'distinctiveness' (e.g. [Merilaita & Ruxton, 2007](#)). We focus on the value of distinctiveness, which has traditionally received less experimental attention as an explanation for aposematism than the value of conspicuously contrasting with background (but see [Merilaita & Ruxton, 2007](#); [Sherratt, 2002](#); [Sherratt & Beatty, 2003](#); [Sherratt & Franks, 2005](#)). The discriminability between prey types represents an important problem for predators attempting to simultaneously find palatable prey and avoid aposematic prey, and these predators are presumably the major selective force in aposematic systems.

When biologists recognize an instance of aposematic signalling, they nearly always do so because the prey animal in question is conspicuously distinct from other prey from a human perspective. This implicit anthropocentrism is problematic because in order to truly understand aposematic signalling systems, we need to understand distinctiveness from the perspective of the intended receivers. Empirical studies of aposematism, however, typically do

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not measure distinctiveness or discriminability based on the perception of predators. Moreover, several studies that have measured distinctiveness of aposematic prey and their mimics, from the predator's perspective, indicate that the predator's perception of prey does not match perfectly with our own (Dittrich, Gilbert, Green, McGregor, & Grewcock, 1993; Green et al., 1999). Even if we were to accept that human sensory abilities map crudely to the abilities of many predators, we still have the problem that 'distinctiveness' is simplest to describe categorically (i.e. prey types are distinctive or not), and this results in an imprecise description of predator recognition. For example, to ask how distinctive a prey item must be to obtain the advantages of aposematism, we need to manipulate the degree of discriminability, and to do this we need to measure it quantitatively.

This paper presents a laboratory simulation of aposematic signalling that uses a quantitative, nonanthropocentric measure of discriminability derived from the theory of signal detection (Green & Swets, 1966). There exists a wide range of literature in psychophysics and experimental psychology that models and tests nonhuman animal discrimination using signal detection theory (reviewed in Alsop, 1998; Blough, 2001). We extend these approaches by structuring the consequences of receiver actions (correct accepts, false alarms, etc.) after the ecological problem of foraging in a system with unprofitable prey. Our goal is not to measure or model discrimination capability, per se, but to identify the protective effects of predator discrimination (i.e. the protection experienced by prey) given a specific arrangement of costs and benefits. First, we develop an experimentally tractable model of aposematic signalling, and briefly review the basic ideas of signal detection theory.

## A BASIC APOSEMATISM MODEL

Consider a predator encountering a prey item. The prey item may be good, yielding a value (or net benefit to the predator) of  $v_{\text{good}}$ . Or the prey may be bad, yielding value  $v_{\text{bad}}$ . Upon encounter, the predator can choose to attack or ignore the prey item. If it ignores the prey item, we assume it pursues an alternative activity (e.g. looking for more prey elsewhere) that yields value  $v_{\text{alt}}$ . We assume that  $v_{\text{good}} > v_{\text{alt}} > v_{\text{bad}}$ . Now, to reduce the number of variables, we rescale the three  $v$ s such that  $v_{\text{good}} = 1$ ,  $v_{\text{alt}} = 0$  and  $v_{\text{bad}} = -b$  such that  $b$  represents the relative unprofitability (or 'badness') of the bad prey type (i.e. the units are now based on the difference between  $v_{\text{good}}$  and  $v_{\text{alt}}$ ). In addition, we let  $p$  be the proportion of prey in the environment that are bad. Finally, we assume that the prey signals its type via an externally detectable pattern. A signal indicating the good type is denoted by  $S+$ , while a signal indicating the bad type is denoted by  $S-$ . A 'signal follower' attacks the prey if it observes  $S+$ , but it adopts the alternative activity if it observes  $S-$ . The expected gains due to signal following are therefore  $Y_{\text{follow}} = 1 - p$  per encounter; the signal follower obtains one unit when it observes pattern  $S+$  and attacks a good prey item (which occurs on a portion  $1 - p$  of encounters), and it obtains 0 units when it encounters pattern  $S-$  because it exploits the alternative resource gaining 0 units when it observes  $S-$ . Assuming the predator can discriminate perfectly between the  $S+$  and  $S-$  states of the signal, the payoff for following the signal is  $Y_{\text{follow}} = (1 - p)$ .

While this assumption of perfect discrimination (i.e. prey types are perfectly distinct) may be reasonable for some forms of aposematic signalling, ultimately it represents a problem. To fully explore the hypothesis that aposematic signalling is valuable to unprofitable signallers because it distinguishes them from other prey, we need to systematically vary discriminability. Research on gradations of discriminability (such as studies on imperfect mimics and aposematic prey) often use qualitative categories of discriminability

(e.g. good versus poor replicas: Caley & Schluter, 2003; Schmidt, 1958; or a graded continuum of an arbitrary trait: Duncan & Sheppard, 1965). Another study goes a step further, manipulating discriminability on a finer scale (McGuire, Van Gossum, Beirincx, & Sherratt, 2006), but does not quantify discriminability based on measures of perception. To address the problem of manipulating discriminability, and thus vary distinctiveness from the profitable prey, we use ideas from the psychophysical framework of signal detection theory. Although several recent papers cover signal detection, we briefly review the key points below.

## Signal Detection Theory

Signal detection theory came to prominence in psychophysics in the 1960s and 1970s (Egan, 1975; Green & Swets, 1966; Swets, 1996). More recently, several behavioural ecologists have recognized the significance of signal detection theory for behavioural ecology (e.g. Getty, Kamil, & Real, 1987; Lynn, Cnaani, & Papaj, 2005; McGuire et al., 2006; Stephens, 2007; Wiley, 1994, 2013). We illustrate the basic ideas with our system of profitable and unprofitable prey in mind. Say that a predator encounters a profitable prey item and observes a signal of the good type ( $S+$ ). Noise causes stochastic variation in the perceived signal magnitude, and as a result, its sensory apparatus draws a sample from a normal distribution of possible signal magnitudes. If, instead, the prey item is unprofitable and the predator observes a signal of the bad type ( $S-$ ), the predator draws a sample from a different normal distribution (see Fig. 1 for a graphical illustration). The predator must decide which of the distributions its observation came from and act accordingly. These two distributions, specifically the distance separating them and their variances, tell us whether the predator faces an easy discrimination problem (little overlap) or a hard discrimination problem (high overlap). Although it is somewhat 'nonstandard' (for signal detection theory), we assume that the distribution for the bad prey is shifted to the right of the distribution for the good prey. The theory assumes that the animal 'discriminates' by setting a threshold  $x^*$  such that the animal accepts the encountered item if it observes a signal intensity less than  $x^*$  and rejects it otherwise.

Traditionally, students of signal detection use the variable  $d'$  to describe the difficulty of the discrimination problem. The parameter  $d'$  measures the separation between the two signal distributions in standard deviation units (assuming distributions with equal variance), which provides a dimensionless measure of how difficult the discrimination problem is for the animal. If  $d'$  is small (say, under 0.1), the animal faces a very difficult discrimination problem, and if  $d'$  is large (say, 3.0), the animal faces a very easy discrimination problem. We can estimate  $d'$  from the frequency of attack when we present  $S+$  and compare this to the frequency of attack when we present  $S-$ . Mathematically, we calculate  $d'$  for an experienced subject as

$$d' = Z[1 - P(\text{Attack}|S-)] - Z[1 - P(\text{Attack}|S+)] \quad (1)$$

where  $Z$  is the inverse function of the standard normal distribution (Gescheider, 1997; but note our  $S-$  distribution is shifted right). This equation quantifies the difficulty of the discrimination problem (and the separation of the two stimulus distributions). We remark that alternative estimates of discriminability are possible, in particular the use of ROC curves, and these alternatives can provide a more complete description of the discrimination process (Macmillan & Creelman, 2005). Our goal, however, is to generalize about the effects of 'discriminability', and its interactions with payoffs and prey prevalence, on predator decisions and so we use the simpler  $d'$  technique because of its simplicity and broad applicability. Note our use of  $d'$  assumes that the signal and noise

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