Do unprofitable prey evolve traits that profitable prey find difficult to exploit?

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Prey that are unprofitable to attack (for example, those containing noxious chemicals) are often conspicuously patterned and move in a slower and more predictable manner than species lacking these defences. Contemporary theories suggest these traits have evolved as warning signals because they can facilitate both associative and discriminative avoidance learning in predators. However, it is unclear why these particular traits and not others have tended to evolve in unprofitable prey. Here we show using a signal detection model that unprofitable prey will evolve conspicuous colours and patterns partly because these characteristics cannot readily evolve in profitable prey without close mimicry. The stability of this signal is maintained through the costs of dishonesty in profitable prey. Indeed, unprofitable prey will sometimes evolve a conspicuous form to reduce mimetic parasitism, even in the unlikely event that this form can be more closely mimicked. This is one of the first mathematical models of the evolution of warning signals to allow for the possibility of mimicry, yet our analyses suggest it may offer a general explanation as to why warning signals take the form that they do. Warning signals and mimicry may therefore be more closely related than is currently supposed.

Keywords: mimicry; crypsis; warning signals; aposematism; honest signalling

1. INTRODUCTION

Prey that are unprofitable to attack (such as those which have stings, or contain toxins) are often conspicuously coloured and patterned (Wallace 1867; Poulton 1890). However, unprofitable prey also show a tendency to engage in slower and more predictable movement (Bates 1862; Hatle & Faragher 1998; Sherratt *et al.* 2004; Srygley 2004) and, in insects at least, are overall more likely to occur in aggregations than related profitable prey (Tullberg & Hunter 1996; Nilsson & Forsman 2003). It is not entirely obvious why natural selection should lead to these well known associations. However, it is noteworthy that conspicuousness, slow movement and aggregation would render any profitable prey species that exhibited these traits highly vulnerable to attack in the absence of close mimicry. One possibility therefore, is that traits such as these are not as strongly selected against in unprofitable prey compared to profitable prey (Gagliardo & Guilford 1993; Sherratt *et al.* 2004; Beatty *et al.* 2005; Speed & Ruxton 2005). Put another way, unprofitable prey can avail themselves of opportunities that are not open to profitable prey. Alternatively, or in addition, unprofitable prey may have evolved these distinguishing traits as signals of defence because they are amongst the least susceptible to exploitation by profitable prey (Chai 1996; Sherratt & Beatty 2003; Srygley 2004). Indeed, unprofitable prey may even be willing to pay an energetic cost to achieve slow, conspicuous flight (Srygley 2004).

The general idea that unprofitable prey species are under some form of selection to evolve distinguishing traits was central to the early discussions of the concept of warning signals. Wallace (1867) for example, is reported

to have emphasized the importance of unpalatable prey adopting signals that were markedly different in appearance from palatable prey. Fisher (1930) similarly emphasized the relationship between adopting a signalling trait and avoiding mimicry by profitable species, noting (page 148) ‘to be recognized as unpalatable is equivalent to avoiding confusion with palatable species’. While contemporary theories of warning signals have tended to suggest that unprofitable prey have evolved traits to exploit the associative biases of predators (Guilford 1988, 1990; Speed 2001), parallel approaches such as those based on peak shift (Leimar *et al.* 1986; Yachi & Higashi 1998) and predator-induced filtering effects (Sherratt 2002a; Franks & Noble 2004) have continued to emphasize and explore the importance of discriminative learning in generating selection for traits in unprofitable prey.

Despite the simplicity of the proposal that conspicuous warning signals have evolved in unprofitable prey as a way of avoiding confusion with potential mimics, surprisingly little work has been done to question the validity of this argument, or examine its implications. For example, we know of no mathematical model of the evolution of warning signals that has formally considered the possibility of mimicry. Similarly, we know of only one set of models dealing with the evolution of mimicry that has explicitly considered prey conspicuousness (Charlesworth & Charlesworth 1975a,b,c), and even here the unprofitable prey species was not free to evolve. If profitable prey species can evolve either crypsis or mimicry as a means of avoiding attack, then many evolutionary trajectories of profitable prey may simply be towards increasing crypsis, rather than towards more complex co-evolutionary chases of mimic and model (e.g. Gavrillets & Hastings 1998). Similarly, unprofitable prey may be selected to evolve

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crypsis if any conspicuous form they take is readily mimicked. This paper represents an attempt to address this shortfall, with the primary aim of elucidating whether unprofitable prey experience selection to evolve traits that profitable prey would find difficult to exploit.

2. THE MODEL

We begin by assuming that there are two forms of a given species of unprofitable prey species U (densities U_1 and U_2) and two forms of a profitable prey species P (densities P_1 and P_2)—see [Gavrilets & Hastings \(1998\)](#) for a similar approach. The two analogous forms of the two species (1 and 1, 2 and 2) look alike to predators to a certain degree (measured as s_1 and s_2 , $0 \leq s_1, s_2 \leq 1$, see below), however we assume that the two forms 1 and 2 are themselves sufficiently distinct that there is no confusion between them. If predators attack a profitable prey item then they gain benefit b , but if they attack an unprofitable prey they incur cost c . We let the probability of a predator detecting an item of forms 1 and form 2 on encounter be measured by q_1 and q_2 , respectively, which we assume is directly proportional to prey conspicuousness. For convenience, we also assume haploid genetic control of the different visual forms, with a per capita rate of mutation of m , and logistic population growth parameters r and K (identical for both species). Given these conditions, the dynamical rate equations for U_1 , U_2 , P_1 and P_2 can be represented as follows.

Unprofitable prey

$$\frac{dU_1}{dt} = rU_1\{1 - \frac{\text{growth}}{(U_1 + U_2)/K}\} - mU_1 + mU_2 - f_1(b, c, s_1, U_1, P_1) q_1 U_1, \quad (2.1)$$

$$\frac{dU_2}{dt} = rU_2\{1 - (U_1 + U_2)/K\} - mU_2 + mU_1 - f_2(b, c, s_2, U_2, P_2) q_2 U_2. \quad (2.2)$$

Profitable prey

$$\frac{dP_1}{dt} = rP_1\{1 - (P_1 + P_2)/K\} - mP_1 + mP_2 - g_1(b, c, s_1, U_1, P_1) q_1 P_1, \quad (2.3)$$

$$\frac{dP_2}{dt} = rP_2\{1 - (P_1 + P_2)/K\} - mP_2 + mP_1 - g_2(b, c, s_2, U_2, P_2) q_2 P_2. \quad (2.4)$$

Predation functions $f_1()$, $f_2()$, $g_1()$, $g_2()$ refer to the probability of attack of a given form on encounter with a predator. Signal detection theory ([Oaten *et al.* 1975](#); [Staddon & Gendron 1983](#); [Getty 1985, 1987](#); [Greenwood 1986](#); [Johnstone 2002](#); [Sherratt 2002b](#)) provides one such optimal solution based on the relative probabilities that an encountered prey type is profitable or unprofitable, weighted by the benefits and costs of attacking these prey types. Such a formulation does not explicitly involve learning and therefore circumvents the problem of the initial spread of conspicuous forms from rarity, for which there are now many solutions (e.g. [Ruxton *et al.* 2004](#); [Marples *et al.* 2005](#)). Using [Staddon & Gendron's \(1983\)](#) power curve approximation (see also [Greenwood 1986](#))

we have:

$$g_1() = [(P_1 b s_1)/(U_1 c)]^{(s_1/(1-s_1))}, \quad (2.5)$$

$$f_1() = g_1()^{(1/s_1)}. \quad (2.6)$$

Similarly,

$$g_2() = [(P_2 b s_2)/(U_2 c)]^{(s_2/(1-s_2))}, \quad (2.7)$$

$$f_2() = g_2()^{(1/s_2)}, \quad (2.8)$$

subject to the constraint:

$$0 \leq f_1(), f_2(), g_1(), g_2() \leq 1.$$

The signal detection component allows us to model predator generalization and recognition errors; with parameter s_1 and s_2 we can control the level of mimicry by modifying the degree to which unprofitable prey will be confused with profitable prey. Thus, when $s_1 = 1$ (perfect mimicry) then the payoff-maximizing probabilities of predators attacking profitable and unprofitable prey of form 1 on encounter are identical $\{f_1() = g_1()\}$, whatever the specific solution. By contrast, if $s_1 = 0$ (the species versions of form 1 are completely different in appearance) then $g_1() = 1$ while $f_1() \rightarrow 0$. Taken together, when $s_1 > s_2$ and $q_1 < q_2$ then for a cryptic unprofitable prey to become distinctive it must degrade its cryptic protection.

3. MODEL EXPLORATION

Equations (2.1–2.4) were solved numerically from fixed starting points $\{U_{10}, U_{20}, P_{10}, P_{20}\}$ using a standard fourth-order Runge–Kutta approach. So long as population growth was high enough to replace individuals lost due to predation (e.g. $r = 1$, $K = 1000$), then the proportion of individuals of a given species in one form or another was insensitive to the precise growth rate parameters (indeed it is possible to formulate an analogous model based only on payoffs in a game). The mutation rate m was assumed low in all cases ($m = 0.001$) so that differences in attack rates on the different forms were the primary source of population-level genotypic change. To explore the model we first examine what forms each species evolve in extreme circumstances and then assess its implications under more general conditions.

(a) *The two species forms are both perfectly mimetic*

In this extreme case we ask what forms the profitable and unprofitable species evolve when the parallel forms are perfectly mimetic ($s_1 \rightarrow 1$ and $s_2 \rightarrow 1$). When $b > c$ then profitable prey tend to undermine any signalling that evolves in unprofitable prey. Under these conditions, both the profitable and unprofitable species evolve their most cryptic forms (effectively, the most highly protected common denominator) whatever the start conditions ([figure 1a](#)). By contrast, when $b < c$ then the system generally has enough unprofitable prey to deter predation and both the profitable and unprofitable species evolve a 50% combination of both forms (graph not shown), maintained simply by mutational balance.

(b) *The two species forms are readily distinguishable*

In this second extreme case we ask what forms the profitable and unprofitable species evolve when the

Figure 1. Evolution of profitable and unprofitable species' appearance as a consequence of optimal predator behaviour. The smooth line denotes unprofitable prey, and the dotted line denotes profitable prey. Parameter values: $b=2$, $c=1$, $m=0.001$, $r=1$, $K=1000$, $q_1=0.1$, $q_2=0.2$, $U_{10}=0$, $U_{20}=500$, $P_{10}=0$, $P_{20}=500$. In (a): $s_1=0.999$, $s_2=0.999$ (perfect mimicry). In (b): $s_1=0.2$, $s_2=0.2$ (imperfect mimicry).

parallel forms are distinct ($s_1 \rightarrow 0$, $s_2 \rightarrow 0$). In this case the profitable species always evolves its most cryptic form whatever the relative value of b and c . Since unprofitable prey are always avoided by payoff-maximizing predators this species evolves a 50% combination of both forms, maintained by mutational balance.

(c) Coarse differences in mimicry and conspicuousness between forms

Here we consider the ways in which the two species evolve when one mutational form is much more conspicuous than the other ($q_1 \ll q_2$), and one form is much more discriminable than the other ($s_1 \ll s_2$ or $s_1 \gg s_2$)—see table 1. When the form that is most cryptic is also more readily differentiated, then both species evolve this cryptic form. By contrast, when the most conspicuous form is the most discriminable, then the unprofitable species tends to evolve this form while the profitable species evolves cryptic.

We now turn to elucidating the form that evolves in profitable and unprofitable species under a broader range of conditions. For parsimony we have restricted ourselves here to showing results in the case of $b > c$ and when both prey species start initially in form 1. However, all of our central findings hold under a range of values $b < c$ and when both prey species start exclusively in their form 2.

(d) Varying the degree of mimicry

When both forms of the two prey species can be discriminated to an extent ($0 < s_1, s_2 < 1$) and one form is considerably more conspicuous than the other, then unprofitable prey tend to evolve this more conspicuous form under a range of different combinations of s_1 and s_2 (figures 1b, 2a). By contrast, the profitable prey species often remain predominantly in their cryptic form (figures 1b, 2b). This difference in the type of trait that evolves in profitable and unprofitable prey is most marked when the conspicuous form of the two species can be readily distinguished ($s_2 \leq 0.4$ in figure 2a,b). Yet discriminability is not the only factor that influences the outcome. For instance, when prey forms can be more readily distinguished in their cryptic state ($s_1 < s_2$) then unprofitable prey sometimes evolve the more conspicuousness form, while profitable prey remain cryptic.

When one prey form is only slightly different in conspicuousness than the other then the conditions under which a (marginally higher) conspicuous form would evolve in unprofitable prey become somewhat more restricted (figure 2c,d). Under these cases however, whenever a high proportion of unprofitable prey evolve to adopt their (marginally) more conspicuous form, then so do the profitable prey.

(e) Varying the degree of conspicuousness

When form 1 of prey are much more readily confused than form 2 prey ($s_1 \gg s_2$) then the unprofitable species tends to evolve form 2, regardless of its relative degree of conspicuousness (figure 3a, see electronic supplementary material). Thus, unprofitable species will even evolve a more cryptic form in the unlikely scenario that it allows them to be much more readily distinguished from profitable prey (cf. Sherratt & Beatty 2003; Wüster *et al.* 2004). By contrast, profitable prey are much more sensitive to conspicuousness *per se*—as might be expected, without good mimicry, they tend to adopt the most cryptic form (figure 3b, see electronic supplementary material).

When parallel forms of the two species are both relatively similar ($s_1 = s_2 = 0.7$ say) then (as noted in the case for perfect mimicry) both profitable and unprofitable prey evolve the most cryptic form (figure 3c,d, see electronic supplementary material). When parallel forms are both relatively distinct ($s_1 = s_2 = 0.1$ say) then unprofitable prey evolve the most conspicuous form (figure 2e). In this case, profitable prey rarely becomes mimetic (and thus conspicuous) because they are too readily detected (as also noted in the case of no mimicry). However, there are conditions under which the benefits of mimicry outweigh the costs of higher conspicuousness, particularly when the two forms are similar in conspicuousness (figure 2f).

(f) Model extension: three forms of each prey species

When the model is extended to include 3 forms of unprofitable species and 3 parallel forms of profitable species, then qualitatively identical results pertain. For example when $b=2$, $c=1$, $s_1=s_2=s_3=0.2$ and $q_1=0.1$, $q_2=0.2$, $q_3=0.5$ then the unprofitable species evolves predominantly the most conspicuous form (3), while the profitable species evolves predominantly the most cryptic form (1). The same result holds even if we keep all other parameters the same and make the two species most

Table 1. Evolving a means to avoid predation.

(The equilibrium morphological form exhibited by the vast majority of profitable and unprofitable prey at $t = 1000$ under various combinations of parameters q_1, q_2, s_1, s_2, b and c . Exact parameter values given in square brackets. Other parameter values $r = 1$, $K = 1000$, $m = 0.001$. These conclusions remained the same whether all prey start as form 1 ($U_{10} = 500$, $U_{20} = 0$, $P_{10} = 500$, $P_{20} = 0$) or all prey start as form 2 ($U_{10} = 0$, $U_{20} = 500$, $P_{10} = 0$, $P_{20} = 500$).)

		$b > c$ [$b = 2, c = 1$]	$b < c$ [$b = 1, c = 2$]
$q_1 < q_2$ [$q_1 = 0.2, q_2 = 0.8$]	$s_1 < s_2$ [$s_1 = 0.2, s_2 = 0.8$]	unprofitable: cryptic profitable: cryptic	unprofitable: cryptic profitable: cryptic
	$s_1 > s_2$ [$s_1 = 0.8, s_2 = 0.2$]	unprofitable: conspicuous profitable: cryptic	unprofitable: conspicuous profitable: cryptic

readily distinguishable in their cryptic form ($s_1 = 0.1$). Thus (as noted in §4) avoiding parasitism by being conspicuous can sometimes be more effectual when imperfect mimicry is involved, than adopting a more cryptic and even more distinguishable form.

4. DISCUSSION

Conspicuous warning signals and mimicry are amongst the best known forms of anti-predator adaptations (Ruxton *et al.* 2004), yet remarkably little work has been done to elucidate how these phenomena might be related. Previous approaches to Batesian mimicry have implied that *any* mutant form of the mimic which brings the mimic closer in appearance to the unpalatable model will be favoured by individual natural selection. This may indeed be the case if signal magnitude is unrelated to conspicuousness, but by no means inevitable if the unprofitable model is highly conspicuous (Charlesworth & Charlesworth 1975a,b,c). In fact, if a noxious species is highly conspicuous then there may be far less scope for the gradual improvement of mimetic resemblance of a Batesian mimic through intermediate stages because mutant individuals displaying these intermediate forms would be more easily seen than their conspecifics, although still readily recognized (Charlesworth 1994).

The results of the model we have presented allow us to make several key points:

- the clearest conditions for the divergence in appearance between profitable and unprofitable prey occurs when the conspicuous form of an unprofitable prey is both highly conspicuous and different in appearance from any potential mimic;
- since conspicuousness can render profitable prey vulnerable to attack, unprofitable prey will sometimes evolve conspicuousness to avoid Batesian mimics, even if a conspicuous form is less readily distinguished than an alternative cryptic form;
- unprofitable prey should evolve crypsis along with profitable prey if they have the potential to attract an excessive mimicry burden in any form they take.

It is our hope that some of the simple predictions made here could be formally tested. The ‘evolving pastry’ experimental approach of Thomas *et al.* (2004) offers a direct way of assessing what forms evolve under controlled conditions, as does the approach using humans foraging on artificial computer-generated prey (e.g. Sherratt & Beatty 2003).

Note that our results are not simply a re-statement of Wallace’s argument that unprofitable prey will adopt forms that help distinguish themselves from profitable prey. Thus, the results portrayed in figure 1b in which $s_1 = s_2$ cannot be explained in the basis of discriminability alone. Indeed, our analysis suggests that unprofitable prey will sometimes evolve a conspicuous form to avoid mimetic parasites, even if that form is *less* readily distinguished than an alternative, more cryptic, form.

Considering our original question: ‘Do unprofitable prey therefore evolve traits that profitable prey find difficult to exploit?’ The model presented here suggests that the answer is a qualified ‘yes’—higher conspicuousness can indeed act to reduce the mimetic burden on unprofitable prey by rendering imperfect profitable mimics more vulnerable, and this effect alone can sometimes sufficient to generate selection on unprofitable prey in this direction. Conspicuousness is not however a panacea—the same model suggests that when mimicry is widespread (s_1 and s_2 high), then conspicuousness *per se* will not be enough to secure protection. Under these conditions unprofitable species themselves will also evolve cryptic traits if there is no way to escape intense exploitation by accurate mimics. The marine sea butterfly *Clione antarctica* is one potential example of a chemically defended yet inconspicuous (to fish) species (Ruxton *et al.* 2004). Endler & Mappes (2004) similarly argued that crypsis could evolve in unprofitable species, and listed several potential examples including larvae of *Dryas julia* butterflies, pine sawfly larvae (*Neodiprion sertifer* and *Diprion pini*) and certain shield bugs (Acanthosomatidae, Heteroptera). However, here their arguments were based on a rather different (but complementary) set of reasons—variation among predators in their tendency to attack defended prey.

As noted above, unprofitable prey species and profitable prey species most clearly diverged in appearance (unprofitable prey evolved the conspicuous form while profitable prey evolved the cryptic form) when ($s_1 \gg s_2$) and ($q_1 \ll q_2$) or vice versa, i.e. when the conspicuous form is highly conspicuous and readily discriminable—see table 1. These conditions may well hold in a variety of natural systems. For instance, Guilford & Dawkins (1991) proposed (page 3) ‘Aspects of a signal that lead to its being increasingly detectable may also lead to its being increasingly discriminable’. This will particularly be the case if predators have a longer time to observe conspicuous prey before making an attack (Guilford 1986). Similarly, prey that adopt crypsis may be more limited in colour variation possibilities and it may be reasonable to assume that there will be a higher level of generalization over them.

Figure 2. Proportions of unprofitable and profitable prey that evolve to form 2 after $t=1000$ for a variety of values (0.05–0.95 in steps of 0.05) of s_1 and s_2 (a–d), and of q_1 and q_2 (e, f). In all cases equilibria were reached. Parameter values: $b=2$, $c=1$, $m=0.001$, $r=1$, $K=1000$, $U_{10}=500$, $U_{20}=0$, $P_{10}=500$, $P_{20}=0$. In 2a, b: $q_1=0.1$, $q_2=0.5$ (form 2 is more conspicuous). In 2c, d: $q_1=0.1$, $q_2=0.11$ (form 2 is marginally more conspicuous). In 2e, f: $s_1=0.1$, $s_2=0.1$ (both forms are equally discriminable—note the non-monotonic nature of the response for profitable prey).

Of course it is possible that some unprofitable prey species may be able to reduce their degree of Batesian parasitism by evolving a distinct (s1 low) but cryptic form (q1 low). Under such conditions one would expect that unprofitable prey would evolve this cryptic form, especially if in so doing they became cryptic to their own prey. Such a condition might well apply to the venomous European adder (*Vipera berus*) which has inconspicuous but distinctive markings and whose patterns are avoided by predators (Wüster *et al.* 2004).

In our case, we did not include any plausible additional advantages to conspicuousness such as sexual selection or improved thermoregulation (Speed & Ruxton 2005) and neither did we assume any inherent receiver biases of predators such as quicker avoidance learning of more conspicuous forms (see Rowe & Skelhorn 2004 for a recent review). Therefore, here aposematic prey were not availing themselves of opportunities not available to profitable prey, or responding to some innate predatory preferences, but simply capitalizing on a more reliable way of signalling their unprofitability. In support, Sherratt & Beatty (2003) found using an artificial experimental system, that unprofitable models eventually evolved the only colour form that could not be mimicked, even if this form was cryptic.

Although this work is amongst the first to formally explore the evolution of conspicuous colouration in the context of mimicry (or in a general sense, confusion), one limit of the approach is that it considers only two species each with a maximum of three different forms with fixed similarity coefficients (i.e. the level of mimicry is fixed). Future work using an individual-based modelling approach will allow us to further relax some of our assumptions, and evaluate the robustness of our arguments for a far wider set of circumstances, and examine the implications of the approach for signalling traits other than conspicuousness.

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