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REVIEW

The evolution and ecology of multiple antipredator defences

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Abstract

Prey seldom rely on a single type of antipredator defence, often using multiple defences to avoid predation. In many cases, selection in different contexts may favour the evolution of multiple defences in a prey. However, a prey may use multiple defences to protect itself during a single predator encounter. Such “defence portfolios” that defend prey against a single instance of predation are distributed across and within successive stages of the predation sequence (encounter, detection, identification, approach (attack), subjugation and consumption). We contend that at present, our understanding of defence portfolio evolution is incomplete, and seen from the fragmentary perspective of specific sensory systems (e.g., visual) or specific types of defences (especially aposematism). In this review, we aim to build a comprehensive framework for conceptualizing the evolution of multiple prey defences, beginning with hypotheses for the evolution of multiple defences in general, and defence portfolios in particular. We then examine idealized models of resource trade-offs and functional interactions between traits, along with evidence supporting them. We find that defence portfolios are constrained by resource allocation to other aspects of life history, as well as functional incompatibilities between different defences. We also find that selection is likely to favour combinations of defences that have synergistic effects on predator behaviour and prey survival. Next, we examine specific aspects of prey ecology, genetics and development, and predator cognition that modify the predictions of current hypotheses or introduce competing hypotheses. We outline schema for gathering data on the distribution of prey defences across species and geography, determining how multiple defences are produced, and testing the proximate mechanisms by which multiple prey defences impact predator behaviour. Adopting these approaches will strengthen our understanding of multiple defensive strategies.

KEYWORDS
antergy, defence portfolio, defence syndrome, intraspecific variation, predation sequence, predator cognition, secondary defences, synergy, trade-offs

1 | INTRODUCTION

Prey use a remarkable diversity of defences to protect themselves from predation (Caro, 2005; Cott, 1940; Poulton, 1890; Ruxton et al., 2018). Often, they rely on more than one antipredator defence (Caro et al., 2016; Caro & Ruxton, 2019; Stevens, 2007), for example, a combination of concealment, motion dazzle and warning signals (e.g., Arias et al., 2019; Barnett & Cuthill, 2014; Umeton et al., 2019; Valkonen et al., 2011, 2020), or signals, toxins, spines, or other weapons (Marples et al., 2018). To glimpse the complexity of prey defences, consider the insect orders Hemiptera (Figure 1a) and Lepidoptera (Figure 1b). The variation in combinations of defences used by species within these groups suggests that certain combinations may be favoured over others. The overrepresentation of some combinations of defences is an interesting problem in evolutionary biology, because it allows us to ask about selective and non-selective factors that promote the integration of multiple traits into complex, adaptive phenotypes. Some explanations for the function of multiple defences depend on specific systems, such as visual perception (Barnett & Cuthill, 2014; Caro et al., 2016; Cuthill et al., 2017; Stevens, 2007). However, our general understanding of how an individual should invest its limited resources in defences, whether they be single or multiple, is less complete. In this review, we aim to provide a broad intellectual scaffold that researchers interested in this problem can use to identify specific questions and to contextualize their studies. We examine both ultimate and proximate factors that promote and constrain the number of defences. We focus on the current state of the art, including current and new hypotheses and evidence where possible, whilst providing practical suggestions for the experimental designs and methods that can best test critical predictions.

We define a defence as a mechanical, chemical, sensory (influencing how an organism is perceived, e.g., colour), or behavioural trait that has either been wholly or partly selected for its antipredator function, or has aspects of its form maintained by selection for an antipredator function. We use the term “multiple defences” to describe a single organism's phenotype that includes different defensive traits. We also point out that multiple defences could form “syndromes”. We use the term “syndrome” to describe patterns of defences that co-occur together, exhibiting statistical covariance across species (e.g., Figure 1; Agrawal & Fishbein, 2008) or within species (Jandt et al., 2014). Both between- and within-species comparisons are potentially informative for understanding the evolution of multiple defences.

There are at least two general hypotheses for why an individual might have multiple defences. One is that an individual has different defences to contend with different enemies (Rojas et al., 2017; Sih et al., 1998; Zvereva et al., 2018). This is reasonable since most species face multiple types of predators in natural food webs (Ings et al., 2009). The hypothesis assumes that each type of predator imposes a distinct selective pressure on prey, driving the evolution of alternative defences. The multiple-predator hypothesis can generate predictions about relationships between specific defences, such as a balance between crypsis and aposematism (warning signals)

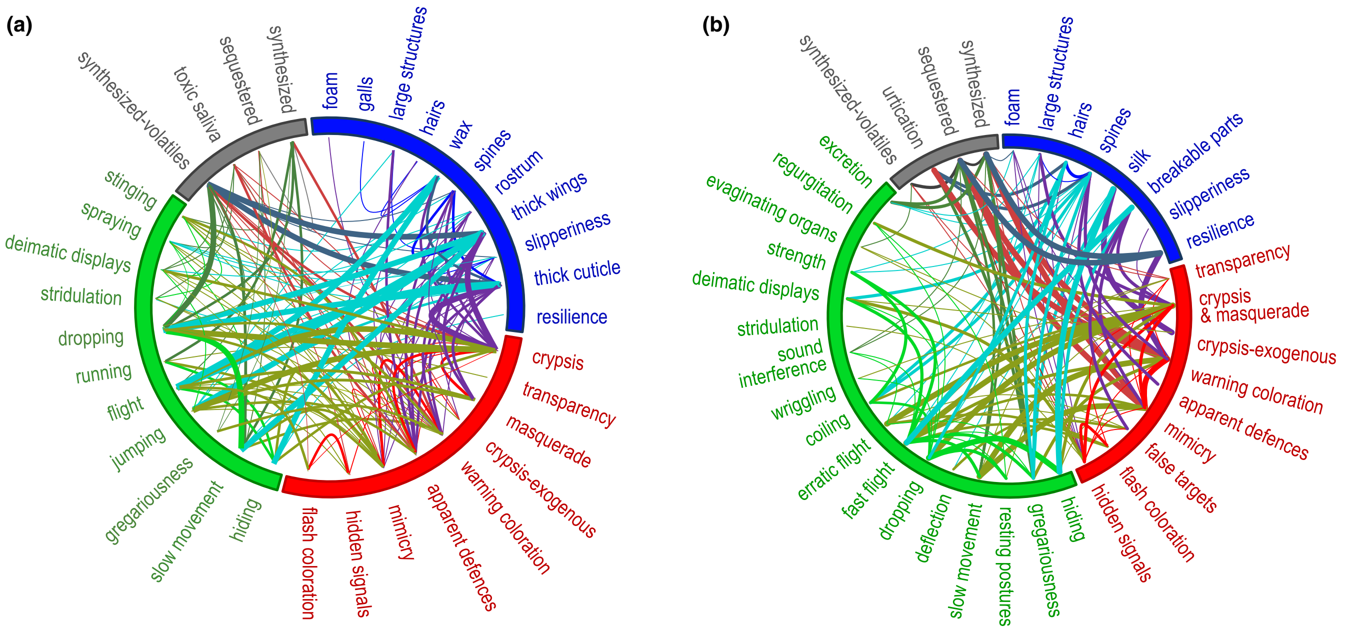


FIGURE 1 Combinations of mechanical (blue), visual (red), behavioural (green) and chemical (grey) defences found in two insect orders: Hemiptera (a) and Lepidoptera (b). Within each category, defences are arranged according to their position along the predation sequence. Connecting lines represent combinations of particular defences, and line colours correspond to the defence categories involved. The thickness of connecting lines corresponds to the number of species in which defence combinations are represented (thick: widespread, medium: common and found in several species; thin: specific to certain species). Prevalence distribution was chosen to represent a 1:2:4 ratio of the thick:medium:thin lines in each insect order. For trait-combination data, species-specific examples, and references that underpin (a) and (b), see Tables S1 and S2, respectively.

(Endler & Mappes, 2004). Indeed, specialist snake predators have been shown to select for camouflage in venomous adders, whereas generalist predators favour aposematism in adders (Valkonen et al., 2012). A variation on the multiple-predator hypothesis is that different defences may function better than others in different contexts (e.g., habitats, times of day), which may expose them to different predators or the same predators in a different foraging mode (reviewed in Caro et al., 2016; Caro & Koneru, 2021). At this point, the possibility of multiple defences to deter multiple predators is a relatively mature and well-studied hypothesis that should be considered whenever multiple defences co-occur in a study organism.

On the other hand, a second hypothesis for why a prey has multiple defences is that it deploys them during a specific instance of interaction with an individual predator. Although it has implicitly been addressed in the study of aposematism (Mappes et al., 2005) and deimatism (Drinkwater et al., 2022; Umbers et al., 2017), we do not know if there is a general explanation or set of explanations that more broadly govern the evolution of defences used against a single predator. Here, we define the subset of a prey's defences that may be used together (simultaneously or sequentially) during an encounter with a particular predator as a "defence portfolio" (Britton et al., 2007). A prey species may have multiple defence portfolios that work against different types of predators, and some defences may be part of multiple portfolios. The general hypothesis that multiple defences co-occur due to selection to function in a defence portfolio is not well-investigated. Therefore, we emphasize current research on this problem. However, much of the content of this review is relevant to both the multiple-predator hypothesis and the evolution of defence portfolios.

The "predation sequence" is a useful framework for thinking about the function of defences (Caro, 2005; Ruxton et al., 2018). Endler (1986, 1991) suggested that the interaction between predator and prey usually consists of six stages: (1) encounter, (2) detection, (3) identification, (4) approach (attack), (5) subjugation and (6) consumption. Within this sequence, defences are frequently placed into the two broad categories of 'primary defences', i.e., those that act before the predator initiates any prey-catching behaviour, and 'secondary defences', i.e., those that act after a predator has made contact with its prey (Edmunds, 1974; Ruxton et al., 2018). Multiple defences can act simultaneously (in the same stage of the predation sequence) or be deployed sequentially across various stages. Although there can be ambiguity about the stage of the predation sequence in which a particular defence functions, this framework remains a helpful tool for investigating predator–prey interactions. We refer to the predation sequence throughout the review where it is relevant to the evolution of multiple defences, and particularly, to defence portfolios, which often deter a single predator at specific stages of the sequence.

We first describe how trade-offs created by resource limitations and functional interactions between traits could shape multiple defences. This provides an ultimate, selective perspective that is not always explicitly considered. We survey empirical evidence for different kinds of trade-offs involving defences reported in the literature. This lays groundwork for a section where we discuss theoretical formalizations of defence portfolio evolution. We add novel theory on how traits can interact non-additively to deter predators. We devote the rest of the manuscript to additional factors and mechanisms that could affect the predictions of the basic theory. We consider ecological conditions that may favour the evolution of defence syndromes, and summarize the results of broad phylogenetic studies. Because there is a dearth of such studies, we provide recommendations for assembling and analysing data to test comparative hypotheses. Subsequently, we examine how genetics and development are likely to impact the ways that multiple defences will respond to selection. We emphasize approaches that will be necessary to discriminate among mechanisms. Finally, we review functional hypotheses for how multiple defences interact with predator cognition. Predator cognition likely plays an important role in defence function when early-acting defences influence the efficacy of later-acting defences, or when interactions between simultaneously deployed defences affect predator response. To understand how complex antipredator adaptations arise, we need clearly envisage all these factors that affect the evolution of defence portfolios, and multiple defences more broadly.

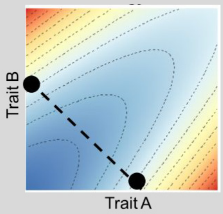
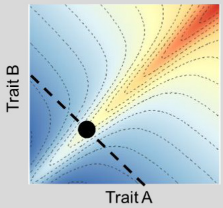
2 | THE BIG PICTURE: RESOURCE LIMITATION AND FUNCTIONAL INTERACTIONS BETWEEN TRAITS

Resource limitations and functional interactions among traits are pervasive themes of adaptative evolution (Stearns, 1989). Antipredator defence is no exception, and most studies of antipredator defences implicitly or explicitly acknowledge some aspect of this. However, the entire range of potential relationships among defences (and other traits) that we give below are seldom considered simultaneously in the literature. Having a detailed road map of all these potential relationships paints a fuller picture of multiple defence evolution and illuminates novel pathways for future work.

The first consideration is resource availability, which constrains an organism's investment into defences. Investment in each defence is constrained by **resource trade-offs**. For example, investment in armour might limit the resources that can be invested in claws. Defences also trade off against other life history traits. For instance, defended algal clones exhibit a marked decrease in reproductive rate relative to undefended clones (Yoshida et al., 2004).

Within a defence portfolio, the optimal resolution of resource trade-offs depends on functional interactions among defences (Table 1; Dewitt et al., 1999; Havlikova et al., 2020; Partan & Marler, 2005). The relative contribution of each defensive trait to a portfolio's total deterrent effect can be affected by other defences, i.e., defence value of trait A conditional upon the value of trait B (Broom et al., 2010; Caro & Koneru, 2021). When increasing investment in one trait decreases the efficacy of another, there is a **functional trade-off** between the traits. A functional trade-off takes place in **antergy**, which we define as occurring when the fitness

TABLE 1 Examples of how trade-offs and synergies can affect the presence and expression of predator defence.

	Definition	Context	Examples
Resource Trade-off		**Investment in one defence limits investment in another.**	• **Sequestration of defensive chemicals** in milkweed bugs trades off with their **synthesis de novo** (Havlikova et al., 2020)
		Investment in defence limits investment in non-defensive trait (e.g., reproduction, growth).	• **Defence-growth trade-off** for algae (Yoshida et al., 2004) • Tadpoles **grow slower** around predators (Van Buskirk, 2000)
Functional Trade-off		**Increased efficacy of one defence reduces the efficacy of (or need for) another defence.**	• Bivalve shells optimized for **burrowing** reduce **crush resistance** (Johnson, 2020) • **Morphological defences** are negatively correlated with **escape speed** in butterflyfish (Hodge et al., 2018)
		A defence protects against one predator at the cost of vulnerability to another.	• Predator-induced **tail shape** in tadpoles (Benard, 2006) and **behavioural responses** in roach (Eklöv & VanKooten, 2001) protect against one predator but reduce protection against others
		Defensive phenotype interferes with non-defensive trait (e.g., mobility, thermoregulation).	• **Tonic immobility** lowers **mating success** in flour beetles (Nakayama & Miyatake, 2010) • Butterflies with **warning signals** pay **aerodynamic costs** (Srygley, 2004)
Synergy		**Two defensive traits that provide more protection when possessed (deployed) together than either separately.**	• Prey using **deimatism** also benefit from **crypsis** (Kang, Moon, et al., 2017 • Many prey combine **morphology** and **behaviour**, thereby enhancing mimetic fidelity (Penney et al., 2014)
Multi-role traits	Defensive Function ↑ **Trait** ↓ Non-defensive Function	A defensive trait has non-defensive functions that increase survival or reproduction. The investment does 'double duty'.	• **Anal fluid** in burying beetles aids in **parental care** and **chemical defence** (Lindstedt et al., 2017) • In *Heliconius erato*, effective **aposematism** was positively correlated with **mating success** (Finkbeiner et al., 2014)

Note: Trade-offs may reflect resource allocation among defences, or between defences and other non-defensive traits. Limited resources mean that trait combinations must lie at or below the dashed line in the "definition" column; however, the line can move if resource availability changes. Warmer colours represent higher values. Functionally, defences may be independent, synergistic, functional trade-offs (including antergy), functionally redundant with each other, or play multiple roles. Rows in grey denote cases that only pertain to interactions between defences (as opposed to non-defensive traits).

benefit of two defences is smaller when they are deployed together than when they act alone. Additionally, some traits can render other traits **functionally redundant** (even if they are not in conflict, i.e., antergistic), which we define as occurring if they simply make the defensive effect of another trait irrelevant. Thus, with redundancy, the effect of just one trait decreases due to the effect of another (note that this does not necessarily mean that selection will completely eliminate a redundant defence, as it may still add some small benefit, unless it is always completely redundant). We define **synergy** between defences as occurring when the benefit of using two defences together is greater than the benefit of those two defences acting independently. **Independence** occurs if the probability of the prey surviving when it uses defence B is unchanged whether or not the prey deploys defence A. Synergy, antergy, and independence between defences in the same portfolio may occur within or between stages of the predation sequence.

Resource trade-offs and functional trade-offs may occur between a defensive trait and a non-defensive trait, defences against one type of predator and defences against another, or defences within a single defence portfolio. Some defensive traits also have other, non-defensive functions. Large investments into a trait that has an essential, non-defensive function can provide a defence that appears to be a "free" evolutionary by-product. We call these **multi-role traits**, which increase fitness through both defensive and non-defensive functions. Traits with predatory functions are often effective as antipredator defences (e.g., Stankowich et al., 2011), and therefore meet the definition of a multi-role trait. The predatory soil bacterium *Myxococcus xanthus* produces a range of secondary metabolites for lysing and digesting prey cells (Thiery & Kaimer, 2020). These metabolites have been hypothesized to function in antipredator defence as well (Findlay, 2016; Mayrhofer et al., 2021). Multi-role traits can confer potent defences acting late in the predation sequence (e.g., venoms). We suggest that this may create conditions favouring the evolution of other, earlier-acting defences such as aposematism.

How important are each of these different types of trade-offs and synergies to the evolution of multiple defences? In surveying the literature, we find that most trade-offs fall into three categories: resource trade-offs between a single defence and another life-history trait, functional trade-offs between defences, and functional trade-offs between defences in a portfolio and other life history traits (including defences against another type of predator) (Tables 1 and S3). Several studies reported resource trade-offs under changing nutrient levels, or allocation to antipredator defence in organisms that respond with plastic defence strategies. For example, Ehrlich et al. (2020) found a concave growth-defence trade-off in lake phytoplankton that favoured fast growth and intermediate defence. Some studies used predator responses to prey defences to test functional trade-offs. Stevens et al. (2011) successfully designed an experiment where humans caught fewer computer-generated prey that moved and had striped patterns, or were stationary and had camouflage patterns, but prey with other trait combinations were more easily caught (Table S3). Correlational studies of behavioural and morphological defences have also been used as evidence of trade-offs (Blanchard & Moreau, 2017; Hodge et al., 2018; Table S3). From correlational studies, it is difficult to determine whether trade-offs are functional or resource-based. However, note that variation in resource availability can lead to positive correlations between pairs of resource-dependent defensive traits (van Noordwijk & de Jong, 1986), regardless of any underlying resource trade-off. We found a few cases where correlations are consistent with synergy (Table S3). For example, Hossie et al. (2017) found increased morphological and behavioural defences in tadpoles that were exposed to predators, though more evidence is needed to test causality. Finally, we also found cases where no trade-offs were detected (Table S3). The potential for a "file drawer effect", where negative results are not reported, makes it hard to generalize about the ubiquity of trade-offs. We need more studies that use experimental approaches to simultaneously test multiple hypotheses for the potential relationships among defensive traits.

3 | THEORY ON THE ALLOCATION OF DEFENCES BETWEEN AND WITHIN STAGES OF THE PREDATION SEQUENCE

Formal theory can clarify specific predictions about how investment will be made among defences. Most of the theory to date primarily asks where an organism should allocate resources among multiple defences within the predation sequence. Trade-offs figure prominently in these models. There are many possibilities, such as incorporating potential synergy among multiple defences, that have yet to be formalized.

Some previous studies have addressed optimal defence portfolios in the case of sequentially deployed defences. Brodie et al. (1991) predicted that early defences should trade-off with late defences due to increased selection for one strategy reducing selection for the other. Subsequent studies have modelled these trade-offs, often agreeing that defences should be concentrated early in the predation sequence (Bateman et al., 2014; Broom et al., 2010; Wang et al., 2019). Some specific exceptions exist—for instance, when late-stage defences are much more effective than early-stage defences, multiple defences should be concentrated later in the predation sequence (Wang et al., 2019). Early-stage defences should also be more stable over evolutionary time than late-stage defences, but this again reverses when late-stage defences are more effective (Carmona et al., 2011; Wang et al., 2019). When the costs of late-stage defences are low, their evolution is favoured (Sherratt & Kang, 2018), and distinct defence syndromes of early vs late-stage specialists may stably coexist (Bateman et al., 2014; Broom et al., 2010).

We highlight two general considerations to orient readers interested in theoretical treatments of multiple defences. The first contrasts the benefits of multiple defences with a single defence. Multiple defences will have a greater survival benefit for the prey whenever their benefit exceeds the maximum of the benefits of any single defence (over evolutionary time). The second formalizes how defences interact. With p_A (resp., p_B) being the probability of the predator failing to overcome a defence A (resp., B), the two defences A and B act independently if the probability of survival when deploying both is $Pr(survival \mid A \& B) = 1 - (1 - p_A)(1 - p_B)$. This value serves as a reference along a continuum of interactions between defences, ranging from a negative interaction (antergy) when $Pr(survival \mid A \& B) < 1 - (1 - p_A)(1 - p_B)$ to a positive interaction (synergy) when $Pr(survival \mid A \& B) > 1 - (1 - p_A)(1 - p_B)$. The same continuum can be used to compare the benefit of multiple defences over single defences; multiple defences will have a greater survival benefit for the prey if $Pr(survival \mid A \& B) > max(p_A, p_B)$.

When defences are deployed simultaneously, we give novel theoretical predictions for how much should be invested in each. Box 1 presents a simple model of simultaneously deployed defences to illustrate how different defences are selected depending on defence effectiveness, the rate of potential encounters with predators, defence cost, and level of synergy between defences.

Future theoretical treatments that incorporate various types of trade-offs and potential synergistic or antergistic effects into optimal defence investment would be welcome. Additionally, incorporating multi-role traits into existing theory on the evolution of multiple defence may alter predictions about investment into early- versus late-acting defences. Some models predict heavy investment in late-acting defences when they are cheap (Broom et al., 2010; Sherratt & Kang, 2018). Multi-role traits may fit this description. However, it would be interesting to understand how general this prediction is when incorporating the additional function that a multi-role trait plays in an organism's ecology, and under what conditions, if any, multi-role traits can *increase* investment in early-acting defences. For example, we suspect that under some circumstances, venoms used in predation may promote the evolution of aposematism. We also need theory that connects multiple defences to ecology, genetics, and predator cognition and behaviour. We cover each of these topics below.

4 | CORRELATIONS AMONG DEFENCES, ECOLOGY, AND PHYLOGENY

Our literature survey on multiple defences in Tables 1 and S3 revealed an incomplete picture, with more studies investigating some types of trade-offs than others, and uncertainty due to possible underreporting of negative results. A more systematic approach is needed, and moreover, attempts must be made to link multiple defences to organismal ecology. Comparing the ecology and evolution of multiple defences across species and at large spatial and/or temporal scales could help us understand the ultimate forces that shape antipredator defences (McGill et al., 2019). Such a comparative framework would blend macroecological and macroevolutionary approaches. Typically, macroecological studies make use of regional to global biogeography, meta-analysis, and coordinated experiments

BOX 1 A model of simultaneously deployed, non-independent defences

Consider a prey species with a single reproductive episode at the end of its life (i.e., it is semelparous). The prey has two possible types of anti-predator defence (*A* and *B*) at its disposal, which can be simultaneously deployed. Defences *A* and *B* come at fecundity costs c_A and c_B, respectively, independently of how often they are deployed. Let the probability of the predator failing to overcome defences *A* and *B* when deployed alone be p_A and p_B, such that $Pr\left(survival \mid A \,\&\, B^C\right) = p_A$ and $Pr\left(survival \mid B \,\&\, A^C\right) = p_B$. Note that the superscript *C* denotes complement. We assume that if no defence is deployed, the prey will not survive an encounter with a predator. We seek to identify the combination of defences (if any) that would be selected for when the defences: (i) work independently to protect the prey, (ii) are synergistic or (iii) antergistic (see main text for definitions). Following these definitions, we define *z* as a measure of the departure of the combined probability of survival assuming complete independence, with $z = 0$ representing a case in which the two defences work independently to protect the prey, such that $Pr(survival \mid A \,\&\, B) = p_{AB} = 1 - \left\{\left(1 - p_A\right)\left(1 - p_B\right)\right\}^{1+z}$(*z* falls within the interval $-1 < z < \infty$, where $z > 0$ corresponds to synergy between defences, $z < 0$ to antergy).

Let predators encounter prey at random, so that putative encounters with individual prey are Poisson distributed with mean and variance λ. Under these conditions, the expected probability of an individual prey surviving a series of random encounters with predators is:

$$\sum_{i=0}^{\infty}\left(\frac{e^{-\lambda}\lambda^{-i}}{i\,!}\right)s^i = e^{-\lambda(1-s)},$$

where *s* is the probability of survival per putative encounter (the probability of having *i* encounters with predators is equal to $\frac{e^{-\lambda}\lambda^{-i}}{i\,!}$). The fitness *w* associated with each combination of defences will depend on the rate at which predators encounter the prey, the degree to which the defences protect the prey and the reproductive price they have paid to ensure it. Specifically, fitness is calculated as the product of prey surviving to reproduction and their fecundity if they do survive:

$$w_{none} = e^{-\lambda}(b)$$

$$w_A = e^{-\lambda\left(1-p_A\right)}\left(b - c_A\right)$$

$$w_B = e^{-\lambda\left(1-p_B\right)}\left(b - c_B\right)$$

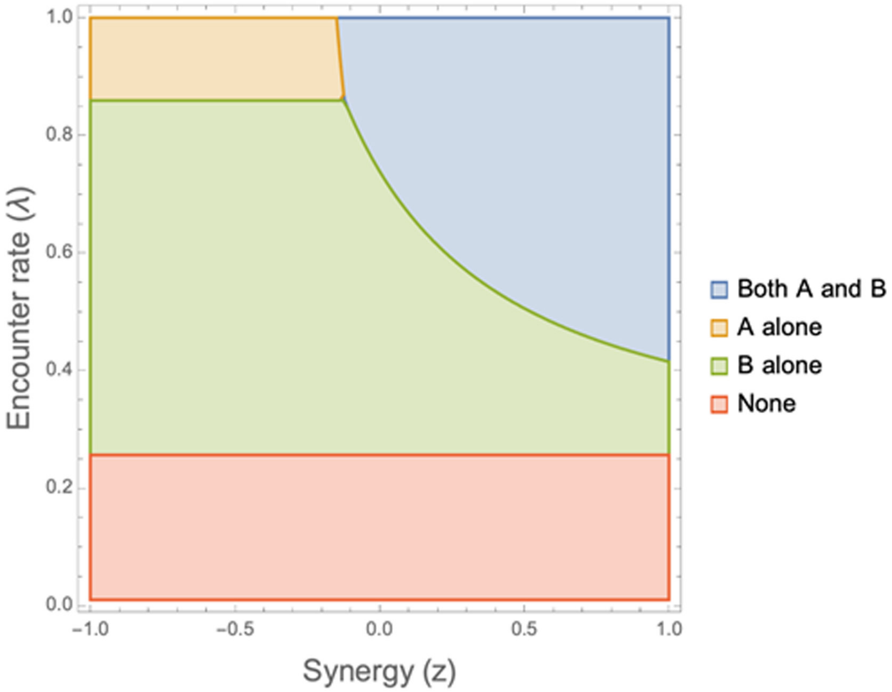
$$w_{AB} = e^{-\lambda\left(1-p_{AB}\right)}\left(b - c_A - c_B\right)$$

(Continues)

BOX 1 (Continued)

where b is the mean fecundity of surviving prey before paying for any defences. A similar approach can be used to calculate the fitness of the prey if it continually reproduces, i.e., is iteroparous (e.g., Kang, Zahiri, et al., 2017).

We can now identify the strategy that would be selected for at a given level of synergy (z) and mean rate of encounter with predators (λ). In the figure below for example, we consider the case in which defence A is better at protecting against the predator, but it costs more (specifically $p_A = 0.4$, $p_B = 0.2$, $c_A = 0.2$, $c_B = 0.05$, $b = 1$). Having no defence at all is only selected for when the mean rate of encounter of prey with predators λ is low (red region). For intermediate λ, the cheaper defence (B) is favoured (green region). For high λ, the level of synergy (z) determines which defences are favoured. Both defences are favoured when the two defences are synergistic (blue region). By contrast, the more effective yet costlier defence A is favoured when the two defences are antergistic (yellow region). To sum up, the strength of synergy (or antergy) between defences (z) as well as the need for defences (controlled by λ), affect which combination of defences is favoured. For an illustration of how survival probability of prey depends on the nature of the interaction between its defences, see Figure S1.



across multiple sites (e.g., Carmona et al., 2011; Nielsen et al., 2016; Roslin et al., 2017), while macroevolutionary studies use phylogenetic comparative methods to reconstruct the evolution of phenotypic traits, and estimate correlated evolution and diversification rates (e.g., Arbuckle & Speed, 2015; Nielsen et al., 2016; Stankowich & Romero, 2017). These approaches would be powerful for testing a wide array of factors that affect the evolution of defences, and will identify cases where experimental efforts offer the greatest power to test predictions.

Macro approaches have yet to be applied extensively to elucidate the ecology of multiple prey defences. Aposematism, which operates as a multiple defence because it relies on predators associating a warning signal with a secondary defence, provides perhaps the best examples thus far (reviewed in Caro & Ruxton, 2019). Ratcliffe and Nydam (2008) compared 37 chemically defended tiger moth species signalling with visual and/or acoustic cues to bird and bat predators, and suggested that multiple predators contribute to the evolution of multimodal aposematism. In poison frogs, specialized diets may facilitate the evolution of aposematism (Santos et al., 2003), and conspicuous coloration is correlated with large body size (Hagman & Forsman, 2003). Correlations between defences are also commonly studied as indicators of signal honesty in aposematism (e.g., mushroom coloration, odours, and toxins; Sherratt et al., 2005; carnivore coloration and noxious secretions; Stankowich et al., 2011; Crofts & Stankowich, 2021), or in terms of trade-offs between different defences (e.g., defensive behaviour and morphology in scorpions; Van Der Meijden et al., 2013). Macro approaches have also been used to uncover the evolutionary sequence of defence adaptations. For example, in spiders (Pekár, 2014) and millipedes (Rodriguez et al., 2018) warning colouration only evolves after chemical defence. Recently, Loeffler-Henry et al. (2023) found that intermediate states where warning signals are hidden could, in conjunction with chemical defence, better explain the evolution of aposematism. These phylogenetic correlations have rarely been tested experimentally (but see Riipi et al., 2001). Kikuchi et al. (2021) and Kunte et al. (2021) discuss how ecology and evolution determine the prevalence of aposematism and mimicry.

We are not aware of many other studies that use macro approaches to study the ultimate drivers of multiple defences in animals. Stankowich et al. (2014) found no instances of sociality occurring together with noxious chemical sprays in mammals, suggesting that these defence strategies may be mutually incompatible, or that they may function against predators in different prey niches (diurnal prey would be exposed to raptorial predators and nocturnal prey to mammalian predators, respectively). In addition to the scarce application of macro approaches to multiple defence in animals, few studies treat defences as a composite trait (but see Stankowich & Romero, 2017). The plant defence literature may provide inspiration for future studies of animals. For example, in a meta-analysis, Carmona et al. (2011) collated measurements of genetic correlation between various plant traits and susceptibility to herbivory. They used this dataset, covering 40 species from 19 plant families, to ask which types of traits most strongly predict resistance to herbivores. Secondary metabolites were assumed to be the most important defence in plants, but the results of Carmona et al. (2011) suggested an alternative hypothesis: herbivores exert greater selection pressure on life-history (e.g., flowering time) and morphological (e.g., plant height) defence traits, and secondary metabolites only gain importance in defence portfolios because they are relatively less constrained by pleiotropic effects of other defence traits creating trade-offs.

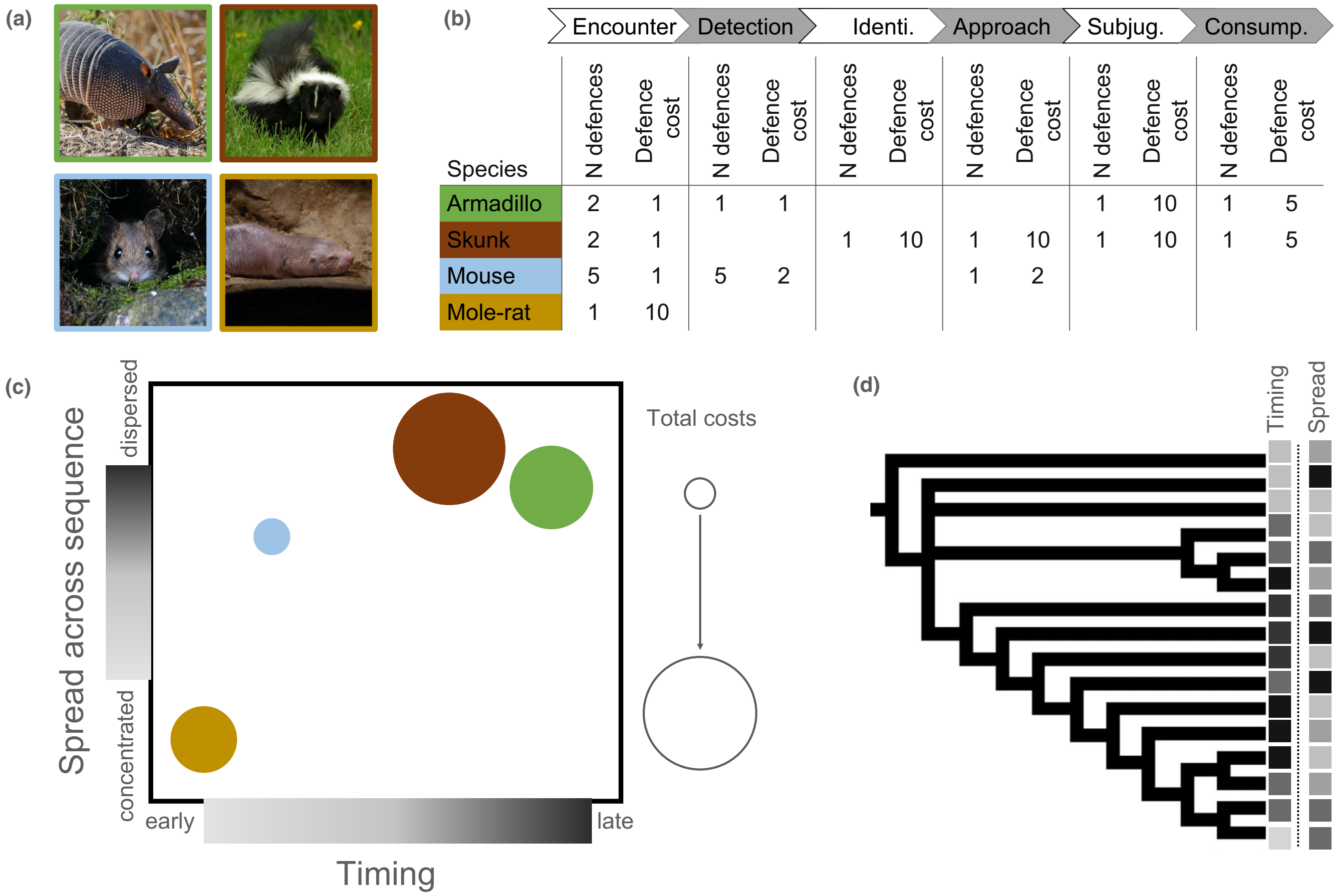
Plant studies may also help guide the way in analytical methods. Previous attempts to quantify multiple prey defences have collapsed traits into one 'defence score' (Stankowich & Romero, 2017). The plant literature employs approaches such as principal components analysis, hierarchical cluster analysis and dendrograms to identify defence syndromes and predict how and why multiple trait combinations evolve repeatedly across species (Agrawal, 2011; Moles et al., 2013; Sheriff et al., 2020). Particularly, many difficulties in the ecology and evolution of multiple defences may be surmounted by implementing an analytical framework that quantifies investment in defences throughout the predation sequence. Subsequently, ordination could be used to examine variation among particular defence portfolios (Figure 2a–c) (Sheriff et al., 2020). Depending on the research question, integrating and summarizing information on multiple defence types across species is likely to involve a degree of abstraction—for example, treating investment in different 'encounter' stage defences such as nocturnality and fossoriality as equivalent. This may be a necessary step in preparing for a comparative study (Figure 2d). We encourage researchers investigating defences using phylogenetic methods to consider a workflow like that envisaged in Figure 2, as it would produce high-quality data applicable to a diversity of questions in antipredator defence.

The approach that we have described above would especially yield a dataset tailored to addressing ultimate questions concerning multiple defences. We give five such questions that would provide key advances to our understanding.

1. How does the diversity of defences accumulate over time? Is it possible that multiple defences arise (nearly) simultaneously, as might be expected from diverse and dynamic predator communities, or gradually increase in number, as might be expected under Red Queen dynamics within stable predator–prey systems? Additionally, the number of defences through time could be clustered around a certain threshold or be highly variable. The accumulation of new defences might also slow down through evolutionary time if there are diminishing returns on reducing predation.
2. Do defences evolve in a predictable pattern, as has been demonstrated for chemical defence evolving before warning colouration in some taxa?
3. Do multiple defences exist in repeated 'defence syndromes'? If so, how many distinct defence syndromes are there in a given taxon and how strong is convergent evolution towards these combinations? How does coevolution (sympatry or allopatry) with important enemy species impact syndromes of defences?
4. Assuming defence syndromes exist, how do they vary between taxa? For instance, it could be that hymenopterans have different defence syndromes compared to snakes, or there might be widespread convergence between distantly related taxa.
5. How does ecological variation influence multiple defence strategies? For instance, does the defence strategy systematically vary with predation risk, latitude, habitat, body size, specialist-generalist axes of the prey or their predators, or other attributes of predator communities?

Latitudinal gradients in multiple defences are one aspect of this last question where some progress has been made. A comparative analysis of primary defences in spiders revealed that the relative frequency of species using crypsis increases with latitude, but frequency of species using Batesian mimicry decreases (Pekár, 2014). This may be because, at lower latitude, spiders are under selection from specialized predators, while at higher latitude spiders are under selection from generalists. If this is a more general pattern, then at lower latitudes prey should be selected to possess defence portfolios that are highly effective against a limited number of specialized predators, whereas at higher latitudes multiple defence strategies that are more generally effective should predominate, which might involve an increase in the number of defences with increasing latitude.

Another example of how ecological variation will be important in understanding multiple defences is the relationship between multiple defence strategy and life history strategy, which has a key role in many



	Encounter		Detection		Identi.		Approach		Subjug.		Consump.	
Species	N defences	Defence cost	N defences	Defence cost	N defences	Defence cost	N defences	Defence cost	N defences	Defence cost	N defences	Defence cost
Armadillo	2	1	1	1					1	10	1	5
Skunk	2	1			1	10	1	10	1	10	1	5
Mouse	5	1	5	2			1	2				
Mole-rat	1	10										

FIGURE 2 Example of a comparative framework. Abstracted defence use throughout the predation sequence. (a) Four examples of mammalian species. (b) Number of defences and defence costs quantified through predation sequence. Data are an illustrative, hypothetical example. Encounter stage defences include nocturnality and fossoriality, which mole rats rely on to avoid predation. Detection stage defences include crypsis, other camouflage strategies and cryptic behaviours. The armour and rolling-into-a-ball behaviour of armadillos defends against subjugation and consumption but carries significant costs. The aposematic colouration of a skunk is a defence at the identification stage, with noxious spraying deterring approach, subjugation and consumption. For mice, speed of escape is a partially effective defence at the stage of approach. (c) Ordination techniques such as PCA could be used to summarize and quantify axes of defence strategy across diverse species. (d) These could be used as composite traits in comparative analyses.

community-level processes such as responses to environmental stochasticity and succession (Connell & Slatyer, 1977). Early-successional species often have 'fast' life history traits, characterized by short life cycles but high reproductive potential, while late-successional species often have 'slow' life histories which prioritize future reproduction. As a result, at early stages of succession, species with limited investment in multiple defences should occur, and over succession be replaced by species with richer and higher-cost defences.

Comparative studies have great power to unveil fascinating patterns that are consistent with or contrary to the predictions of certain hypotheses. However, they lack mechanistic descriptions and strong inference. To provide these, it can be helpful to experimentally measure factors that produce fine-scale variation among individuals within populations, as the population is the unit in which microevolutionary change occurs. To measure the effectiveness of defences, especially within a defence portfolio, evaluating mechanisms of their function against relevant predators is essential. We cover these approaches in the next two sections.

5 | GENETICS AND DEVELOPMENT: FACTORS THAT MAY CONSTRAIN OR PROMOTE ADAPTATION

Various proximate mechanisms generate defence phenotypes. These mechanisms can have important implications for how well theoretical models of selection are able to predict the evolution of multiple defences. As such, any treatment of multiple defences needs to take these into account.

Some variation is genetically canalized. For example, in garter snakes (*Thamnopsis ordinoides*), selection favours a genetic correlation between cryptic or conspicuous colour patterns and different evasive behaviours (Brodie, 1989, 1992). In other cases, defences respond plastically to environmental conditions, as seen in the poison frog *Oophaga pumilio*, whose chemical defences vary according to spatio-temporal availability of the arthropod prey from which they sequester their toxins (Saporito et al., 2006). Finally, individual variation within and between populations can arise from interactions between genotype and environment (GxE interactions), whereby genetically distinct individuals respond differently to environmental variation. This can be seen in genotypes of *Daphnia* that differ in their reaction norms for defence induction after exposure to predator cues (Hammill et al., 2008). Additionally, state variables such as organismal size can depend upon the nutrients available in the environment, resulting in size-dependent changes in the expression of defences. Some lepidopteran larvae switch strategies from masquerade to crypsis or aposematism as individuals advance through instars to adulthood (Gaitonde et al., 2018; Medina et al., 2020). Studies that test whether genetic, environmental, and GxE interactions determine defence phenotype would give us greater insight into the mechanisms most likely to result in certain defence syndromes.

Additional proximate mechanisms may prevent selection from producing the phenotypes that are predicted by idealized optimality models, such as those we presented above. To illustrate this, consider functional trade-offs and synergies between defences. They can arise from single traits with multiple functions. However, similar correlations can also arise from pleiotropy, in which a single gene affects more than one trait (Lande, 1979; Lande & Arnold, 1983). In defence portfolios, as with any other set of traits, pleiotropy has the potential either to facilitate adaptive evolution by leading to combinations of traits that work well together or to limit the combinations that are generated (Carmona et al., 2011). For instance, pleiotropy has been shown to constrain the evolution of chemical defences in *Boechera stricta*, a wild relative of *Arabidopsis*, where a single locus is largely responsible for defences under antagonistic selection in fruits and leaves (Keith & Mitchell-Olds, 2019). In species that go through metamorphosis, pleiotropy among defensive traits can also occur between life stages (Lindstedt et al., 2016). A similar effect of evolutionary constraint can arise from linkage among genes, with certain combinations made less likely by low levels of recombination (Charlesworth, 2016). Many antipredator traits are likely to be quantitative and polygenic, making it more difficult to understand the links between genotype and phenotype (Kooyers et al., 2020). The interplay of these factors could—in combination with the general consideration of environmental and genetic contributions to phenotype—predict which combinations of defences are evolutionarily possible for a species. Theory that predicts the genetic architecture underlying different defence syndromes would be of exceptional value, as would experiments that test it.

Knowing the proximate basis by which different defences arise does not necessarily tell us about their adaptive value. Variability in defences may occur above or below the thresholds at which survival is affected. As we have seen above, genetic and environmental sources of variation in phenotype indicate caution when examining correlations among defences within a population. Even if variation is adaptive, any selective benefits of defences happen because they impact progression through the predation sequence. Most defences are hypothesized to work by affecting predator cognition and behaviour. Thus, understanding the mechanisms of how predators respond to multiple defences is indispensable. We turn to this in the next section.

6 | THE FUNCTIONAL PERSPECTIVE: PREDATOR COGNITION AND MULTIPLE DEFENCES

Despite the fact that predator cognition is a key factor driving the evolution of many forms of defence (Skelhorn, Halpin, et al., 2016; Skelhorn & Rowe, 2016; Umbers et al., 2017), work in this area has largely focused on single defences. To understand the functional significance of multiple defences, and to test mechanisms underpinning correlative patterns, we need to consider how multiple defences may interact to exploit predator cognition.

We take a broad view of predator cognition, defining it as any mechanism related to information processing, which includes perception, attention, learning, memory, and decision-making (Shettleworth, 2009). Whilst a number of experiments have established that the benefits of multiple defences can exceed that of a single defence (Skelhorn, Holmes, et al., 2016; Winters et al., 2021), the mechanisms by which multiple defences in a portfolio exploit predator cognition are not clear. Predator cognition may underpin synergistic or antergistic relationships between defences, and thus affect prey survival and defence evolution. Here, we consider cognitive mechanisms of predators that could cause defences to interact in the ways outlined earlier in the text and in Box 1. We focus on defences deployed either immediately before or upon attack, since they usually target multiple sensory modalities and cognitive responses of the predator (Rojas et al., 2019; Rowe & Halpin, 2013), and emphasize how defences may work synergistically or antergistically, as the default assumption has typically been independence (Rowe, 1999; Rowe & Halpin, 2013; Ruxton et al., 2018).

There are a number of mechanisms through which multiple defences may exploit predator cognition and produce potentially synergistic effects. **Multisensory integration**, i.e., integrating sources of information from different sensory modalities, is well understood at the neuronal level (Stein & Stanford, 2008). Multimodal neurons (i.e., neurons sensitive to stimuli in several modalities) show stronger responses to a multimodal stimulus than to any of its unimodal components (Stein & Meredith, 1993). Moreover, neuronal responses can be superadditive, that is, they exceed the sum of the responses to unimodal stimuli (Stein & Stanford, 2008). This increase in perceptual sensitivity, called **multisensory enhancement**, leads to increased stimulus salience, better detection, faster reaction times, more accurate localization, and improved discrimination between stimuli (Munoz & Blumstein, 2012; Stein et al., 2020). Comparative studies indicate that common principles underlie multisensory integration across vertebrates (Stein et al., 2020). This may help to explain why multimodal warning signals are so widespread (Rowe & Halpin, 2013). Multisensory enhancement that speeds up a predator's reaction may provide a fitness benefit by stopping attacks early enough to avoid damage (Rowe, 1999). Multisensory enhancement may also reduce speed-accuracy trade-offs in prey discrimination (Chittka & Osorio, 2007). Enhancing prey salience to predators through multimodal displays is consistent with the importance of conspicuousness in aposematism (Mappes et al., 2005; Stevens &

Ruxton, 2012), and probably in other defence strategies such as deimatism (Umbers et al., 2017). Multimodal defences may also exploit predator cognition through their effects on learning and memory. For example, bats learn to avoid chemically defended fireflies faster when they use bimodal signals (sound and bioluminescence) than either of these modalities alone (Leavell et al., 2018). Whilst the neural mechanisms of multimodal enhancement are well-known, showing that these mechanisms are at play in the context of predation requires further work.

Another possible mechanism through which multiple defences may exploit predator cognition is **cross-modal correspondence**, where a defence in one modality may change the way a defence in another modality is perceived, producing potentially synergistic effects. Whilst such a mechanism has been demonstrated in humans (Spence, 2011), direct evidence is lacking in the context of predator–prey interactions, where cross-modal correspondence may potentially play a role in hidden innate aversions to aposematic displays. For instance, interaction between olfactory and visual warning signals triggers innate aversions to aposematic prey in birds (Rowe & Guilford, 1996) and spiders (Vickers & Taylor, 2020), but the exact cognitive mechanisms responsible for these aversions remain unknown.

Defences may also act synergistically if multiple defences are inherently more surprising or less predictable than single defences. Several forms of defence involve a sudden appearance of unexpected stimuli (e.g., display of previously hidden signals; Kang, Moon, et al., 2017; Umbers et al., 2017; Riley et al., 2022) and may exploit the effects of **surprise** on predator cognition. Since one important function of the brain is to reduce uncertainty about the external world (Clark, 2013), unpredictable stimuli increase the brain computational load, which increases neural activity and reaction times to external events (Jakobs et al., 2009). Multiple defences are likely to increase cognitive load, and may thus delay or alter a predator's decision to attack (Holmes et al., 2018; Kang, Zahiri, et al., 2017). Surprising events also indicate change and increase uncertainty, which may lead to enhanced subsequent learning (Courville et al., 2006). Sudden appearance of unexpected defences may therefore increase the speed at which predators learn to avoid defended prey (Kang et al., 2016; Rowe, 2002; Skelhorn & Rowe, 2005). More broadly, possessing multiple defences may make prey more 'unpredictable'. If predators cannot predict which form of defence prey are likely to use, it may be more difficult for them to develop counter-strategies. Interactions between sequential defences may have synergistic effects if one stimulus increases a predator's response to a subsequent stimulus, a mechanism known as **priming** (Shettleworth, 2009). For example, highly volatile pyrazines, which are part of defensive secretions of many aposematic insects and act as olfactory signals (Moore et al., 1990) may increase a predator's subsequent response to gustatory cues, such as bitter-tasting toxins (Siddall & Marples, 2008; Winters et al., 2021).

In other cases, prey defences may act antergistically. Multiple signals may, for instance, compete for predator's attention, and competition may occur both within the same modality and across modalities (Dukas, 2002). For example, simultaneous processing of two streams of auditory information by foraging bats may lead to decreased performance in both tasks (Barber et al., 2003). Multiple signals may also interfere with each other in prey avoidance learning, and this may result in stimulus overshadowing, whereby predators associate prey unprofitability with the most salient of simultaneously presented stimuli (Aronsson & Gamberale-Stille, 2008; Kazemi et al., 2014; Sherratt et al., 2015). Nevertheless, even if defences act antergistically, having multiple defences can still be beneficial provided the benefit of deploying multiple defences is greater than the benefit of deploying the best defence alone.

Investigating how multiple defences affect the cognition of relevant predators would enable us to determine how defence portfolio design impacts prey survival. This would also allow us to address key questions concerning multiple defences and predator cognition: (1) Do defences that are displayed earlier and later in the predation sequence exploit different cognitive responses of predators? (2) Which aspects of predator cognition are targeted in simultaneous versus sequential deployment of multiple defences? (3) When does synergy need synchrony of the multiple defences, and when does it not? (4) How are multiple defences related to the concepts of surprise and uncertainty and to their effects on predator cognition and behaviour? Moreover, understanding the function of synergistic multiple defences can offer novel insights into diverse aspects of predator cognition, including both individual experience and use of social information.

Testing theoretical predictions about the effects of multiple defences on predator cognition will require carefully designed experiments involving manipulation of prey defensive traits (Ottocento et al., in press; Rojas et al., 2019) as well as costs and benefits associated with predator decisions to attack or avoid (Sherratt & Holen, 2018). As cognition and hunting strategies of predators, and their sensitivity to prey defences can vary greatly, model predators should be as ecologically relevant as possible. Ideally, several different predators would be compared (Rojas et al., 2017). Because direct observations of predator–prey interactions in the wild remain rare, recent technological advances, such as camera traps (Akcali et al., 2019; Smith et al., 2020) and eDNA analysis (Rößler et al., 2020) can help identify natural predators. Since human respondents frequently substitute for predators in experiments focused on, for instance, prey detectability (Loeffler-Henry et al., 2018) or signal categorization (Kikuchi et al., 2019), validating these tests using natural predators would allow for better interpretation and generalization of their results (Penney et al., 2012).

7 | CONCLUSION

Multiple defences are a ubiquitous phenomenon with at least two general classes of hypotheses to explain them: that multiple predators (or multiple selective environments) favour them, or that they are functionally integrated to deter a specific instance of predator attack. The former is far better understood than the latter.

Formulating arguments about how an organism's limited resources would be best allocated among defences depends not only upon the efficacy of individual defences in deterring predation, but also upon their trade-offs and functional interactions with other traits. New theory that incorporates these interrelationships would produce more general hypotheses about the integration of defences. For example, synergistic and antergistic interactions among defences deserve more attention, because, as we have shown in the model of simultaneous defences (Box 1), synergy (or antergy) among defences may affect the conditions under which different combinations of defences would be selected for. Likewise, multi-role traits that serve non-defensive functions could change our expectations for which combinations of defences are most likely to evolve and when.

We advocate using phylogenetic approaches to test for broad-scale patterns among defences and other traits, including various aspects of ecology. We emphasize that quantifying defences that function across different stages of the predation sequence and using ordination methods to derive summary statistics for phylogenetic analysis will improve the inferences we can make (Figure 2). At the same time, we caution that correlative evidence should be accompanied by experimental tests. Specifically, the genetic and environmental basis of variation in defences is poorly known, although it could have a critical influence on how closely an organism's phenotype matches adaptationist arguments. Finally, we have pointed out potential mechanisms through which multiple defences may exploit predator cognition (e.g., multisensory integration, cross-modal correspondence, surprisingness of the defences, and cognitive priming) and produce synergistic effects on predator behaviour and prey survival. Experiments targeting these mechanisms could simultaneously tell us about the fitness effects of multiple defences, and how those effects are produced.

We are optimistic that with the diversity of theoretical and experimental approaches now available or soon to be available this field will progress rapidly to offer a more complete picture of the evolution and maintenance of defence portfolios and antipredator defences in general. The study of multiple defences encourages an integrative perspective on trait evolution that acknowledges the many problems organisms face. It also emphasizes the diversity of solutions—sometimes complementary, sometimes conflicting—that prey evolve.

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AUTHOR CONTRIBUTIONS

David W. Kikuchi and Alice Exnerová are co-organizers; other authors listed alphabetically.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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