

An individual-based profitability spectrum for understanding interactions between predators and their prey

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There is confusion in the animal behaviour literature over the use of the terms ‘toxicity’ and ‘unpalatability’, which are commonly used interchangeably when describing the function of chemical compounds in prey, although these terms describe very different functions. Toxic chemicals cause fitness-reducing harm, whereas unpalatability provides aversive taste but no reduction in fitness. Furthermore, chemical defences are only one aspect of prey profitability. We argue that if predators are maximizing fitness, all prey can be described in terms of their costs and benefits to predators across all currencies, giving each prey item a positive or negative position on a ‘profitability spectrum’. Adaptively foraging predators should be selected to eat only prey with a positive profitability. The context of each predator–prey encounter also alters the profitability of the prey. Given that profitability is a function of the current state of both the predator and the prey individuals, we explain why it should be considered to be an attribute of a particular encounter, in contrast to its present usage as an attribute of a prey species. This individual-centred perspective requires researchers to investigate, through both theoretical models and empirical studies, the complex conditions in which predators and prey meet in real life.

ADDITIONAL KEYWORDS: aposematism – chemical defence – distasteful – mimicry – predator – prey – profitability spectrum – toxic – unpalatable – warning signal.

INTRODUCTION

All predators need to make adaptive decisions about whether or not to eat different items of prey that they encounter. The fitness implications of the decisions that predators make, and how they decide which prey to eat, have been investigated since Darwin’s time (Darwin, 1859; Wallace, 1889; Poulton, 1890). It is clear that predators need to acquire information about the prey that they are consuming, because not all prey are of the same value to the predators. Furthermore, different individual predators may make different foraging decisions in the same circumstances if they differ in their traits and physiological state. In this discussion paper, we firstly highlight the important differences between unprofitable prey (often defended by toxins)

and distasteful prey, which despite their aversive taste, need not be unprofitable for the predator (Holen, 2013). We then propose the concept of a ‘profitability spectrum’ as an adaptive framework for thinking about the bewildering diversity of predator–prey interactions represented by the wide range of unprofitability types, levels and currencies, signalled in a variety of different sensory modalities. We propose this paradigm to describe these interactions in terms of overall prey profitability and emphasize the need to take into account the characteristics of both the individual predator and the individual prey that are interacting. The points that we raise are important for a number of reasons.

1. The current inconsistent use of terminology obscures the direction of selection pressures.
2. It is important to integrate all relevant influences on the profitability of a prey item, in order to understand fully the foraging decisions made by predators.

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3. It is essential to develop an individual-level (rather than a species-level) approach, to appreciate the differences in selective context in which each individual exists. This individual selective context can be used to explain the diversity of foraging decisions found within a single species of predator and the diversity of responses of a community of predators to a single species of prey.

DEFINITIONS OF UNPALATABLE, DISTASTEFUL AND TOXIC

There is a widespread tendency to use the terms ‘toxicity’ and ‘unpalatability’ interchangeably, using both words to indicate unprofitability, or to use the term ‘unpalatable’ to mean that the prey will necessarily be avoided (e.g. Muller, 1879; Fisher, 1930; Cott, 1940; Edmunds, 1974; Smith, 1979; Alatalo & Mappes, 1996; Tullberg & Hunter, 1996; Speed & Turner, 1999; Lindström *et al.*, 1999; Abrams, 2000; Mallet & Joron, 2000; Speed *et al.*, 2000; Tullberg *et al.*, 2000; Ruxton *et al.*, 2004). These usages are unfortunate because they conflate two very different phenomena, as outlined below. Despite several authors pointing out this error (e.g. Turner & Speed, 1996; Mappes *et al.*, 2005; Ruxton & Kennedy, 2006; Skelhorn & Rowe, 2010; Holen, 2013), the problem still persists.

The concept of a ‘palatability spectrum’ was introduced by Turner (1984) to emphasize that not all chemically defended prey are equally aversive, but vary from fully palatable to highly unpalatable. The term ‘unpalatable’ was first applied by Bates (1862) in the context of aposematism, to describe chemically defended prey. This usage of ‘unpalatable’ was continued by Brower (1984) along with the term ‘noxious’ as the terms of choice to describe prey that are ‘chemically defended’. We argue that this usage has become changed over time, where the term ‘unpalatable’ has come to be used synonymously with ‘distasteful’ (as highlighted by Ruxton & Kennedy, 2006; Holen, 2013). This new usage implies that the item carries an unpleasant taste or smell but does not necessarily do any harm to the predator. Thus, it appears that Brower’s original usage of the term ‘unpalatable’

(where the chemical is fitness reducing, i.e. toxic) was different from the current usage (where the chemical is fitness neutral).

Brower (1984) separated chemical defences into two categories, class I and class II, and defined class I defences as noxious chemicals, causing actual harm, with ‘capacity to irritate, hurt, poison and/or drug an individual predator or parasitoid’, whether or not the chemicals can be detected on ingestion. Class II chemicals were defined as ‘innocuous chemicals which harmlessly stimulate the predators’ olfactory and/or gustatory receptors’. This distinction between classes of chemical defences we find helpful to some extent, because it emphasizes that the stimulation of taste and/or olfactory senses can be carried out completely independent of the fitness cost to the predator of eating a toxic prey item. Specifically, class II defences can be psychologically aversive, but do not directly reduce fitness. In Brower’s classification, these different functions are performed by different chemicals. However, chemicals may have both effects, both stimulating the senses and reducing the fitness of the animal. Therefore, it seems more helpful to talk in terms of class I and II functions, rather than class I and II chemicals (Table 1).

The term ‘noxious’ was used by Brower (1984) to mean something with a negative physiological effect. However, the term ‘noxious’ has, at least in common usage, come to be associated with gaseous irritants (Cambridge English Dictionary, 2017), which are not necessarily fitness reducing. Therefore, we suggest the exclusive use of the term ‘toxic’ to refer to the class I function; specifically, a chemical which, when consumed, reduces the fitness of the consumer. The terms ‘unpalatable’ or ‘distasteful’ are so widely used that we assume both will persist in the literature, but for consistency they should both be used only to mean an item which has an aversive taste or smell to a given predator, but which would be classified as having a class II function only, in that it does not have any direct fitness costs associated with its consumption. How the animal responds to that taste can, of course, have fitness consequences (see section 7.40 Profitability is also a function of individual predators), but, in contrast to toxic defences, the distasteful chemical itself is not directly costly to the predator.

Table 1. Classification of terms and effects associated with class I and class II functions of protective chemicals

Function	Effect on profitability/fitness	Effect on senses/perception/psychology	Terms that indicate this class
Class I	Negative	Neutral	Toxic (but not distasteful/unpalatable)
Class II	Neutral	Stimulatory/psychologically aversive	Distasteful/unpalatable (but not toxic)
Class I and Class II	Negative	Stimulatory/psychologically aversive	Toxic and distasteful

If a single chemical has both class I and class II functions, then it should be described specifically as being both toxic and unpalatable.

THE IMPORTANCE OF TREATING UNPALATABILITY AND TOXICITY AS TWO SEPARATE PHENOMENA

A clear distinction between ‘unpalatability’ and ‘toxicity’ is important because if class I and class II functions are caused by two different chemicals, then prey items could be toxic but not palatable, or palatable but not toxic (Holen, 2013). Thus, the variability in class I function leads to a spectrum of toxicity equivalent to, but separate from, a spectrum of palatability that relates to variability in class II function. This is a crucial distinction to make because the separate functions (class I and class II) have different consequences for predator foraging decisions, the resulting selection pressure on prey and the co-evolution of prey and their predators.

It is important to draw a clear distinction between class I and class II functions when addressing the evolution of defensive chemicals in prey species. Fisher (1927) pointed out that when attacked by naïve predators, prey types that have only a class I function (i.e. are toxic but palatable) are more likely to be killed because there is no early warning of their toxicity until the predator has learned the meaning of other signals, such as colour patterns, which may be associated with the toxicity. In contrast, prey that have both class I and class II functions in their defence (i.e. are both toxic and unpalatable) are better protected even from a naïve predator, because predators may reject the unpalatable prey on first tasting without the prey being killed (Wiklund & Järvi, 1982). Prey individuals that are unpalatable but not toxic (class II function only) are effectively Batesian (deceptive) taste mimics of toxic models bearing the same or a similar taste. On the contrary, if toxic prey are not unpalatable then their defences rely on signals in other modalities, which have been shown to be less effective than multimodal signals that include taste, and avoidance learning by the predators may therefore be less effective (Marples *et al.*, 1994). Thus, different combinations of class I and class II functions will result in different selective pressures on the prey.

Empirical evidence supports the view that predators exhibit different responses to class I functions (toxicity) and class II functions (unpalatability). For example, animals will continue to eat prey that is only unpalatable but not toxic (Marples *et al.*, 1989, 1994; Rowland *et al.*, 2013), yet exhibit long-lasting aversion to toxic prey regardless of its taste (Garcia *et al.*, 1955). Where both class I and class II functions are

present, predators have been shown to exhibit both taste rejection and accelerated aversion learning (i.e. classic taste aversion learning; Kalat, 1985; empirically shown by Skelhorn & Rowe, 2006; Rowland *et al.*, 2013). Therefore, prey species might often be expected to benefit by having both toxicity (class I function) and unpalatability (class II function) in their chemical defences, because this favours them via individual selection. However, it is easy to imagine scenarios in which only one class of function might evolve; for example, if toxicity required chemicals that were unavailable or expensive to synthesize, sequester or store (Ruxton *et al.*, 2004: pp. 59–60). It is also possible that a chemical defence for one enemy, such as a chemical that is toxic to a parasitoid wasp, might not be toxic to a different enemy, such as a predatory bird, for which the chemical defence might be merely unpalatable.

The distinction between toxicity and unpalatability/distastefulness highlights the evolutionary importance of the different processes involved in chemical protection. Under this definition of terms, it is likely that there is a selective advantage for a predator to eat unpalatable but non-toxic items because of their nutritional benefits, but there would be strong selection pressure for predators to avoid consuming toxic items (because of the fitness costs that they carry). The challenge for foraging animals is to be able to distinguish unpalatable prey that are also toxic (class I and II functions in their defensive chemicals) from unpalatable prey that are not toxic (class II function only). This distinction typically requires experience, which will involve consumption of toxic prey, which carries a cost (Holen, 2013). Therefore, there may be a cost to eating distasteful prey even if it is not toxic, because of the costs of learning to distinguish between distasteful prey that also carry toxicity and distasteful prey that do not.

How frequently might predators encounter prey that are unpalatable but not toxic? It is often assumed that aversive taste is reliably associated with toxicity, but there is little evidence to support this assumption (Ruxton & Kennedy, 2006). Indeed, it has been shown that there is little consistency between the strength of distastefulness to a predator species and the toxicity of the chemical involved (Glendinning, 1994). Thus, the assumption that highly distasteful prey should normally be toxic is called into question. There appears to be extraordinarily little empirical study of this association, although Ruxton & Kennedy (2006) stated that ‘distasteful non-toxic prey items may be widespread’. Despite this assertion, we were able to discover only one example in the literature of a prey species that is known to be non-toxic yet unpalatable. This example is the two-spot ladybird, *Adelia bipunctata*, which is not toxic to blue tits, *Cyanistes caeruleus* (Marples *et al.*, 1989), or to the ant *Lasius niger* (Marples, 1993c). However, this species is unpalatable

to blue tits because the ladybird contains an alkaloid (adeline), which carries a bitter taste (Marples *et al.*, 1989). Despite the bitter taste, blue tits regularly provision their nestlings with two-spot ladybirds (Marples *et al.*, 1989). This contrasts with the seven-spot ladybird, *Coccinella septempunctata*, which also has a strong bitter taste from a different alkaloid (coccinelline), but which is also very toxic (Marples *et al.*, 1989). Seven-spot ladybirds are avoided by blue tits (Marples *et al.*, 1989); thus, it may be that the two-spot ladybird gains protection by its taste mimicry of the bitter toxin of the seven-spot ladybird.

The reasons for unpalatability in the absence of toxicity in prey organisms remain uncertain. In some cases, this might be attributable to taste mimicry or a signal of other aspects of unprofitability, but in other cases unpalatable chemicals might simply be products of other physiological processes, not selected specifically for their taste.

THE NEED FOR A 'PROFITABILITY SPECTRUM'

Toxicity and unpalatability are by no means the only forms of protection from predators. Ruxton *et al.* (2004) divided defences into three categories: in addition to chemical defences, they defined behavioural and morphological types of defences. 'Behavioural defences' include adaptations to increase predator search time (e.g. through crypsis, masquerade and other forms of hiding from predators), and 'morphological defences' include adaptations to increase the difficulty of capture and to increase handling time, by the use of physical attributes (e.g. spines, teeth, stings and armour). Given that any or all of these forms of protection contribute to the costs to a predator of feeding on a particular prey individual, the decision by a predator should be based on the net profitability of the prey, rather than on the costs attributable to any single mode of defence.

The first instance that we can find in which 'unprofitability' was explicitly considered (as opposed to toxicity alone) was in consideration of defences of birds against predation, by Baker & Parker (1979). They introduced the idea that the prey might signal that they have detected the predator, and that the predator should take this into account when assessing the profitability of attacking that prey individual. There are many factors that would influence the profitability of a prey item to a given predator. The most widely recognized of these focus on attributes of the prey, such as the level of chemical and physical defences and the ease of detection. However, they identify that there are many other attributes, both of the predator and of the prey, that influence prey profitability. Some of these include familiarity of the prey to the individual

predator, the relative abundance of that prey compared with other familiar palatable foods, the location, ease of handling, digestibility and the nutritional content of the individual prey (reviewed by Ruxton *et al.*, 2004).

Not only are there a range of attributes of predator and prey individuals influencing the probability of attack, but the decision by a predator of whether or not to eat a prey item is also made across a range of different currencies. Such currencies might include the nutritional, temporal, physiological and psychological aspects of the predator-prey interaction, to name but a few. The complexity of deciding whether or not it is adaptive for a predator to eat a particular prey individual, using all these influences on the predator, presents a bewildering task to an ecologist. However, the predator itself has a somewhat easier job; that of simply learning through experience whether a particular prey type in a particular situation is likely to be profitable or not, irrespective of the individual reasons for that profitability. We would expect a predator to hone its prey choices as it gains more information about a particular prey type in a particular setting.

A predator should be adapted to consume any prey that has a net fitness benefit across all currencies, i.e. the nutritional fitness benefits plus the informational benefits, minus all of the summed fitness costs imposed by the various modes of defence and other attributes affecting the cost of attack. Therefore, a predator should be selected to eat anything, however distasteful or however toxic, as long as there is a net benefit of eating the prey, i.e. the position of the prey on the profitability spectrum is positive. There are a number of studies showing clearly that predators do indeed consume toxic prey in some circumstances (Marshall, 1908; Fink *et al.*, 1983; Brower & Calvert, 1985; Stephens & Krebs, 1986; Belovsky & Schmitz, 1994; Kokko *et al.*, 2003; Sherratt, 2003; Orłowski & Karg, 2013; Oudman *et al.*, 2014), but there remains a need for studies to examine the net benefits of eating toxic prey. Likewise, the predator should avoid any prey with a negative profitability. Although the response of the predator to profitability is dichotomous (they either eat the individual prey item or they do not), there is, nonetheless, a spectrum of profitability, in that some prey individuals are highly profitable, whereas others are only marginally profitable; likewise, unprofitable prey range from marginally to highly unprofitable. Therefore, we propose the concept of the 'profitability spectrum', by which predator foraging decisions can be understood. This spectrum provides a holistic framework for classifying all prey items by their net benefit, across all currencies. We emphasize that by 'all currencies' we mean absolutely everything that affects the decision of the predator, not only the attributes of the prey that have traditionally been considered to be part of their anti-predator defences (for examples see

Table 2). The optimal foraging literature acknowledges this all-inclusive trade-off between costs and benefits of different food choices (Stephens & Krebs, 1986), but the true diversity of influences on the profitability of individual prey is rarely recognized.

The processes by which a predator assesses the cost of each prey and its benefits, in terms of nutrients and other resources, are not always clear but can involve learning by direct experience of the prey type (e.g. Speed *et al.*, 2000; Lindström *et al.*, 2004; Ihalainen *et al.*, 2008; Webb *et al.*, 2008; Halpin *et al.*, 2014). The process of learning about an unfamiliar prey type may be costly (e.g. it is likely to involve sampling some toxic prey), and thus the novelty or familiarity of prey may be an important element of the profitability of the prey. What matters to predators is the net effect of eating the prey, not the individual costs and benefits that make up that profitability; therefore, the decision to eat should depend solely on whether the prey item confers an overall profit or a net loss to the fitness of the predator on that occasion. Thus, the learning task for the predator can be understood as a process of learning about whether prey exhibiting a particular combination of traits, in a particular ecological context, tend to be profitable or not.

A few prey species are unprotected and always highly profitable, depending for their survival on superabundance to swamp predation pressure, e.g. periodical cicadas (*Magicicada* spp.; Williams & Simon, 1995) and various reptiles and amphibians (Doody *et al.*, 2009). However, it has been suggested that even in these cases, an excess of a particular nutrient might become toxic and therefore the prey might become unprofitable when eaten in excess (Turner & Speed, 2001). Some prey are so well defended that they are probably always unprofitable to any predator, e.g. poison arrow frogs (*Dendrobates* spp.; Maan & Cummings, 2012), but the vast majority have a profitability nearer to zero, such that they are neither strongly profitable nor strongly unprofitable. These prey are worth eating, at least in some circumstances, but the predators incur costs in doing so. These prey are of particular interest because where they lie on the spectrum depends on the exact state of both the predator and the prey individual, and the ecological context, as discussed below. Indeed, there is evidence that predators are able to make adaptive state-dependent decisions about what to eat, depending on the relative profitability of potential prey (Sherratt, 2003; Sherratt *et al.*, 2004; Mappes *et al.*, 2005; Barnett *et al.*, 2007; Skelhorn & Rowe, 2007). Therefore, the location of any prey individual on the profitability spectrum is highly context specific, such that profitability should be viewed as a dynamic, spatially and temporally varying property of the individual predator–prey interaction, rather than a fixed property of each prey species.

PROFITABILITY IS AN ATTRIBUTE OF AN INDIVIDUAL PREY ITEM

The usage of such terms as ‘toxic’ or ‘unpalatable’ is almost always applied to a species as a whole rather than to individuals within that species, yet the profitability of a prey item will depend not only on what species it is, but also on the state of that particular prey individual (Stephens & Krebs, 1986; Sherratt, 2003; Mappes *et al.*, 2005). These differences in net benefit to the predator exist in several different currencies. The current nutritional content of the prey may differ between prey species or between sexes, or even within one sex. For instance, a gravid female praying mantis (*Mantodea* spp.) would be considerably more nutritionally beneficial as a prey item than one that has just laid its eggs (Barry, 2010). The location of the prey item with respect to other prey may also influence its cost. For example, nests at the edge of a seabird colony may be more profitable for a predator to attack than a nest located in the middle of the colony, where the predator must suffer the cost of being mobbed by birds defending their nests (Curio, 1978). The visibility of the prey depends partly on the crypsis or conspicuousness of its patterning, but also on the background against which it is currently viewed, and whether it is currently stationary or active (Ruxton *et al.*, 2004). For instance, a moth flying past a bird might constitute a low-cost prey item in terms of search time, but search time may be substantially higher if the moth is motionless on a matching background. The absolute abundance of a given prey type may also influence its profitability, because the formation of an effective search image reduces search time (Tinbergen, 1960; Pietrewicz & Kamil, 1979; Bond, 1983). Repeated experience also increases the familiarity of the predator with the prey, potentially reducing handling time (Ruxton *et al.*, 2004) and increasing knowledge of how variable that prey is in terms of its profitability (Hughes, 1979; Holen, 2013). For similar reasons, relative abundance compared to other profitable and unprofitable prey may influence the decision by a predator about which prey to eat (Allen & Clarke, 1968; Allen & Anderson, 1984; Church *et al.*, 1994; Kokko *et al.*, 2003; Lindström *et al.*, 2004; Halpin *et al.*, 2013; Carle & Rowe, 2014).

Some prey species can take proactive evasive action when threatened; therefore, their perception of the predation threat may affect their profitability. Examples of such evasion include fleeing, feigning death and dropping out of sight, or emitting defensive fluids, such as reflex blood (Ruxton *et al.*, 2004). In addition, in chemically defended prey there may be differences between individuals of a species in their level of defence. This could be because of variation in the toxicity of the food that they are eating, their ability to sequester or synthesize chemical defences, the type

Table 2. Examples of factors that influence the profitability of a given prey item to potential predators

Factor influencing profitability	Effect on profitability
Features of the prey	
Toxicity	Negative
Distastefulness	Neutral/slightly negative
Behavioural defences, e.g. speed, thanatosis	Negative
Morphological defences, e.g. spines, hairs	Negative
Difficult to find, e.g. cryptic	Negative
Difficult to handle	Negative
Low digestibility	Negative
Low nutritional value	Negative
Unfamiliar	Negative
Uncommon	Negative
Positioned near alternative prey	Negative
Pursuit deterrent signals	Negative
Batesian mimic	Negative
Unpredictable defence level	Negative
Features of the predator	
Body size and condition of predator	Positive/negative
Current toxin load of predator	Positive/negative
Susceptibility to toxin	Positive/negative
Prior handling experience	Positive
Ability of predator to learn	Positive/negative
Hunger level	Positive
Prior experience of unprofitability	Negative
Novelty of prey	Negative
Foraging strategy, e.g. dietary wariness, generalist/specialist	Positive/negative
Social learning available	Positive/negative
Perceived level of competition for prey type	Positive/negative
Perceived abundance of alternative prey	Positive/negative
Perceived risk by predator of being attacked	Positive/negative
Perceived risk of starvation	Positive/negative
Harshness and unpredictability of environment	Positive

of toxins sequestered, and how they present these toxins to the predator (Turner & Speed, 2001; Sherratt, 2003; Skelhorn & Rowe, 2005; Maan & Cummings, 2012). Profitability may also depend on the age, size and sex of the prey individual, concentration of body fluids, and a host of other factors. For instance, in a ladybird (*Adalia* sp.) the effectiveness of defence varies depending on how recently it has been attacked, because it will have lost some of its reflex blood after the attack and so carry less of a cost to a predator than one which is still fully defended (de Jong *et al.*, 1991; Holloway *et al.*, 1991). Furthermore, Halpin *et al.* (2014) showed that the balance between the nutritional value and the chemical costs of a prey item alters its profitability. In their study, nutrient-enriched mealworms (*Tenebrio molitor* larvae) injected with 4% quinine sulphate suffered increased predation by foraging European starlings (*Sturnus vulgaris*) compared with non-enriched mealworms treated in a similar manner.

These issues apply to greater or lesser extents in different taxa. For example, plants may respond 'behaviourally' to herbivore attack (e.g. by synthesizing additional protective secondary compounds; Feeny, 1970), but the response is often too slow to influence the immediate profitability of the current herbivory event. In contrast, most animals can respond sufficiently quickly to alter their profitability to the current predator [e.g. a hedgehog (*Erinaceus europaeus*) can curl up in time to defend itself]. There is little information about how readily predators can assess both the toxin and the nutrient content of a prey item (Skelhorn *et al.*, 2016), but herbivores commonly make foraging decisions based on both toxicity and nutrient content of alternative foods (Freeland & Janzen, 1974; Marsh *et al.*, 2005, 2007; Nersesian *et al.*, 2012).

Thus, the position of a given individual on the profitability spectrum changes constantly, both because of factors that are under the control of the individual, such as food

choice, resting position and foraging location, and because of changes in the state of the prey individual, such as age, health, and nutritional and toxin content. Not only are prey individuals likely to change their location on the profitability spectrum, but also some species are more flexible in their location than others. This, in itself, may make that species less attractive to a predator, because it is less predictable in its profitability and therefore harder to learn about (Barnett *et al.*, 2012; Holen, 2013; Skelhorn & Rowe, 2005, 2007, 2010). This flexibility in profitability may have many unexpected consequences. For instance, one intriguing prediction is that prey species that are dietary generalists may be more variable in their profitability than dietary specialists. This is because generalists will contain a wider range of chemicals from their more diverse food types and are more likely to be found on different backgrounds in consecutive encounters, whereas specialists will be less variable in these respects.

Although each of these influences on the profitability of prey is widely understood to influence decisions made by predators (as discussed above), it is extremely rare for either empirical studies or theoretical models to attempt to account for them. However, theoretical consideration of predator–prey interactions needs to encompass overall profitability, including all variables in all currencies, before terms such as ‘aposematic’, ‘unprofitable’ or ‘toxic’ are assigned and inferences made about whether a predator should eat an individual prey. Therefore, we urge caution in assuming that prey species are aposematic simply because they are brightly coloured and contain a toxin. Furthermore, we suggest that attributes of prey such as ‘aposematic’ should not be used as a description of a species as a whole, but as a description of a specific prey item in a specific context.

PROFITABILITY IS ALSO A FUNCTION OF INDIVIDUAL PREDATORS

Not only are prey variable in their position on the profitability spectrum, but there is also substantial variation in the degree to which a prey item is profitable to an individual predator. Indeed, profitability may vary as a feature of the predator as much as of the prey. This occurs in three distinct ways. Firstly, different predator species, or different individuals within a species, may differ in their susceptibility to different toxins (e.g. Gleadow & Woodrow, 2002; Marsh *et al.*, 2005; Speed & Ruxton, 2014). Secondly, predators differ substantially in the degree to which they can detect bitterness (Li & Zhang, 2014), which is often used as a warning signal. Thirdly, predators may differ in their foraging strategy, influencing the frequency with which they encounter different prey, hence the perception by the predator of new prey items (Marples *et al.*, 1998).

One of the costs to a predator of new and therefore unfamiliar prey is that each individual predator needs to learn during their lifetime about the profitability of each new prey type that they encounter (see above). They must do this by risking consumption of potentially dangerous prey and, almost certainly, consuming unprofitable prey in the process, in order to learn the profitability of each prey type and how variable that profitability is between prey individuals of that species (Sherratt, 2011; Holen, 2013). It has recently been suggested that apparent errors in predator foraging could be intentional information gathering by the predator, rather than simply mistakes in prey choice (Skelhorn *et al.*, 2016). It has been shown that different individuals in a predator species may have different foraging strategies, such that some predator individuals are much more willing to consume novel prey types than others, and thereby gain experience in different ways (Marples *et al.*, 1998). These two foraging strategies have been described as dietary conservatism (DC) and adventurous consumption (AC), respectively (Thomas *et al.*, 2010), and shown to be genetically based traits (Marples & Brakefield, 1995). Whether an individual predator has a DC or AC foraging strategy will make a fundamental difference to its ability to learn about the profitability of different prey types, through direct experience. An AC predator, which readily samples novel food, will gain a wide range of experience of different prey types but will not eat so many of each type, so may not learn as quickly about any particular prey as a DC predator would. In contrast, a DC predator specializes on only a very few food types and will learn much more quickly about those food types and their variability, but at the expense of failing to discover other profitable prey (McMahon *et al.*, 2014). Thus, AC predators will sample a variety of prey from across the profitability spectrum, consuming much more unprofitable prey with the risk of being poisoned, but will eventually eat prey of a wider spectrum of profitabilities. Indeed, they theoretically should eat everything that has a positive net profitability. In contrast, DC predators would be expected to specialize quickly on a small number of profitable prey types and therefore exploit only a small section of the profitability spectrum, missing out on profitable prey but rapidly gaining specific foraging expertise, allowing them to exploit their preferred food type more efficiently. The relative costs and benefits of AC and DC foraging strategies may differ between ecological contexts, which in turn may influence the selection pressures on predator behaviour and prey responses.

In addition, the day-to-day physiological and psychological state of the predator will vary, influencing the profitability of a given prey type to that individual predator at that time. Physiological factors of the

predator include its body size, body condition, age and amount of the toxin already ingested (e.g. Marsh *et al.*, 2005; Skelhorn & Rowe, 2007). We know from recent work that some predators are able to assess their toxin intake and adjust their future foraging decisions accordingly (Skelhorn & Rowe, 2007). Likewise, predators have been shown to adjust their intake of prey that they know to be toxic, depending on their current body condition (Barnett *et al.*, 2007, 2012). The cognitive decision about whether to eat the prey will be informed by the predator's perception of itself and the environment around it, such as its own risk of starvation, perceived abundance of alternative prey, and the perceived risk of foraging on prey in different locations (Kokko *et al.*, 2003; Sherratt, 2003; Sherratt *et al.*, 2004). For instance, in a classic experiment by Milinski & Heller (1978) it was shown that three-spined sticklebacks (*Gasterosteus aculeatus*) preferred to feed on low-density prey (*Daphnia*) when they had recently seen a predator (a common kingfisher, *Alcedo atthis*), but preferred to feed on high-density prey when they had not. This indicates that perceived predation risk alters the profitability of foraging in each situation.

PROFITABILITY IS ALSO A FUNCTION OF THE ENVIRONMENT

The environment in which the forager finds itself will alter its probability of eating a given prey type (Whittingham & Evans, 2004). The distance of the food from cover, combined with the number and types of predators in the area, may alter the probability of the forager eating a given prey item (Hegner, 1985; Vytienis & Godin, 1991; Brown, 1999; MacLeod *et al.*, 2005). Local climate conditions of the area, such as ambient temperature (Chatelain *et al.*, 2013), will alter the energetic needs of the predator and may alter the profitability of a given prey for that predator. The relative availability of the focal prey type (a combination of relative abundance and relative crypsis) compared with other familiar and unfamiliar prey in the area will also alter the decision by the predator about whether to eat the prey (Abrams, 2000; Kokko *et al.*, 2003). If the focal prey is unfamiliar and surrounded by many familiar and highly profitable prey, then it is probably adaptive for the forager to eat only familiar prey. Likewise, if the unfamiliar focal prey is surrounded by toxic prey of a type that the predator has recently consumed, then the current toxin load of the predator may dissuade it from sampling anything else that is unfamiliar. In both these cases, a profitable but unfamiliar prey item may gain protection simply by its proximity to the other prey types. In general, proximity to familiar and/or highly profitable prey will reduce the predation risk for any unfamiliar prey type (Kokko

et al., 2003; Lindström *et al.*, 2004; Halpin *et al.*, 2013, 2014; Carle & Rowe, 2014). The competitive environment is also important to predators; the responses of a range of predator taxa to novel prey has been shown to be influenced by the presence of foraging competitors, which can occur through a variety of mechanisms, including social learning (Stephens & Krebs, 1986; Fryday & Greig-Smith, 1994; Richards *et al.*, 2011; McMahon *et al.*, 2014).

UNDERSTANDING MÜLLERIAN AND BATESIAN MIMICRY IN THE CONTEXT OF THE PROFITABILITY SPECTRUM

Classically, Müllerian mimics are defined as defended species that mimic other defended species (Müller, 1879), whereas Batesian mimics are considered to be fully palatable species that obtain their protection from their similarity to defended species (Bates, 1862). Quasi-Batesian mimicry is where a less defended species obtains some degree of incomplete protection by its partial similarity to a more defended species (Speed, 1999; Turner & Speed, 2001). However, all of these defining statements attribute a profitability level to an entire prey species, which as we argue above, is not usually realistic. In addition, these definitions imply that all predators are the same and meet the prey under the same ecological conditions, which we have also argued is not the case. In other words, profitability depends on the current attributes of the individual prey, the individual predator and the current environmental context of their interaction. It may be that an individual prey item is sufficiently defended to act as a Müllerian mimic for one predator individual, for whom the net profitability of eating that prey item would be negative, whereas for a second predator individual (e.g. a larger predator), that prey item is a Batesian mimic because the net profitability of consuming it would be positive. This is an opportunity for theoretical modelling to address a wider range of parameters in which predator decisions are made. For example, by comparing the predictions of models describing classical 'Pavlovian' decision making (e.g. Speed *et al.*, 2000) with exploration–exploitation modelling using 'optimal predators' (e.g. Aubier *et al.*, 2017).

This potential for a given prey item to act both as a Batesian and as a Müllerian mimic in different situations was recognized by Sheppard & Turner (1977) and Speed (1999) and was again highlighted by Turner & Speed (2001) but has somehow escaped wide recognition. It is clear that this idea has not yet been embraced fully, in that the majority of studies refer to entire species as either Batesian or Müllerian mimics. In the same way that the profitability of an aposematic animal is unique to a specific predator in a specific

ecological context, the same can be said of mimetic relationships. Therefore, the type of mimicry is a feature of the specific interaction between two individuals at a specific time, and not a general feature of the prey species as a whole.

IMPLICATIONS FOR THE CO-EVOLUTION OF PREDATORS AND PREY

This view, that aposematism and mimicry are descriptions of interactions between individual predators and individual prey, has major implications for our understanding of the co-evolution of predator and prey populations. The selection pressures on prey populations will depend on the sum of all of the dynamic interactions with their different predators. As discussed in this review, the type of interaction will vary between individual predators and prey within a population; therefore, selection operates at an individual level, but the co-evolution occurs at the species level. The direction of the resulting selection pressures depends on the average response of all predators that consume that prey species at that time. For example, if predators are relatively naïve at some times of year (e.g. fledgling songbirds in summer) but are relatively educated at other times (e.g. older birds in winter) then the direction of selection may switch from favouring crypsis at one time of year to favouring aposematism at another (Waldbauer, 1988; Mappes, 2014).

If a particular prey species is treated by one subset of predators on average as a Müllerian mimic and by another set of predators as a Batesian mimic, then the two sets of predators will drive the co-evolutionary relationship between the mimic and its model in different directions (Turner & Speed, 2001). Specifically, if the prey species is treated on average as a Müllerian mimic, then selection pressure on the prey will favour aggregation (to facilitate predator learning), high abundance (to dilute the cost of educating the predators) and convergent evolution of the colour pattern with any abundant toxic model prey in the area (to share the cost of predator education across the mimicry ring; Ruxton *et al.*, 2004). However, if the prey species is treated on average as a Batesian mimic, then the selection pressure will favour dispersed distributions of prey (reducing the opportunity for the predator to learn of the profitability of the prey) and lower abundance (to avoid the predators devaluing the meaning of the signal; Ruxton *et al.*, 2004). The signals of the models will likewise be selected to converge on the signals of other Müllerian mimics and diverge from those of Batesian mimics. Thus, a single predator species may be exerting completely different selection pressures on a whole assemblage of prey species,

depending on individual differences in the perceptions of the predators of the profitability of individual prey (Abrams, 2000; Kokko *et al.*, 2003).

CONCLUSIONS AND FUTURE DIRECTIONS

Even though considering all aspects of profitability appears to make it almost impossible to comprehend or model the complexity of the interactions occurring in the wild, ignoring the real level of complexity risks an over-simplistic interpretation of predator–prey interactions. Modellers are already starting to disentangle palatability as a proxy for predator decision making (e.g. as a ‘Pavlovian predator’; Speed *et al.*, 2000) from decisions based on the overall profitability of the prey (e.g. as an ‘optimal predator’; Aubier *et al.*, 2017), which allows individual variation in decision making to be modelled. For example, there is a current need for models to integrate the key conditions for predator decision making, such as those we have outlined in this paper, including learning, state dependence and the distinction between unpalatability and toxicity. Incorporating more realistic complexity helps to explain the diversity and variability of predator responses and prey signalling traits. However, empirical ecologists need not despair. It may now be time to move away from a focus on laboratory experiments, in which the psychology of the predators is explored in detail but divorced from ecological context, towards study of the foraging decisions in the complex ecologies in which predators and prey live (e.g. Mappes, 2014). To do this, we need tractable ecological systems, in which we can measure the diversity of alternative prey types, the ecological conditions and the relevant aspects of the predators and prey. Fortunately, technology is making such observation ever more possible, with tiny forager-mounted cameras, physiological monitors and location trackers, allowing foraging decisions to be observed directly in real environments (e.g. Greenstone & Bennett, 1980; Rutz *et al.*, 2007; Mullen *et al.*, 2013; Watanabe & Takahashi, 2013; and reviewed by Ropert-Coudert & Wilson, 2005). Although technological developments may not yet be sufficiently advanced to record all relevant aspects of foraging behaviour, this will undoubtedly progress over the coming years; therefore, we would encourage scientists to consider the ecological complexities of their study system as less of a deterrent and more of a challenge. This is important because, as outlined in this review, consideration of the complexity underlying the net profitability on which selection acts is necessary for understanding the diversity of predator and prey interactions in the real world and how these interactions have evolved.

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