THE ROYAL SOCIETY

Received 29 March 2004
Accepted 18 May 2004

Evasive mimicry: when (if ever) could mimicry based on difficulty of capture evolve?

G. D. Ruxton[1]*, M. Speed[2] and T. N. Sherratt[3]

[1] *Division of Environmental and Evolutionary Biology, IBLS, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK*
[2] *School of Biological Sciences, University of Liverpool, Liverpool L69 7ZB, UK*
[3] *Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada*

We elucidate the conditions under which an easy-to-catch edible prey species may evolve to resemble another edible species that is much more difficult to capture ('evasive Batesian mimicry'), and the conditions under which two or more edible but hard-to-catch species evolve a common resemblance ('evasive Müllerian mimicry'). Using two complementary mathematical models, we argue that both phenomena are logically possible but that several factors will limit the prevalence of these forms of mimicry in nature. Evasive Batesian mimicry is most likely to arise when it is costly in time or energy for the predator species to pursue evasive prey, when mimics are encountered less frequently than evasive models and where there are abundant alternative prey. Evasive Müllerian mimicry, by contrast, is most likely to arise when evasive prey species differ in abundance, predators are slow to learn to avoid evasive prey and evading capture is costly to the prey. Unequivocal evidence for evasive Batesian or Müllerian mimicry has not yet been demonstrated in the field, and we argue that more empirical work is needed to test whether putative examples are indeed a result of selection to signal difficulty of capture.

Keywords: Batesian mimicry; Müllerian mimicry; aposematism; escape behaviour; predation

1. INTRODUCTION

We are familiar with the idea that members of a species that is palatable to a predator can evolve increased protection from predators by mimicking the appearance of another unpalatable species: this is Batesian mimicry (Bates 1862; Mallet & Joron 1999). Here, we ask whether it is feasible to have mimicry on the basis of difficulty of capture or subjugation rather than unpalatability after capture. Specifically, can a prey species that is easy for its predators to catch gain protection by mimicking a species that is sufficiently hard to catch that predators sometimes decline the opportunity to pursue them? We will call this 'evasive Batesian mimicry' and distinguish it from 'locomotor mimicry', which is generally interpreted as the mimicry of the *movement* behaviour of unpalatable prey (Srygley 1999). An analogous form of 'evasive Müllerian mimicry' might in theory occur when two or more evasive species evolve a similar appearance, thereby reducing their mortality (or giving them more time to reproduce) during the course of predator education.

The first to recognize the possibility of evasive mimicry appear to be van Someren & Jackson (1959), who studied a group of African butterflies (*Rhopalocera*), and proposed that

> Protective resemblance exists among relatively edible *Rhopalocera* and can be divided intro three natural groups each involving factors other than distastefulness, as follows.... B. Difficulty of capture.
> (van Someren & Jackson 1959, p.122)

Holling (1965) similarly proposed

> ...effective escape behaviours are common features that inhibit predators, quite independently of edibility.... Thus mimicry among edible species might simply reflect a technique of repelling predators that does not involve taste.
> (Holling 1965, p. 22)

Rettenmeyer (1970) also included an effective escape mechanism in his list of features worth mimicking. An early non-lepidopteran example was reported by Lindroth (1971), who observed visual similarity between sympatric flea-beetles (Alticinae, Chrysomelidae) and ground beetles (Lebia, Carabidae). He suggested that none of these beetles was unpalatable to their predators but that flea-beetles could jump as an effective form of escape from predators, an ability that ground beetles do not have. Lindroth's suggestion was that the unprofitability of the escape ability of flea-beetles to predators formed the basis for evasive Batesian mimicry by the ground beetles, although the palatability of the beetles has since been called into question (see Moore 1979; Brower 1995). Hespenheide (1973) proposed that evasive mimicry occurred, in a predominantly Müllerian form, among a complex involving flies and agile beetles in the American tropics. Similarly, Holm & Kirsten (1979) argued that the remarkable similarity of a complex of scarab beetles in the Namib desert, all with orange-brown elytra, was best explained by a combination of Batesian and Müllerian evasive mimicry. In a related idea, it has been suggested that species use conspicuous coloration to advertise difficulty of capture to predators (Young 1971; Thompson 1973; Baker & Parker 1979; Grewcock 1992; Dittrich *et al.* 1993; Pinheiro 1996; Srygley 1999).

---

[*] Author for correspondence (g.ruxton@bio.gla.ac.uk).

doi:10.1098/rspb.2004.2816

So far, there have been three experimental studies into evasive Batesian mimicry (Gibson 1974, 1980; Hancox & Allen 1991), each of which purported to provide evidence that such mimicry could occur. In contrast, Brower (1995) argued that these studies actually provide no strong evidence in support of evasive Batesian mimicry and that this phenomenon could not in fact occur: Brower (1995) concluded that

> the existence of mimicry between palatable but unpro-fitable prey is disputed on theoretical and empirical grounds.
> (Brower 1995, p. 413)

Despite Brower's contention, evasive Batesian mimicry is still being discussed in the literature (see Srygley 1994, Brower 1995, Srygley 1999 for reviews) and new purported examples of it are being reported (e.g. Balgooyen 1997). In this paper, we will again review the evidence and combine this with the current understanding of the mechanisms behind classical unpalatability-based mimicry: we argue that evasive mimicry is logically possible but that there are fundamental aspects of it that will limit its possible prevalence in nature.

2. METHODS

(a) *Empirical evidence*

Gibson (1974) reported on predation by star finches (*Bathilda ruficauda*) on three types of seeds that differed in colour (green, blue and red). Each seed type was equally attractive to the birds. On each experimental day, three seeds of each colour were presented to a single caged bird. The nine seeds were presented sequentially in random order. Each was placed on a platform painted with blue and green dots, on which the blue and green seeds were considered cryptic (compared with the red). When the bird approached the platform and attempted to feed on the single seed, the platform could be tilted to remove the seed from the bird's reach. During the initial part of the experiment, the platform was always tilted when blue or red seeds rested on it, but the bird was allowed to eat green seeds undisturbed. Birds reacted to this by increasing their latency to attack blue and red seeds. During the second half of the experiment, the platform was never tilted no matter which colour of seed was offered. The birds' latency to attack blue seeds remained higher than their latency to attack green seeds for several days after the change in regime, but it eventually returned to the same level as with green seeds. By contrast, the birds were still much slower to attack red seeds than green ones some two weeks after the regime change, when the experiment ended. This latency could be sufficiently long that the bird never attacked a seed in the two-minute period before Gibson terminated that trial. Gibson considered the red and blue seeds in the first part of the experiment to function as evasive models, whereas the same types in the second half acted as mimics. She interpreted her results as giving support to the plausibility of evasive mimicry, especially if the evasive model were non-cryptically coloured. Reporting a later study, Gibson (1980) presented a very similar experiment, except that robins (*Erithacus rubecula*) were used as predators and colour-banded mealworms (*Tenebrio molitor*) as prey. The results were essentially identical to those described above except that, by 14 days after the regime change, all but one of the six robins had returned to taking all three prey types equally as willingly.

In a related experiment, Hancox & Allen (1991) used unmarked garden birds as predators and cylinders of red and yellow uncooked dough, presented on a bird-table, as prey. A presentation consisted of two yellow and two red prey simultaneously. When a bird landed on the table and attempted to feed on a prey item (of either colour), a mechanism was activated that removed the prey of one colour but not the other from the bird's reach. The colour of the first prey item to be attacked was recorded. On the first day, the prey withdrawal mechanism was not used and birds had a free choice of either prey: the results showed a very slight preference for yellow prey. On days 2–21, yellow prey were made evasive by being withdrawn when the bird attacked the bait. Birds reacted to this with a progressive decrease in the probability that the first-attacked prey would be yellow. On day 22, the evasion mechanism was not used: the first-attacked prey was red on 28 occasions and yellow on 15. On days 23–39 the red prey were now made evasive and the yellow were not, and the birds responded by progressively focusing their attacks on yellow prey. Finally, on day 40, the evasion mechanism was again switched off: the first-attacked prey was red on 10 occasions and yellow on 28. From this, Hancox and Allen concluded that

> . . .birds in their normal surroundings learned to ignore prey that are adept at 'escaping' and instead concentrated on alternative non-escaping food.
> (Hancox & Allen 1991, p. 12)

Of course, designing appropriate experiments to test the plausibility of evasive mimicry can be challenging, not least because a rapid escape movement can also generate a startle response in predators. Nevertheless, Brower (1995) suggested that the above studies actually provide evidence against evasive Batesian mimicry:

> These results showing quick loss of aversion to prey unprofitability by reason of effective escape are in marked contrast to reports of long-term aversion to aposematic prey.
> (Brower 1995, p. 416)

We agree that mimicry requires that predators remember previous encounters with similar-looking prey, and that all three experiments suggest that in the absence of negative reinforcement (through experiencing evasive models) memories fade and with them any protection afforded to non-evasive mimics. However, unlike Brower, we see no evidence in these studies that evasive Batesian mimicry cannot be sustained, only that the mimic would soon lose protection if the predator stops encountering models. However, in principle this may be no different from what would occur if aversion were driven by unpalatably rather than evasiveness.

(b) *A mathematical treatment of evasive Batesian mimicry*

The experiments of Gibson (1974, 1980) and of Hancox & Allen (1991), for convenience, involve a situation where predators encounter exclusively evasive models then exclusively evasive mimics. This might represent the ecological situation where the evasive model species is available for a brief period early in the season, whereas mimics are only available later in the season. Under such circumstances, the experiments seem to suggest that evasive Batesian mimicry would be ineffective. However, this is not the only ecologically realistic situation: it may be that the model and mimic populations occur simultaneously, and hence predators continue to encounter models as well as mimics. Only experiments that allow for periodic experiences with evasive models to potentially 'jog the memory' of predators can evaluate whether evasive mimicry can be sustained in such circumstances. Brower's (1995) dismissal of the feasibility of evasive mimicry on the grounds of these previous experimental results is therefore premature. However, we feel that there are several previously unconsidered factors that will limit the frequency of occurrence of evasive mimicry in the natural world. These are best introduced using a simple mathematical model.

Consider a predator feeding on a palatable species A. We will assume that a searching predator encounters individuals of this species at rate λ_a. On encountering a prey individual, the predator must invest a 'handling time' t_a in pursuing, catching, subjugating and consuming that individual. Searching and handling are incompatible, but after handling a prey item, the predator immediately returns to searching for another. For simplicity, we assume that all encountered prey of species A are caught and yield unit energetic value. It is easy to show that these assumptions lead to a long-term rate of energy gain given by:

$$R_A = \frac{\lambda_a}{1 + \lambda_a t_a}.$$

This is the Holling disc equation (Holling 1965).

Imagine now a more complex ecosystem, where as well as species A, the predator also encounters a species E at rate λ_e. We assume that E individuals can easily be distinguished from A individuals by the predator. Pursuit of individuals of species E takes a finite time (during which searching does not occur). However, this species is highly evasive, and pursuit always ends in escape of the prey. Clearly, the optimal behaviour for the predator would be to ignore any individuals of species E encountered (since pursuing them wastes time for no gain) and focus exclusively on species A, yielding energy at rate R_A.

We now make the system more complex again and add another species M, individuals of which mimic the appearance of the evasive species E. However, if the predator pursues an M individual, that individual can be caught and yields unit energetic reward (identical to species A). Hence, M individuals should be attractive to the predator, but the predator faces the problem that on initial encounter it cannot differentiate between evasive unprofitable E individuals and profitable mimetic M individuals. However, if it invests a time t_s in 'sampling' an encountered individual (say by chasing it), then this sampling does allow differentiation into either species E or M. This sampling time is similar to the recognition time in the diet choice model of Hughes (1979). Clearly, if the individual is of species E then the predator should desist from further time investment in that individual and return to searching. If, however, it is an M individual then a further time t_m must be invested in catching, subduing and consuming that individual. Using standard time-budget methods (e.g. Lendrem 1986; Stephens & Krebs 1986), it is easy to show that the uptake rate for a predator that includes both A and M individuals in its diet is:

$$R_{AM} = \frac{\lambda_m + \lambda_a}{1 + \lambda_e t_s + \lambda_m(t_s + t_m) + \lambda_a t_a}.$$

(Here, we implicitly assume that predators do best by either always or never pursuing individuals of a given type. It is possible to prove that no intermediate probabilistic predator strategy can be optimal in this model, but since this result is intuitive and commonly seen in such models, we omit this proof.)

The condition for mimicry to be effective, in that the predator maximizes its uptake rate by excluding the mimetic M species from its diet, is simply that $R_A > R_{AM}$, which (using the equations above) simplifies to:

$$t_m + t_s\left(1 + \frac{\lambda_e}{\lambda_m}\right) > t_a + \frac{1}{\lambda_a}.$$

This suggests that the following ecological conditions are conducive to evasive mimicry: plentiful alternative prey (high λ_a), high costs of differentiating between model and mimic (high t_s) and high encounter rate with models relative to mimics ($\lambda_e > \lambda_m$). These conclusions lead to predictions about the relative prevalence of evasive mimicry compared with classical unpalatability-based mimicry.

First, evasive (and classical) Batesian mimicry can only be maintained in situations where sampling prey is costly to predators. Imagine that there are zebra of two types: fast-running models and slow-running mimics. When stationary or moving slowly, there is no way of telling one from the other. However, a pack of African Hunting Dogs has only to chase a zebra briefly (akin to the sampling in our model) and it will be revealed as model or mimic. The dogs can desist from attacking models, having invested little time or energy in the 'identification chase', but continue pursuing mimics. In this case (corresponding to a low t_s value in our model), the slow-runners would gain nothing from their mimicry. However, consider another predator that relies on surprise and being able to creep up to their prey undetected: a lion, say. If the lion attacks a zebra that turns out to be a model, then not only will it fail to capture that animal but all other animals in the area will be alerted to the lion's presence, forcing it to pay the perhaps substantial cost of moving on to another area before trying another surprise attack. Against such a predator, mimetic slow-running zebra could gain an advantage, since the best strategy for the lion may be to desist from attacking zebras of all types (because of the potential costs of attacking a model) if there are alternative prey. These costs to the predator may be as simple as the time and/or energy invested in unsuccessful attacks. Hence, evasive mimicry is only feasible if the predators do not have a cheap way to tell models from mimics. Exactly the same restriction applies in classical Batesian mimicry, which would be unsustainable in situations where the predator can sample and reject models without any significant cost. However, evasiveness can be evaluated earlier in a predation sequence than unpalatability (evaluation of which generally requires that the prey individual has been pursued, subdued and taken into the predator's mouth). Hence there seems greater scope for low-cost sampling of evasiveness than low-cost sampling of palatability.

Second, a classical Batesian model can be so highly toxic or otherwise defended that it is actually a danger to predators. In such situations, mimics can exist at high population densities (even outnumbering models) because even sampling occasional models would be highly undesirable to predators. Analogous situations (where the cost of sampling a single model is very high) for evasive Batesian mimicry are likely to be less common (although large amounts of energy could be expended, and possible injury could be incurred when pursuing a prey). However, as our model above demonstrates, if evasive models are highly abundant and evasive mimics relatively rare, then evasive Batesian mimicry could be stable since there will be a prohibitively high cost per successful capture from preying on the model–mimic pair, even when the cost of individual encounters with models is low. This occurs because the predator would do best to exclude both from its diet and concentrate on alternative prey. Our arguments lead to the prediction that if Batesian evasive mimicry does exist, then we would expect (i) evasive models to be very abundant (or very apparent) and (ii) mimics to be considerably less common (or at least less apparent) than their models. Although we consider it unlikely that an evasive Batesian mimic would outnumber its model, it is not impossible (although it is less likely than for classical Batesian mimics).

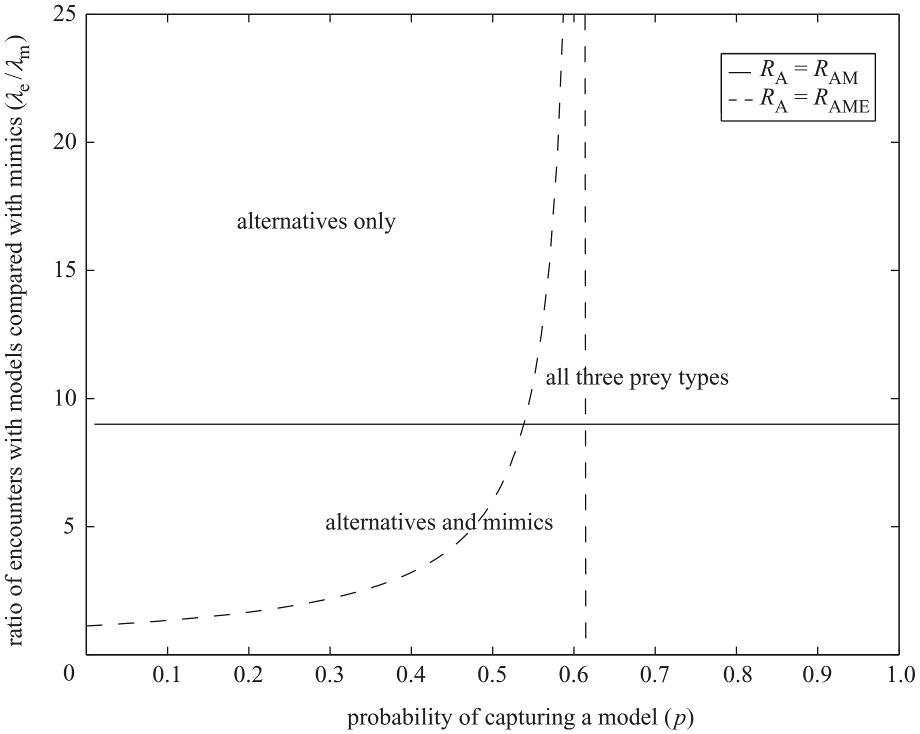

Figure 1. The optimal diet choice of a predator as a function of the ratio of encounters with evasive models and mimics (λ_e/λ_m), and the likelihood that extended pursuit of a model will lead to its capture (p); ($t_a = t_m = 3$; $t_s = 1$; $t_e = 7$; $\lambda_a = 0.1$).

(c) *Extension of the model*

It is possible that the pursuit of prey involves an investment of energy as well as time (see, for example, Stephens & Krebs (1986)). Whereas the prey species that are difficult to catch will be even less profitable under these circumstances, the currency optimized (namely, the long-term rate of energy gain) would remain the same, and qualitatively similar predictions will arise.

Here, we elaborate our model in a rather less obvious direction by including an evasive model that has a probability p of being captured (yielding unit energetic reward) if the predator pursues it for a further time t_e after the initial t_s. Under these conditions the energy gain rate for a predator that pursues all three prey types is:

$$R_{AME} = \frac{\lambda_m + \lambda_a + p\lambda_e}{1 + \lambda_e(t_s + t_e) + \lambda_m(t_s + t_m) + \lambda_a t_a}.$$

For mimicry to be successful we now need to satisfy the same condition as before, $R_A > R_{AM}$, and also the new condition, $R_A > R_{AME}$. These two conditions can be rearranged to give conditions for attacking models/mimics based on the ratio of encounters with evasive models and mimics.

$R_A > R_{AM}$ can be reformed as:

$$\frac{\lambda_e}{\lambda_m} = \frac{t_a + \dfrac{1}{\lambda_a} - t_m - t_s}{t_s},$$

and $R_A > R_{AME}$ becomes

$$\frac{\lambda_e}{\lambda_m} = \frac{t_a + \dfrac{1}{\lambda_a} - t_m - t_s}{t_s + t_e - p\left(\dfrac{1}{\lambda_a} + t_a\right)}.$$

Interpretation of these equations is easiest graphically (see figure 1). When p (the probability that a model will be captured if pursued) is high then, as we would expect, mimicry is ineffective, irrespective of the relative densities of models and mimics, since predators do best if they include all three food types in their diet. This occurs for p values above 0.62 regardless of the values of λ_e and λ_m in figure 1. As p reduces there comes a range when mimicry can be effective (i.e. predators include only the alternative food type A in their diet), provided that the ratio of models to mimics encountered is very high. For a band of intermediate p-values (between 0.54 and 0.62 in figure 1), the predator can include alternatives only, alternatives and mimics or all three types in its diet, depending on prey encounter rates. If models are encountered much more frequently than mimics (above the curved broken line), then only alternatives are consumed and mimicry is effective in offering protection to the mimetic prey type M. For ratios of encounter rates falling below the curved broken line and above the solid line, all three types are consumed. When mimics are relatively common (below the solid line) it pays the predator to focus only on A and M food types. Finally, for low p-values (below 0.55 in figure 1), it is never optimal for the predator to include the evasive prey type in its diet. However, if mimics are rarely encountered compared with models (i.e. above the solid line), then it pays the predator to concentrate on As only and mimicry is effective. The overall conclusions that should be drawn from this are that evasive mimicry is more likely to be effective if evasive models are much more common than mimics and if the models are particularly difficult (or time consuming) to catch. Further, even if the models are highly evasive (i.e. p is near zero in our model), then evasive mimicry will only be successful if mimics are not encountered too frequently by the predator (relative to its frequency of encounter with models).

The third limitation, not considered in our model, on the occurrence of evasive mimicry is that predators may often not be able to learn quickly which prey are more evasive than others. This is unlike the case of palatability, where (ignoring the possibility of automimicry (Brower *et al.* 1967) within the model population) all models that are eaten will be unambiguously detected as being unpalatable and all mimics as palatable. The reason for this difference is that many predators are accustomed to prey escaping from them, and therefore to a low success rate in individual attacks on any prey type. Hence, they need to differentiate between prey on the basis of the proportions of attacks on particular prey morphs that were successful. To put this another way, eating a single prey item, the unpalatability of which can be determined at the point of ingestion, will often allow the predator to identify unambiguously whether it is palatable or not. However, a single experience of a prey item escaping does not give unambiguous evidence of whether it was an intrinsically hard-to-catch prey item or an intrinsically easier-to-catch item that was lucky on this occasion. Thus, learning about palatability will generally be quicker and easier than learning about evasiveness, reducing the ease with which evasive mimicry can occur. However, to mitigate this effect, evasive species may be under selection pressure to aid predator learning (by, for example, aposematic coloration and perhaps amplification of reliable cues that indicate evasiveness prior to attacks). Similarly, predators should be under selection pressure to be good at grading the evasive qualities of prey. Further, it may be possible to test the evasiveness of several individuals simultaneously. Another aid to learning about evasiveness is the close association spatio-temporally between the negative consequences (loss of the prey) and the signal (appearance of the individual). This is not always true for unpalatable prey (where, for example, an emetic effect can occur several minutes after prey ingestion). Hence, the ecological relevance of this restriction on the prevalence of evasive mimicry is less clear than for the two previously discussed restrictions.

(d) *A mathematical treatment of evasive Müllerian mimicry*

Whereas the above treatment of Batesian evasive mimicry identified the optimal strategy set for rate-maximizing predators that already know how difficult certain prey types are to capture, selection for Müllerian mimicry appears to depend more on the educational process itself (Müller 1879; Mallet & Joron 1999; Ruxton *et al.* 2004). Extending Müller's (1879) model (see also Mallet 1999), consider a case in which a predator community must seek to capture n of each distinct type of evasive prey before they avoid them completely. We assume that evasion of attack is energetically costly to the prey, thereby increasing their mortality to a degree (it may also involve additional opportunity costs to the prey that are not explicitly considered here). Under these conditions, one would expect that even highly evasive prey may be selected to avoid pursuit by would-be predators. First, let us consider the case in which two species of distinct-looking evasive prey are at densities a_1 and a_2. Let the n pursuits involved in predator education be randomly (Poisson) distributed among prey with each phenotype. We assume that pursued prey eventually die, with a probability that is dependent on the number of times (x) that they have been pursued (we therefore denote this function $f(x)$). Under these conditions, the survivorships of species 1 and 2 are

$$\frac{a_1 - F(n, a_1)}{a_1}$$

and

$$\frac{a_2 - F(n, a_2)}{a_2},$$

where

$$F(n, a) = \sum_{x=1}^{\infty}\left(\exp\left(\frac{-n}{a}\right)\left(\frac{n}{a}\right)^x\left(\frac{af(x)}{x!}\right)\right).$$

(i.e. $F(n,a)$ = sum of [probability of being approached x times (given Poisson mean (n/a)) multiplied by population size a, multiplied by probability of death after being approached x times] for all possible values of x.)

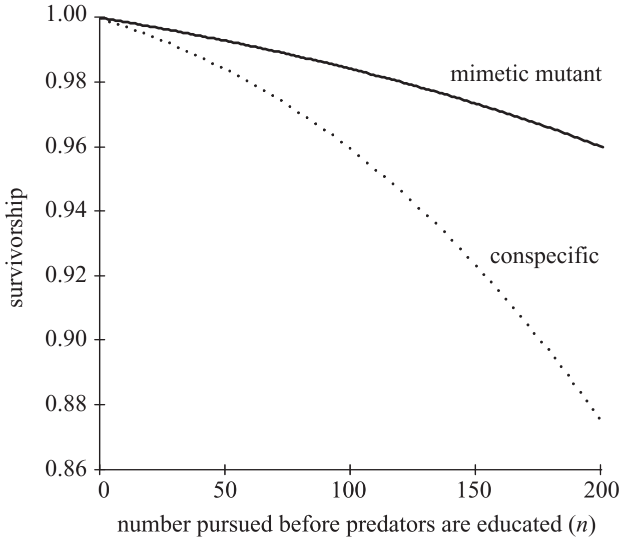

Figure 2. How the survivorship of conspecifics of a distinct evasive species 1 and the survivorship of a mimetic mutant of species 1 change as the number of pursuits necessary to educate predators (n) increases. Parameter values: $a_1 = 100$, $a_2 = 200$, $m = 1$, $k = 1$, $j = 100$. The higher the value of n, the greater the selective advantage to mimicry. When k was reduced to 0.01 (very low mortality from pursuit) then the difference in survivorship between the conspecific and mutant was negligible (even at $n = 200$, the difference in survivorship was 0.003).

When would m mutants of species 1 that looked like species 2 survive better than conspecifics of species 1? This arises when

$$\frac{a_2 + m - F(n, a_2 + m)}{a_2 + m} > \frac{a_1 - m - F(n, a_1 - m)}{a_1 - m}.$$

In the first instance, let us assume that the probability of an individual eventually dying as a result of being pursued is simply directly proportional to the number of times it has been chased, namely $f(x) = xq$, where q is a proportionality constant. Under these conditions, the above inequality reduces to:

$$\frac{a_2 + m - nq}{a_2 + m} > \frac{a_1 - m - nq}{a_1 - m}.$$

This expression in turn reduces to:

$$a_1 < a_2 + 2m.$$

Thus, a very rare (m small) mimetic mutant of evasive species 1 which resembled evasive species 2 would spread if species 1 were rarer than species 2.

To further elucidate the factors that help promote the spread of Müllerian evasive mimicry, we now turn to a more complex model. In particular, it is likely that the relationship between the number of times an individual is pursued and the probability of it dying (for example, through exhaustion) is nonlinear. To reflect this nonlinearity, we have arbitrarily assumed a sigmoid relationship between an individual's mortality and its frequency of pursuit such that $f(x) = e^{xk}/(j + e^{xk})$, where k and j are constants (if k is high then mortality from pursuit more rapidly approaches 1 as x increases). Figure 2 shows how the *per capita* mortality of mimetic mutants and conspecifics varies with n under such conditions.

Table 1. Comparison of our predictions of necessary features of evasive mimicry systems with reported features from previous studies of postulated examples of such mimicry.

reference	system [predator; model; mimic]	alternative prey available?	sampling costly?	high encounter rate with models versus mimics?	notes
Lindroth 1971	birds; flea-beetles (Alticinae, Chrysomelidae); ground beetles (Lebia, Carabidae)	Not discussed but likely.	'A bird repeatedly exposed to this experience [a flea-beetle's rapid escape] may eventually cease to try the hopeless peck.' (p. 46)	'Flea-beetles were much more abundant than Lebia' (p. 41)	Very little consideration is given to ecological considerations in this paper.
Hespenheide 1973	Anolis lizards and birds; flies; beetles in South America	Non-mimetic beetles are also reported from the same surveys.	No direct evidence but arguments that there are likely to be energetic and predation-risk costs associated with failed attacks.	The model flies are described as 'abundant'.	Because most of the beetles are also very quick and elusive, it is suggested that this system is functionally Müllerian.
Holm & Kirsten 1979	jackals, crows, owls, lizards; *Scarabaeus rubripennis* (winged, orange elytra); *Pachysoma denticolle* (wingless, orange elytra)	Yes. There was a high preponderance of black diurnal beetles. Both the orange beetles and the black beetles appeared palatable.	No direct evidence. However, it was argued that *S. rubripennis* is the fastest and most agile species of the orange scarabs in the area.	*S. rubripennis* is found much more frequently in traps than *P. denticolle* but this may be a consequence of their higher activity.	This potential example of Batesian evasive mimicry appears to form part of a more complex community of Müllerian evasive mimics. *P. denticolle* becomes non-mimetic outside the zone of overlap with the model.
Balgooyen 1997	American kestrels (*Falco sparverius*); alfalfa butterfly (*Colias eurytheme*); grasshopper (*Arphia conspersa behrensi*)	Yes. Kestrels fed on 'small vertebrates and invertebrates'	Yes. On average it took 16.2 seconds longer for a young boy to capture a model versus a mimic. Escape rate of models (27.2%) and mimics (1.4%) also differed. Attacks by kestrels on models and mimics often aborted.	No/Yes. The model was 'relatively rare' while the mimic was 'numerically abundant'. However, during 5-minute transects at least one model was visible 100% of the time, but the mimic was only visible 4.2% of the time.	The model appears in the habitat before the putative mimic.
Srygley 1999	probably birds; *Adelpha heraclea* and *A. phylaca* (Nymphalinae); *Doxocopa laure* (Charixinare)	Alternative prey are likely to be common in the neotropical environment.	No direct evidence, although all of these species appear to be difficult to catch, with short, stout abdomens.	This example appears to be a case of Müllerian rather than Batesian escape mimicry.	The three species appear relatively palatable (Srygley 1999 and references therein).

As might be expected, the more individuals that have to be pursued before predators are educated, the greater the selection on evasive prey (as measured by the difference in survivorship) to become Müllerian mimics. Similarly, if pursuit has very few cost implications for the prey (k low) then there is very little difference in mortality between the conspecifics and the mimetic mutants.

In sum, Müllerian evasive mimicry is plausible in theory and is most likely to arise when (i) evasive prey species differ in abundance, (ii) predators are slow to learn to avoid evasive prey and (iii) evading capture is costly to the prey. We note in passing that it can also be shown that selection for Müllerian evasive mimicry is even more intense if the predators have long memories and the rarer evasive species reaches peak abundance later in the season than its co-model.

3. CONCLUSIONS

In summary, we consider that evasive Batesian mimicry should be possible, provided that the predators have alternative prey and that sampling the extent of the evasiveness of an individual prey item is costly to the predator. There is not currently sufficient evidence to judge whether proposed evasive Batesian mimics meet these criteria, although these underlying predictions do not appear to be contravened in any major way (see table 1). Unequivocal evidence of predatory behaviour capable of promoting evasive Batesian mimicry has not yet been demonstrated in the field. Besides formally confirming the palatability of the species involved (see, for example, Lindroth (1971)) and establishing that the species do not resemble one another simply through common descent, it would be helpful to test whether the putative mimic is indeed adversely affected if models were removed, and/or that mimics which are artificially modified in appearance have lower survivorship than mock-treated controls (see, for example, Jeffords *et al.* (1979)). We hope that our clarification of its logical basis will reinvigorate and refocus the search for such evidence. Further, our arguments above should also make clear that (like Hespenheide (1973) and Holm & Kirsten (1979)) we consider that evasive Müllerian mimicry, where two or more hard-to-catch species have similar appearances in order to share the costs of educating predators about their evasiveness, is also logically feasible. Indeed, it may be that evasive Müllerian mimicry will be particularly advantageous if (as we speculate in § 2c) learning about evasiveness is more challenging for predators than learning about unpalatability. However, we would only expect evasive Müllerian mimicry to develop in situations where initiating evasive actions in response to attacks by uneducated predators incurs a significant expense to the prey—expense that Müllerian mimicry could usefully reduce. Such costs have not, to our knowledge, been quantified in previous studies in which evasive Müllerian associations have been postulated.

We thank J. Mallet for advice on an earlier draft of this paper, and two referees for perceptive comments.

REFERENCES

Balgooyen, T. G. 1997 Evasive mimicry involving a butterfly model and grasshopper mimic. *Am. Mid. Nat.* **137**, 183–187.

Baker, R. R. & Parker, G. A. 1979 The evolution of bird coloration. *Phil. Trans. R. Soc. Lond.* B **287**, 63–130.

Bates, H. W. 1862 Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae. *Trans. Linn. Soc. Lond.* **23**, 495–566.

Brower, A. V. Z. 1995 Locomotor mimicry in butterflies? A critical review of the evidence. *Phil. Trans. R. Soc. Lond.* B **347**, 413–425.

Brower, L. P., Brower, J. V. Z. & Corvino, J. M. 1967 Plant poisons in a terrestrial food chain. *Proc. Natl Acad. Sci. USA* **57**, 893–898.

Dittrich, W., Gilbert, F., Green, P., McGregor, P. & Grewcock, D. 1993 Imperfect mimicry: a pigeon's perspective. *Proc. R. Soc. Lond.* B **251**, 195–200.

Gibson, D. O. 1974 Batesian mimicry without distastefulness. *Nature* **250**, 77–79.

Gibson, D. O. 1980 The role of escape in mimicry and polymorphism: I. The response of captive birds to artificial prey. *Biol. J. Linn. Soc.* **14**, 201–214.

Grewcock, D. 1992 The hoverflies: a case of 'poor' mimicry? PhD thesis, University of Nottingham, UK.

Hancox, A. P. & Allen, J. A. 1991 A simulation of evasive mimicry in the wild. *J. Zool.* **223**, 9–13.

Hespenheide, H. A. 1973 A novel mimicry complex: beetles and flies. *J. Entomol.* A **48**, 49–56.

Holling, C. S. 1965 The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* **45**, 1–60.

Holm, E. & Kirsten, J. F. 1979 Preadaptations and speed mimicry among Namib desert scarabaeids with orange elytra. *J. Arid Environments* **2**, 263–271.

Hughes, R. N. 1979 Optimal diets under the energy maximisation premise: the effects of recognition time and learning. *Am. Nat.* **113**, 209–222.

Jeffords, M. R., Sternburg, J. G. & Waldbauer, G. P. 1979 Batesian mimicry field demonstration of the survival value of pipevine swallowtail and monarch color patterns. *Evolution* **33**, 275–286.

Lendrem, D. 1986 *Modelling in behavioural ecology*. Beckenham, UK: Croom Helm.

Lindroth, C. H. 1971 Disappearance as a protective factor. *Entomol. Scand.* **2**, 41–48.

Mallet, J. 1999 Causes and consequences of a lack of coevolution in Müllerian mimicry. *Evol. Ecol.* **13**, 777–806.

Mallet, J. & Joron, M. 1999 Evolution of diversity in warning color and mimicry: Polymorphisms, shifting balance, and speciation. *A. Rev. Ecol. Syst.* **30**, 201–233.

Moore, B. P. 1979 Chemical defences in carabids and its bearing on phylogeny. In *Carabid beetles: their evolution, natural history and classification* (ed. T. L. Erwin, G. E. Ball, D. R. Whitehead & A. L. Halpern), pp. 193–203. The Hague: Dr W. Junk.

Müller F. 1879 Ituna and Thyridia: a remarkable case of mimicry in butterflies. *Proc. Entomol. Soc.* **1879**, xx–xxix.

Pinheiro, C. E. G. 1996 Palatability and escaping ability in neotropical butterflies: tests with wild kingbirds (*Tyrannus melancholicus*, Tyrannidae). *Biol. J. Linn. Soc.* **59**, 351–365.

Rettenmeyer, C. W. 1970 Insect mimicry. *A. Rev. Entomol.* **15**, 43–74.

Ruxton, G. D., Sherratt, T. N. & Speed, M. P. 2004 *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry*. Oxford University Press. (In the press.)

Srygley, R. B. 1994 Locomotor mimicry in butterflies? The associations of positions of centres of mass among groups of mimetic, unprofitable prey. *Phil. Trans. R. Soc. Lond.* B **343**, 145–155.

Srygley, R. B. 1999 Incorporating motion into investigations of mimicry. *Evol. Ecol.* **13**, 691–708.

Stephens, D. W. & Krebs, J. R. 1986 *Foraging theory*. Princeton University Press.

Thompson, V. 1973 Spittlebug polymorphism for warning colour. *Nature* **242**, 126–128.
van Someren, V. G. L. & Jackson, T. H. E. 1959 Some comments on protective resemblance amongst African lepidoptera (Rhopalocera). *J. Lepidopterists' Soc.* **13**, 121–150.
Young, A. M. 1971 Wing coloration and reflectance in *Morpho* butterflies as related to reproductive behaviour and escape from avian predators. *Oecologia* **7**, 209–222.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.