Review

Predicting Predator Recognition in a Changing World

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Through natural as well as anthropogenic processes, prey can lose historically important predators and gain novel ones. Both predator gain and loss frequently have deleterious consequences. While numerous hypotheses explain the response of individuals to novel and familiar predators, we lack a unifying conceptual model that predicts the fate of prey following the introduction of a novel or a familiar (reintroduced) predator. Using the concept of eco-evolutionary experience, we create a new framework that allows us to predict whether prey will recognize and be able to discriminate predator cues from non-predator cues and, moreover, the likely persistence outcomes for 11 different predator–prey interaction scenarios. This framework generates useful and testable predictions for ecologists, conservation scientists, and decision-makers.

Invasions, Extinctions, and Disturbed Interactions

The distribution of predators and their prey are static in neither time nor space. Through range expansions, natural and anthropogenically driven extinctions, and accidental and deliberate introductions, prey can lose historically important predators and gain novel ones. There is a growing theory to predict responses of prey to alien predators, or to reintroduced extinct predators (e.g., naiveté [1]; the multipredator hypothesis [2]; relaxed selection [3]), but these hypotheses are often too specific to permit broadly applicable, *a priori* predictions about the outcomes of new predator–prey interactions. Consequently, the temptation is to use them as *post hoc* explanations rather than as part of a predictive toolbox. When theory is linked to processes that occur in the real world, developing a fundamental understanding of the responses of prey to predators is not of purely academic interest. The ubiquity of invasions and other ecosystem changes worldwide means that the persistence of native prey is inextricably linked to effective antipredator behavior for a range of predators [4,5]. We aim to unify the theory around novel predator–prey interactions in disturbed environments, and to create a synthetic, predictive framework for ecologists and conservation scientists that will predict not only whether prey will respond to a predator but also how (or how effectively) they will respond, and the likely prognosis for prey persistence.

We define 'disturbed' predator–prey interactions as those interactions to which predators have been introduced (e.g., an alien predator) or from which a predator has been lost (e.g., to extinction). The former results in an exotic predator interacting with native species; this is a new predator–prey interaction, and it might also be a novel one (see Box 1 in [6]). The latter scenario, where a native predator is lost, also disturbs native predator–prey interactions, with implications for responses to that same predator (if reintroduced) or other predators (e.g., exotics). For example, the extinction of a native predator can result in the loss of antipredator behavior through relaxed selection [3], or the maintenance of antipredator behavior if other predators

Trends

Global processes of invasion and extinction have disturbed evolved predator–prey interactions worldwide.

A cornucopia of mechanisms have been proposed to explain antipredator behavior in native, new, and novel predator–prey interactions.

Each has, until now, been too specific to enable *a priori* predictions of whether prey will respond appropriately in disturbed interactions.

By integrating two recent frameworks – eco-evolutionary experience and multiple levels of naiveté – we synthesize eight mechanistic hypotheses into an overarching, predictive framework.

This new framework links ecological and evolutionary experience with predators via specific hypothesized mechanisms and the multiple levels of prey naiveté framework, to a predicted persistence outcome for prey under predation from a focal predator.

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remain (multipredator hypothesis) [2]. Conceptually grouping predator loss and predator gain as disturbances to native predator–prey systems enables the synthesis of classic and modern predator–prey theory into a single framework.

The Legacy of Eco-Evolutionary Experience

The eco-evolutionary experience framework describes how heritable experience gained within native biotic interactions (including predation, competition, mutualism, and commensalism) might (or might not) be applicable to new ecological interactions outside the native range. For example, native prey species might be particularly vulnerable to an introduced mammalian predator if they lack eco-evolutionary experience with mammalian predators (e.g., [5,7]). We extend this framework to show how the outcome of all predator–prey interactions, both historically stable and recently disturbed ones, can be predicted by considering eco-evolutionary experience. Whereas Saul and Jeschke [6] focus on predicting invasion success and impact on recipient communities, we use the framework to unite disparate components of predator–prey theory, and to predict how prey will respond to specific predators. We describe native prey responses to a range of predators for the sake of simplicity, but the logic and arguments of our framework can be applied to situations where the prey of interest is exotic and might, for example, encounter native predators (e.g., [8]).

Native prey faced with native predators and native prey faced with highly novel, recently introduced exotic predators represent the two extremes of the eco-evolutionary experience spectrum. A native prey species and its native predator have a long, shared history of experience over both evolutionary and ecological timescales. We therefore expect native prey to respond effectively to native predators [9], and this is generally the case. For instance, yellow-bellied marmots (*Marmota flaviventer*) respond to the sights [10], sounds [11], and scents [12] of their predators, and have a rich repertoire of antipredator behavior that includes emitting alarm calls [13], modifying their vigilance as a function of risk [14,15], the evolution of compensatory responses that link locomotor ability to antipredator vigilance [16], and modifying their habitat by digging escape burrows and using them to escape predators in a risk-sensitive way [17] that can increase fitness [18]. This suite of responses generally protects older marmots from predation. By contrast, native prey that have no eco-evolutionary experience with a predator are unlikely to respond to it effectively because they have neither learned about nor adapted to it [9,19]. For example, many of avifauna of New Zealand, such as the kakapo (*Strigops habrotilus*), have no experience with mammalian predators, and therefore retain traits such as ground-nesting, locatable mating calls, and/or flightlessness [20]. These traits have left kakapo (and other New Zealand birds) extremely vulnerable to predation by invasive mammalian predators, and they are now critically endangered, with a population comprising only 126 individuals [21].

Outcomes for these extremes are straightforward to predict. However, expected outcomes are unclear for disturbed predator–prey interactions across the spectrum of experience. For example, we expect different mechanisms to operate, and different outcomes for native prey persistence, where an extinct, historically important native predator is reintroduced to its historical native range. The classic example is the reintroduction of wolves (*Canis lupus*) to Yellowstone National Park in the USA (reviewed in [22]). Reintroducing Tasmanian devils (*Sarcophilus harrisii*) to the Australian mainland after approximately 900 years of absence would create a similar scenario [23]. Further examples of intermediate eco-evolutionary experience might come from the practice of 'rewilding', where exotic species are introduced to restore a missing ecological function, such as herbivore overabundance due to an extinct native predator [24]. In such scenarios, it would be crucial to accurately predict how prey are

likely to respond to the predator, or, in the case of rewilding, to select a substitute exotic predator that is unlikely to extirpate native prey. We therefore need to understand how experience with the predator of interest, and with other predators more generally, predict the mechanisms underpinning each disturbed predator–prey interaction, and the likely persistence outcomes for prey. Although there is a collection of hypotheses about when prey should respond effectively to predators in a range of scenarios, to date we have not been able to organize them into an overarching synthetic and predictive framework. We show below how the idea of eco-evolutionary experience helps us to unite these hypotheses into an integrative framework that predicts coexistence, or failure to coexist, with particular predators.

A Cornucopia of Predator–Prey Hypotheses

We review here and synthesize eight key hypotheses from the predator–prey literature through their shared implicit reference to the concept of eco-evolutionary experience. Briefly, they include: (i) adaptation [25], the mechanism by which prey evolve over time to deal with ongoing predation risk; (ii) the multipredator hypothesis [2], whereby antipredator behavior for an extinct predator is maintained so long as predation pressure from other predators remain; (iii) 'recoverable templates', where priming or other experiences with predators rapidly re-engage unused, but nevertheless intact, predator-discrimination templates [26]; (iv) relaxed selection [3], whereby costly antipredator responses are lost in the absence of predation risk; (v) the archetype hypothesis [27], whereby prey antipredator responses are effective against specific sets of similar predators, regardless of prior experience with particular predator species; (vi) a group of predator 'labeling' hypotheses suggesting that prey recognize specific 'features' that label an animal as dangerous, regardless of prior experience [28–32]; (vii) the naiveté hypothesis [1,27,33], which predicts that prey will not recognize or respond to novel predators for which they lack prior experience; and (viii) a group of 'rapid change' hypotheses about mechanisms through which prey can rapidly learn and/or adapt in the face of novel predation pressure [34,35] (Box 1 and Figure 1). Each of these hypotheses describes a mechanism behind prey antipredator response in a specific scenario. Importantly, these mechanisms might not be mutually exclusive, and some mechanisms are more proximate (e.g., archetype, multipredator) than others (e.g., adaptation, relaxed selection).

Pathways to Predator Discrimination

Much of the experimental predator–prey literature reports whether prey discriminate predator from non-predator cues because cue discrimination necessarily precedes mounting an antipredator response [36–38]. However, prey might experience substantial predation despite having the ability to discriminate predator cues [9]. In the next section we show that it is not the cue discrimination outcome itself but rather the mechanism behind predator cue discrimination (Box 1) that allows us to predict whether (and in what way) focal prey will respond to the focal predator. We first show how the eco-evolutionary experience of the prey with the focal predator identifies the relevant mechanism of cue discrimination outcome, and the cue discrimination outcome itself (Figure 1). While the 'eco' in 'eco-evolutionary experience' refers to the ecological interaction of interest [6], it is also the history of experience of the prey species with that interaction over ecological and evolutionary timescales that predicts which mechanism of antipredator recognition will operate (Box 1 and Figure 1). Hence, we consider ecological and evolutionary experience separately (Figure 1). Experience at either timescale can also be specific or general, 'applicable' experience [6]. For example, prey might have no specific experience with the focal predator, but have general experience with other predators. The first part of our framework formalizes the taxonomy of the combination of specific and general,

Box 1. Predator Discrimination Hypotheses

Adaptation: with sufficient time and heritable variation, prey will adapt to contemporary threats and ultimately be able to discriminate predators from non-predators (*sensu* [25]).

Multipredator hypothesis: this predicts that prey will retain evolved abilities to respond to extinct predators as long as they retain other predators. An implicit assumption of this hypothesis is that antipredator behaviors are genetically correlated or linked because it would be disadvantageous for the underlying traits to independently assort. This is because a prey species that was able to respond to one of its predators, but not to another predator, would be selectively disadvantaged compared to one that was able to respond to both. Thus, selection is expected to create correlated antipredator systems that should be somewhat resilient to the loss of a specific predator [2].

Recoverable templates: the key idea underlying recoverable templates is that recognition templates exist but are not activated without experience. Experience might include specific exposure to predators (e.g., as seen when cow elk lost a calf to a predator [26], or when fish have one-trial olfactory learning that permits predator identification [51]) or could include priming (which is seen when a non-specific stimulus is required for the later proper performance of a behavior).

Relaxed selection: the assumption under a relaxed selection model is that if recognition and/or discrimination abilities are no longer selected, and if there are any costs to maintaining them, these abilities will be lost [3]. Costs could be energetic (maintaining unnecessary sensory organs or brain tissue is expensive) or opportunity costs (responding to a predator when not present would reallocate time from important activities to an unimportant activity).

Archetypes: the archetypes hypothesis proposes that prey will recognize and respond to introduced predators that are of the same 'archetype' as familiar local predators. Distinctions at the taxonomic level of family are the proposed proxy for a practical interpretation of 'archetypes', but an archetype can also be defined as 'the set of predators against which a given suite of antipredator adaptations is effective' [27].

Labeling: a group of hypotheses suggest that prey use general features common to predators to 'label' a novel animal as being predatory, irrespective of prior experience with that particular predator species. For example, prey might recognize a chemical *leitmotif* [28,30] or sulfurous chemical compounds resulting from meat digestion [52] in the olfactory products of a novel predator. Similarly, large-bodied, faster-moving fish are more likely to be predatory than smaller, more slowly moving fish [53–55], and in some environments animals with large, forward-facing eyes are likely to be predatory [56]. Finally, general fear towards novel stimuli, objects, or environments, also called 'neophobia' [31,32], is another way in which prey might label all novelty as indicative of danger. These features can all be considered predator 'labels'.

Naiveté: naiveté theory predicts that native prey will not recognize or respond to a novel predator because of a lack of experience [1]. More recent formulations posit that there are in fact multiple levels of naiveté, through which prey might progress with time and experience [9,19].

Rapid change: when faced with a novel predator, prey might rapidly develop antipredator behavior via plasticity, learning, and/or rapid evolution [34,35,57,58].

evolutionary and ecological experience that the focal prey has with the focal predator, and uses this information to identify the underlying mechanism behind a cue discrimination outcome.

As previously mentioned, we default here to discussing a native prey species and its native or introduced predators. We have identified 11 eco-evolutionary experience scenarios which we conceptualize as 'pathways' through a decision tree diagram (Figure 1; pathways are shown as lines of different colors). Each pathway begins with the specific eco-evolutionary experience of the prey with the predator of interest (Figure 1, 1A–D), then considers whether prey has any other, potentially applicable experience, on evolutionary (Figure 1, 2A–C) or ecological time-scales (Figure 1, 3A–C). Questions 2B and 2C ask about predator archetypes and cue-labeling components – these are questions about general applicable evolutionary experience because innate responses to other co-evolved predators are required before prey can recognize and respond to archetypes or cue-labeling components [26,37,39]. Each pathway includes only the relevant questions given the information that can already be assumed for prey at the current
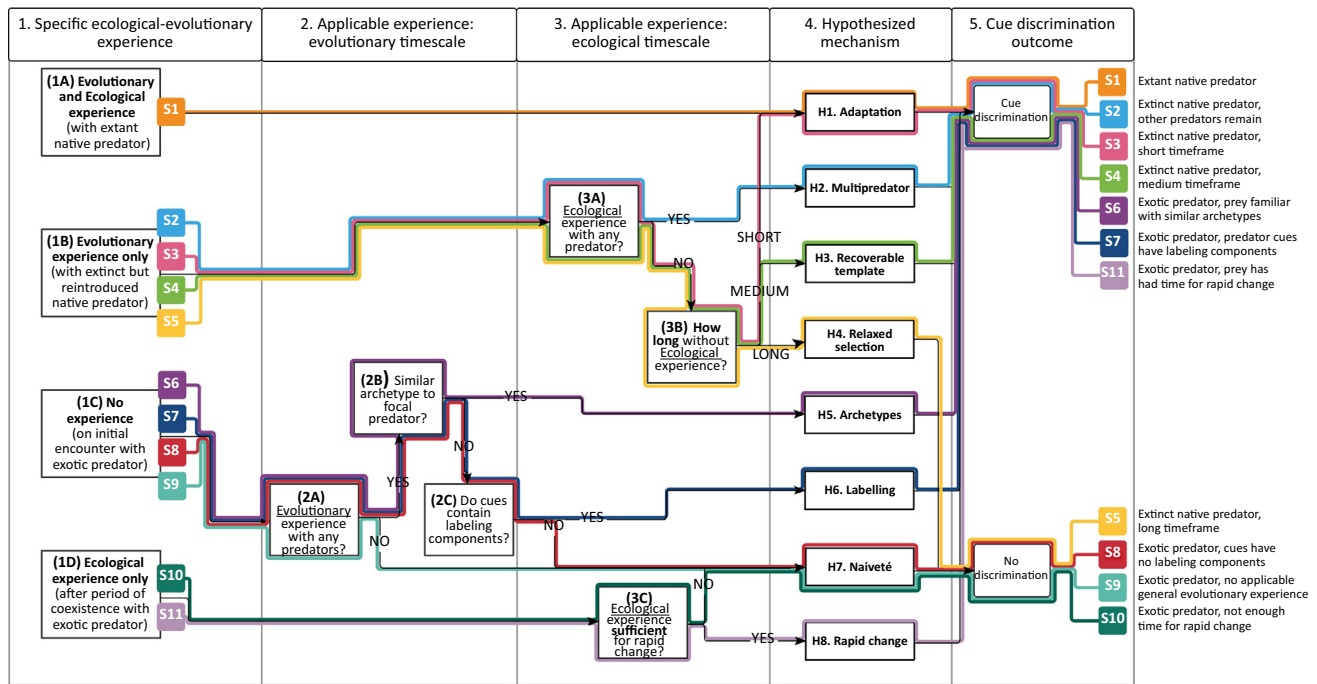
Figure 1. Pathways to Predator Discrimination. Based on a prey species' specific ecological and evolutionary experience with a predator (column 1), applicable evolutionary experience with predators (column 2), applicable ecological experience with predators (column 3), and one of eight hypothesized mechanisms by which prey can recognize predators by being able to discriminate predator cues from non-predator cues (column 4), prey might either successfully discriminate predator cues from non-predator cues or fail to discriminate between them (column 5). Each pathway illustrates a mechanistic process that permits some predictions about the likelihood of prey discriminating the cues of the focal predator from non-predator cues. The four categories of the specific eco-evolutionary experience of the native prey species with a focal predator include (first column): (1A) experience on both ecological and evolutionary timescales (an extant, sympatric native predator), (1B) experience on an evolutionary timescale only (a reintroduced native predator), (1C) no experience (initial encounter with an exotic predator), or (1D) experience on an ecological timescale only (an exotic predator sometime after it was introduced).

Scenario 1. If prey have experience on both evolutionary and ecological timescales with the focal predator (1A), as seen with native prey and their extant native predators, prey will be adapted to that predator (H1 adaptation). The marmot example described in the text illustrates this scenario.

Scenario 2. If prey have specific experience on an evolutionary, but not an ecological, timescale with the focal predator (1B), such as occurs when an extinct native predator is reintroduced, we consider whether prey have recent (ecological) experience with other predators (3A). If so, we predict (H2 multipredator hypothesis) that antipredator responses for the focal predator will be maintained. For instance, the multipredator hypothesis has been used to explain why populations of tammar wallabies (*Macropus eugenii*) that have been isolated on islands without mammalian predators maintain the ability to respond to mammalian predators. On islands where they coexisted with non-mammalian predators, they maintained an ability to respond to mammalian predators, whereas on islands where they were isolated from all predators they rapidly lost mammalian predator-discrimination abilities [59].

Scenarios 3–5. If prey have specific evolutionary but not ecological experience with the focal predator (1B), but no ongoing ecological experience with other predators (3A), as when a native predator goes extinct, and no other predators remain, then we ask how long the prey species has lacked predation pressure (3B). This is because, according to the relaxed selection hypothesis, costly antipredator behaviors will be lost through selection given sufficient time [3]. After a short time without predation risk, our framework predicts that prey will remain adapted to the predator (H1 adaptation), and will discriminate predator cues (scenario 3). In practical terms, 'a short time' might mean less than one prey generation. After a medium amount of time without predation risk, the framework predicts that re-exposure to the predator will rapidly recover antipredator behavior (H3 recoverable templates; scenario 4). In practice, it is impossible to define what a 'medium' amount of time means for a given species. The degree to which antipredator behavior will be lost will relate to several factors including whether prior antipredator behaviors were innate or learned, the generation times of the prey, and so on. Importantly, we do not know the degree to which recognition and behavioral templates for a particular historical predator might be generalizable to other, novel, exotic predators. This requires further study. However, the rapid reinstatement of antipredator behavior for wolves by elk in Yellowstone National Park [26] illustrates this process. Finally, after a long time without predation pressure, the framework predicts that prey will lose costly antipredator responses (H4 relaxed selection, scenario 5), and therefore fail to discriminate the cues of the reintroduced predator. This occurs because the lack of predation pressure allows prey to reallocate energy and resources away from antipredator defense and towards other needs [3]. In practice, a 'long' time would require multiple prey generations without predation pressure, such as takes place in captivity or on islands [60].

Scenarios 6–9. If prey have no specific eco-evolutionary experience with the focal predator (Figure 1, 1C), as for example when a novel exotic predator is introduced, we ask whether prey have any applicable evolutionary experience with other predators (2A). If so, are these other predators of a similar archetype to the new predator (2B)? If they are similar, then the archetypes hypothesis (H5) predicts that prey will recognize the new predator and discriminate its cues (scenario 6). If not, then prey might still discriminate the cues of the new predator if it contains labeling components that identify it as predatory (2C, H6 labeling, scenario 7). If no labeling components are

*(See figure legend on the bottom of the next page.)*

location in the diagram. For example, for prey with specific evolutionary-only experience with the focal predator (Figure 1, 1B), we next consider ecological experience with other predators (Figure 1, 3A). This is because specific evolutionary experience with the focal predator is, by definition, more relevant than any general applicable experience (Figure 1, column 2) for predicting discrimination of the cues of the focal predator. Next, each pathway identifies the relevant hypothesized mechanism (Figure 1, H1–H8; Box 1) before predicting the cue discrimination outcome (Figure 1, 5. Cue discrimination outcome). In all cases, when referring to a 'cue discrimination outcome' we are referring to whether prey are able to discriminate a predator cue from a non-predator cue. We describe the 11 predator–prey interaction scenarios comprehensively in the legend to Figure 1.

Why Mechanism Matters

A mechanistic-based understanding of cue discrimination and how it leads to antipredator response is essential if we wish to knowledgeably manage wildlife populations [16]. Cue discrimination is a function of the perceptual and cognitive capabilities of the prey [40,41], and does not necessarily entail a behavioral response [9]. Of the 11 potential eco-evolutionary experience scenarios outlined in Figure 1, seven result in discrimination of the predator's cue (Figure 1, S1–S4, S6, S7, and S11), and four result in a failure to discriminate the predator's cue (Figure 1, S5, S8–S10). Importantly, while cue discrimination is the measurable variable in an experimental or observational setting, without the theoretical background to infer the mechanism(s) behind that cue discrimination outcome (Figure 1, H1–H8) we cannot predict prey persistence outcomes. This becomes clear once we incorporate the multiple levels of naiveté [9] into our framework (Figure 2).

Predator naiveté was originally conceived as a binary response, whereby native animals were either naïve to introduced predators or they were not [1], as inferred by whether prey discriminated a predator cue (visual, acoustic, or olfactory; e.g., [42,43]). However, theoretical (e.g., [9,19,27,33]) and experimental (e.g., [44–48]) work has since revealed great complexity in the possible types of naiveté (reviewed in [19]). The multiple levels of naiveté framework suggests that level 1 naïve prey do not recognize the predator, precluding any antipredator response. Level 2 naïve prey recognize the predator but show an inappropriate antipredator response (such as freezing in response to a scent-hunting predator), and level 3 naïve prey respond appropriately but ineffectively (for example, they might be 'out-run' by a novel predator) [9]. Finally, level 4 naïve prey suffer excessive sublethal costs of predation by 'over-responding' to an exotic predator – for example by hiding for longer than necessary, and not being able to engage in other activities such as foraging during that time [19]. Each level of naiveté indicates the relative amount of eco-evolutionary experience prey must possess to have effective and appropriate responses for that predator. It follows that prey that require extensive experience (and hence time) to develop or evolve effective antipredator responses are more likely to become extinct. Hence, the multiple levels of naiveté framework [9] is the final component to our synthetic framework, allowing us to link eco-evolutionary experience to predicted conservation outcomes. That is, we can use eco-evolutionary experience to predict the mechanism underpinning a cue discrimination outcome (Figure 1), and then use that

present (2C), then we expect that this prey, when faced with a novel exotic predator for the first time, will be naïve and fail to discriminate the cues of the predator (H7 naiveté, scenario 8). Similarly, if prey without specific eco-evolutionary experience with the focal predator (1C), or have no applicable evolutionary experience with any predators (2A), then they have no general eco-evolutionary experience to draw on, and are expected to fail to discriminate predator cues (H7 naiveté, scenario 9). *Scenarios 10–11.* Once a novel exotic predator has persisted in its new environment for some time, prey will have interacted with it, meaning they have gained ecological experience with this predator (1D). If insufficient time has passed for rapid change, prey will be naïve (H7 naiveté) and will not discriminate predator cues. However, if sufficient time has passed so that prey have learned or adapted to it (3C), then the suite of rapid change hypotheses (Box 1) predict that prey will discriminate the cues of the predator from non-predator cues (H8 rapid change, scenario 11).
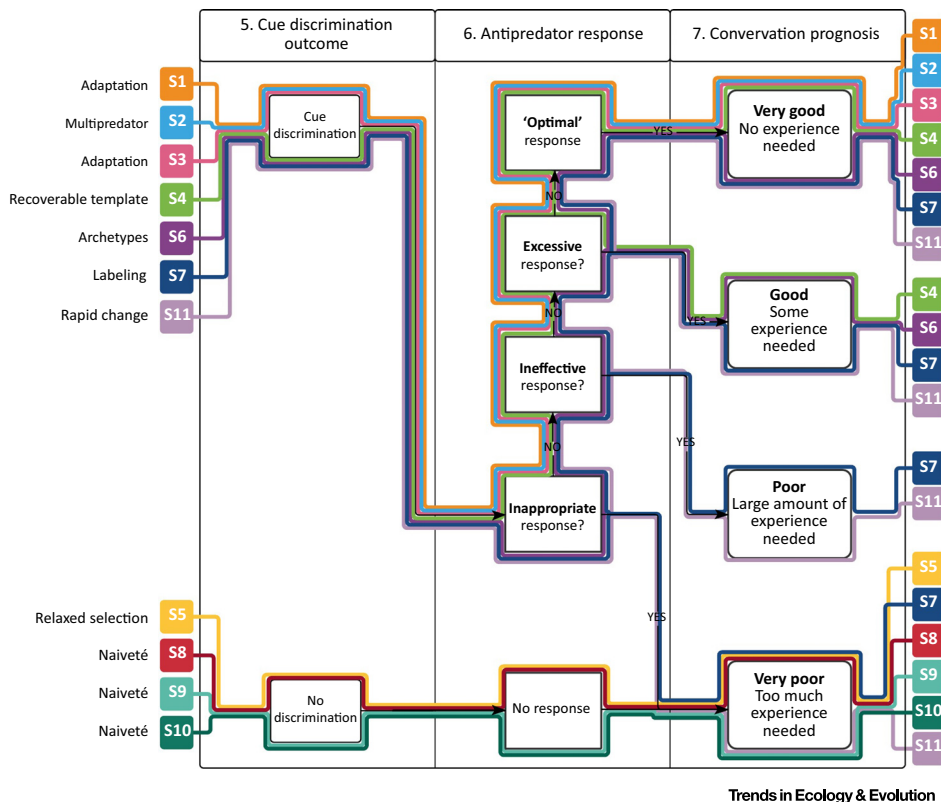
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Figure 2. Diagrammatic Representation of Banks and Dickman's [9] Multiple Levels of Naiveté Framework Linking Cue Discrimination Mechanism and Outcomes (from Figure 1) to Predicted Conservation Outcomes. Moving from left to right through the diagram, the first column (5. Cue discrimination outcome) is the link to Figure 1, with the seven scenarios that resulted in predator cue discrimination (S1–S4, S6–S7, S11), and the four scenarios that did not (S5, S8–S10). The second column (6. Antipredator response) asks about the appropriateness and effectiveness of antipredator responses, reflecting the multiple levels of naiveté framework [9]. The final column reveals the predicted conservation outcome for prey showing each type of response (7. Conservation prognosis). Scenarios 1–3 predict a 'good' conservation outcome for prey (column 7) because prey are adapted to the predator or have maintained adaptations for that predator via the multipredator hypothesis [2] – thus no experience is needed for prey to perform appropriate and effective antipredator responses. Scenario 4 prey retain an innate, recoverable template for responding to the focal predator, but require some experience to reactivate it. These prey might have a 'very good' conservation outcome if very little experience is required, or a 'good' outcome if more experience is required (column 7). Scenarios 5, 8, 9, and 10: these four scenarios without cue discrimination are predicted to lead to a very poor conservation outcome for prey (column 7) because cue discrimination is a prerequisite for any antipredator response. Scenario 6, wherein prey recognize the archetype of the predator, has either a 'very good' or a 'good' predicted outcome. An archetype refers to 'the set of predators against which a given suite of antipredator adaptations is effective' [27], thus prey in this scenario show effective antipredator behavior but are in danger of over-responding (level 4 naiveté [19]). If we assume that over-responding is less detrimental than inappropriate or ineffective responses, this scenario predicts a 'good' conservation outcome (column 7). Prey that use one of the labeling hypotheses to recognize a predator (scenario 7), or have had sufficient time for rapid change to occur (scenario 11), will discriminate the predator cues from non-predator cues, but might still show inappropriate, ineffective, or excessive antipredator responses, meaning that conservation outcomes will range from 'very good' to 'poor' in both scenarios (column 7).

mechanism, via the multiple levels of naiveté framework, to predict prey persistence outcomes for disturbed predator–prey interactions (Figure 2).

Using the Framework to Predict Conservation Outcomes

For ease of interpretation we have split our model into two parts (Figures 1 and 2), but they join at '5. Cue discrimination outcome'. We have created categories of 'very good', 'good', 'poor', and 'very poor' conservation outcome (based on prey persistence), representing a spectrum of potential outcomes. In practical terms, 'very good' conservation outcomes would translate to long-term population persistence, whereas 'very poor' would suggest likely decline to extinction. 'Good' and 'poor' suggest prey populations will decline either slowly ('good') or more

rapidly ('poor'), but might persist with conservation intervention. We recognize that these are somewhat subjective categories, and we also recognize that, for these predictions to be useful for managers, more research must be conducted into the consequences of cue discrimination for persistence. We hope that this framework will stimulate such research. However, in the absence of other information, even these subjective outcomes may be valuable. There is precedence for using such an approach as a starting point to understanding conservation risk, as exemplified by the use of similar 'rough' categories in early versions of the International Union for Conservation of Nature (IUCN) Red List v. 2017-1 (www.iucnredlist.org).

Linking the cue discrimination outcomes to a conservation prognosis (as described in Figure 2) reveals the key role of the cue discrimination mechanism in predicting the level of naiveté of prey, and hence the expected conservation outcome under predation pressure from the focal predator. Predator cue discrimination is a prerequisite for effective antipredator responses, meaning that disturbed predator–prey interactions, in which prey do not discriminate the cue of a predator (Figure 2, S5, S8–S10), are expected to lead to level one naiveté, and a very poor conservation outcome (Figure 2, 7. Conservation prognosis). Indeed, failure to discriminate the cue of a predator is part of the classic definition of prey naiveté [9,27]. However, our framework demonstrates that, even in scenarios where prey have cue discrimination abilities (S1–S4, S6–S7, S11), a positive conservation outcome is not guaranteed. Scenarios 7 and 11 most clearly demonstrate the importance of decoupling cue discrimination from an assumption of predator-wariness. Prey in scenario 7 might, through labeling mechanisms, recognize 'danger', 'predation risk', or 'a particular predator archetype' – each of which represents increasing recognition specificity. If prey recognize 'danger' or 'predation risk' then they might perform an antipredator response from their repertoire that is inappropriate or ineffective because it is targeted for a different, native predator (level 2 or 3 naiveté; Figure 2). If, however, as described in scenario 7, prey use a labeling mechanism to recognize a familiar predator archetype, then the archetypes mechanism (H5, Figure 1) [27] is operating, and by definition their primary risk is an excessive response (level 4 naiveté; Figure 2). As for scenario 7, prey in scenario 11 might learn or evolve the ability to recognize a predator and discriminate its cue, but they might also subsequently initiate an inappropriate, ineffective, or excessive antipredator response that was learned or evolved in response to a different, native, predator [9]. Here again, cue discrimination is not sufficient for a positive conservation outcome (Figure 2). Predictions of conservation outcomes for each of the 11 predator–prey interaction scenarios are described in greater detail in the legend to Figure 2.

All scenarios describe the outcome of a particular predator–prey interaction at one timepoint and to one predator. Importantly, the mechanisms of learning and adaptation (the rapid change hypotheses, H8; Figure 1) can then act on any of these scenarios to improve the conservation outcome for the prey species over time and in the face of different predators. Nevertheless, prey that are furthest from achieving 'optimal' antipredator responses are still most likely to become extinct before they achieve this (Figure 2). Our synthesis reveals that, to predict the likely conservation outcome of a particular disturbed predator–prey interaction, we must not only understand whether but also why the prey do or do not discriminate the predator cue, by identifying the mechanism underlying cue discrimination.

Of course, conservation outcomes for native prey depend on more than interactions with predators. Habitat disturbance and loss, as well as climate change and other forms of human-induced rapid environmental change, will all play a role. In some cases the effects of these variables might interact with or even overshadow the effects of disturbances to evolved predator–prey interactions. However, there is ample evidence that introduced predators exert

strong effects on native prey populations [4], and in many cases are the driving force behind native prey extinctions [5,49] as well as the failure of reintroductions and translocations for conservation (e.g., reviewed in [50]). We therefore believe that a focus on the conceptual and mechanistic underpinnings of disturbed predator–prey interactions is justified, although we acknowledge that the framework addresses the likelihood of prey persistence only in terms of the effects of predation pressure.

In sum, then, our new synthetic framework enables us to link the eco-evolutionary experience of a prey species with a focal predator to a hypothesized mechanism behind a cue discrimination outcome (Figure 1), and then, through the multiple levels of naïveté framework, to a predicted conservation outcome under predation pressure from that predator (Figure 2).

Concluding Remarks

We have illustrated how eight different hypothesized mechanisms that predict the response of prey to a novel predator result in 11 different conceptual pathways that lead to either discrimination or a failure to discriminate predators from non-predators. Moreover, we have linked these mechanisms, via the multiple levels of prey naiveté framework, to predictions about prey persistence. We have thus illustrated how knowledge of underlying mechanisms can be used to manage wildlife populations that have either gained a novel predator or lost an historical one. These predictions require formal testing, but we have demonstrated, with examples, that there is already support for many of these pathways. We envisage that this unified conceptual framework will lead to future researchers refining, and ideally quantifying, objective measures upon which to base the categories of experience and predicted conservation outcomes that we have used here (see Outstanding questions). Decision-makers faced with responding to the introduction of a novel predator [e.g., red foxes (*Vulpes vulpes*) in Tasmania, cane toads (*Rhinella marina*) in the Australian Northern Territory, wolves in North America, or brown tree snakes (*Boiga irregularis*) in Guam] might find this framework immediately useful in their deliberations over allocating scarce wildlife management funds.

Outstanding Questions

How can we develop a quantitative evaluation of actual conservation outcomes?

To what degree are recognition and behavioral templates for a particular historical predator generalizable to other, novel, exotic predators?

How common is experience-based recovery whereby the abilities to respond to predators are relatively rapidly recovered following any experience with predators?

Is a detailed understanding of the response to the cues of each predator essential to be able to predict outcomes to multiple predators, or can we assume that they are lost and recovered in similar ways?

What is the precise timecourse of trait loss?

Are cues in different modalities (e.g., visual, acoustic, or olfactory) lost and recovered at the same rate, or are some modalities more resistant to loss?

Are cues in some modalities learned or adapted to more readily for some species?

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