Title: Enhancing the ecological realism of evolutionary mismatch theory

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Abstract:

Following rapid environmental change, why do some animals thrive, while others struggle? We present an expanded, cue-response framework for predicting variation in behavioral responses to novel situations. We show how signal detection theory can be used when individuals have three behavioral options (approach, avoid, or ignore). Based on this theory, we outline predictions about which animals are more likely to make mistakes around novel conditions (i.e., fall for a trap or fail to use an undervalued resource) and the intensity of that mismatch (i.e., severe versus moderate). Explicitly considering three options provides a more holistic perspective and allows us to distinguish between severe and moderate traps, which could guide management strategies in a changing world.

Main Text:

Behavioral responses to evolutionary mismatches

Behavior is a proximate response to human-induced rapid environmental change (HIREC) [1–3]; however, substantial variation exists in behavioral responses to HIREC among species, populations, and individuals [4]. Rapid change can create mismatches between **cues** (i.e., see Glossary) and previously adaptive responses, leading animals to make suboptimal decisions [5], including instances when animals choose an overly costly option (i.e., an **evolutionary trap**) or fail to choose a beneficial option (i.e., an **undervalued resource**). **Signal detection theory** (SDT) has previously been used to help explain specific mismatches [6]. Here we extend SDT to consider the conceptual similarities between traps and undervalued resources [7] and explain patterns of variation in these alternative forms of '**evolutionary mismatches**'

(Table 1). Importantly, by expanding the standard two-choice SDT to a three-choice view, we generate new insights on factors influencing these mismatches.

The three-option approach

Current theory on behavioral mismatches has largely considered the organism’s choice between two behavioral options – avoid or not, or approach or not. Here, we expand to a three-option view that explicitly acknowledges that *ignoring* an option differs from the more behaviorally active options of ‘attraction’ or ‘avoidance’ (Box 1).

If the best option is to actively avoid a low-fitness option (e.g., a predator, or toxic food), it is clearly maladaptive to be attracted to that stimulus; but, in some circumstances, ignoring a low-fitness option can also be highly costly. We suggest that an important factor is whether the organism ‘interacts’ with the dangerous stimulus, even when the stimulus is ignored. If that stimulus (e.g., a predator or parasite) actively attacks an organism that ignores it, then ‘ignore’ is almost as costly as attraction. If the low-fitness option is toxic food or low-quality habitat, ignoring the stimulus should be similarly beneficial to avoidance. However, if passive interaction rates are high enough (e.g., when edible foods and pollutants are both consumed in the same mouthful), then actively avoiding the stimulus, if possible, can be substantially better than ignoring it.

If the best option is attraction (e.g., a valuable food item or habitat), ignoring the stimulus can be as costly as avoidance. Organisms that ignore an undervalued resource save on the direct costs of active avoidance, but still suffer the opportunity costs. A key aspect is whether the organism ‘interacts’ with the option even though it is ignoring it. If the organism incidentally consumes an otherwise ignored food item or ‘settles’ (e.g., runs low on energy and stops searching) in habitat that it was 'ignoring', the opportunity cost of undervaluing a resource is reduced.

Finally, in some cases, the best option is to ignore the stimulus. This is the case for stimuli that are safe but appear dangerous (e.g., harmless humans like ecotourists or human structures [8,9]). Actively avoiding these stimuli can have high direct and opportunity costs [10,11], both of which would be reduced by ignoring the stimuli. Many objects are likely ignored because they have little to no fitness effect. In addition, animals might ignore stimuli, even if they have a net benefit, if a better option is present. Decision theory emphasizes that if committing time or energy to a mediocre option reduces the possibility of utilizing a better option, then the mediocre option should be ignored [12]. Of course, mis-assessments of the value or availability of different options, which may also change due to HIREC, can result in animals falling into traps or not utilizing undervalued resources.

Acknowledging all three behavioral options can help to explain when and how organisms might escape from traps or switch to adopt undervalued resources. Avoiding an undervalued resource gives the organism little or no opportunity to experience, re-evaluate and adopt an (initially) undervalued resource [13]. In contrast, because organisms may passively interact with options they have chosen to ignore, they can still gather information that can inform future choices. For example, attraction to a dangerous option may result in death, whereas at least sometimes, ignoring it can be both relatively safer and provide information that facilitates re-assessment.

Signal detection theory as a framework

Evolutionary mismatches can be understood as an error in an animal's **cue-response system** that results from a change in the relationship between a cue and its historic payoff [14,15]. An established body of theory, **signal detection theory** (SDT; [16,17]) — also termed 'receiver operating characteristic analysis' [18] or 'error management theory' [19–21] — explicitly models optimal decision-making based on imperfect cues.

A key premise of SDT is that organisms make decisions without perfect knowledge of the state of the environment. SDT assumes that organisms compare cue inputs to a cue-response threshold that combines the historic background level of risk, the benefits of responding appropriately, and the costs of potential errors, to guide an action. Recent models extend basic SDT to predict responses to HIREC by positing that organisms use their previously adaptive cue-response thresholds to respond to novel situations [9,22,23]. SDT models typically analyze cues along a single cue-axis, with the understanding that multiple sources of information can be combined into a single score (e.g., a principal component factor score) for a one-axis simplification. SDT solves for an optimal cue-response threshold and posits that the organism's response depends on whether the strength of a cue emitted by a stimulus is above or below the threshold. For example, for a potential predator, if the cue is above the threshold (e.g., the potential predator is large and approaching rapidly) the organism flees. If the cue is below the threshold, the organism does not flee. Responses to a novel stimulus depend on the novel cues' relationship to the evolved threshold.

Expanding SDT to consider that animals have three options (Box 2), adds a second threshold to each analysis. For a novel predator, if it exhibits cues below a high "danger threshold", two-option SDT predicts that the animal should ignore it (i.e., not flee [23]). Three-option SDT adds a lower "safety threshold" that predicts that if the novel predator exhibits cues below that threshold (i.e., if it appears safe or beneficial like predators with a 'lure' [24]), then naïve prey animals should be attracted to it – a more severe trap.

Factors that influence the breadth of the cue ranges of these thresholds determine whether a novel stimulus is likely to result in an evolutionary mismatch. For example, factors that increase a naïve prey animal's danger threshold (i.e., make it bolder), increase the likelihood that the animal will ignore a novel predator versus actively avoid it [23]. The three-option view adds the insight that factors that affect the prey's safety threshold determines whether a naïve prey might not just ignore but be attracted to a novel predator. This should be particularly important for novel sit-wait predators that require prey to approach the predator.

For novel habitats or toxic foods, the key mismatch occurs at the attraction vs ignore threshold that has been addressed by previous two-option SDT models [25]. However, if toxic foods could be incidentally consumed by animals that do not actively avoid, then the ignore vs avoid threshold is also important. Conversely, for undervalued resources, the usual two-option view emphasizes the attraction vs ignore threshold; however, as noted earlier, if 'ignoring' an object provides experience with that object, that could be an initial step towards later adopting it, the ignore vs avoid threshold is also important [26].

Variation in attract-ignore-avoid thresholds can occur at a species level. Generalist species accept a wider range of stimuli, and thus might be more likely to fall for traps, but also more likely to exploit novel resources than specialists. However, if novel cues fit into a specialist's narrow acceptance range, it can be particularly detrimental, since their preferred options are already limited. Studies on interspecific variation in plastic consumption by birds, fish, and sea turtles [27–29] support this prediction. Some specialist species—specifically olfactorily-oriented foragers [30–33] — are more severely trapped by plastics because of the similarity between odors associated with plastic and with actual food [33,34]. While generalist predators appear chronically trapped at low levels [35], when specialists are trapped, they are likely to consume plastic frequently [28,33].

SDT makes predictions on other factors affecting susceptibility to traps and undervalued resources (Figure 1). We next outline major predictions, highlighting novel insights from three-option SDT, along with pertinent empirical examples. While at the species level, thresholds are shaped by evolutionary forces; variation in individual-level thresholds could be shaped by personal experience, learning, or genetic differences. Here we discuss thresholds generally because on a conceptual level the consequences remain the same (i.e., evolving with many predators versus growing up with many predators have similar effects on optimal thresholds).

Predictions: factors that affect mismatch likelihoods

I. Cue similarity

The well-established ‘cue similarity’ hypothesis [36,37] predicts that organisms are more likely to respond well to novel predators if they resemble familiar ones, but that naïve prey often fail to respond appropriately to novel predators when the cues emitted by exotic versus native predators are different [6,38,39]. For example, a meta-analysis found that prey generally fail to recognize introduced predators when they lack congeneric native predators [40]. The three-option view adds that if exotic predators are ignored rather than approached (i.e., native prey fail to recognize danger, but do not perceive a signal of safety), introduced predators are more likely to become a **moderate trap**. However, if prey actively approach or congregate near predators — if for example they resemble historically safe or even beneficial options — novel predators could be a **severe trap** [41]. Native predators can become more dangerous, for example, if changes in their diet in response to HIREC elicit different cues that lead prey to ignore or even become attracted to things they historically avoided [6].

Following HIREC, animals can also be attracted to toxic prey items that they should ignore. In a classic example, cane toads (*Bufo marinus*), resembling native Australian prey, appear to be particularly attractive to many naïve predators. Since Australian predators have no evolutionary history of exposure to the bufotoxins produced in cane toad skin, many predators become ill or die after ingesting cane toads [42]. Similarly, recent evidence suggests that the maladaptive decision to consume plastic is more likely to occur when species are misled by plastic-associated visual and chemosensory cues [30,31,33,34].

Moderate undervaluation can occur when organisms ignore novel items they should approach because those novel items fail to resemble historically good options. Supporting this prediction, phylogenetic similarities (that often reflect similarities between native food and introduced plants in the chemistry of attraction-deterrence) can be a useful predictor of herbivorous insect adoption of edible novel plants [43,44]. The three-option view emphasizes that more severe undervaluation occurs when organisms do not just ignore, but actively avoid neutral or beneficial options because they resemble ones that were dangerous in the past. For example, species with a history of being hunted or harassed may continue to respond to humans as predators even after the cessation of threat (i.e., trait retention after relaxed selection [45]). Hunting can lead to rapid shifts in space use [46], changes in behavior [47] and selection for less bold behavioral types [48] which can persist long after hunting has stopped, causing animals to pay unnecessary costs avoiding humans that no longer pose a threat.

Cue discrimination has long been understood as an important factor for predicting predator recognition [49], however factors that affect response thresholds should lead to better predictions for how different cues can be while still eliciting the same response and thus affect the likelihood of HIREC-associated mismatches. SDT addresses three such factors (discussed below).

II. Past cost of errors

Regarding perceived risk, organisms should be more likely to ignore novel risky situations (that they should avoid) if the past cost of erroneously ignoring danger was low (e.g., past predators were only mildly dangerous), or the past cost of unnecessarily avoiding safe situations was high (e.g., organisms were food limited). As noted earlier, for animals that have experienced lethal human hunting in their past, the cost of ignoring humans was historically high, resulting in frequent over-avoidance even after humans stop hunting. In contrast, because the ability to rapidly escape [50–52] or find refuge [53] reduces the costs of incorrectly ignoring (or approaching) a dangerous option, animals in these situations are less inclined to over-avoid humans. Instead, as predicted by SDT, animals are more likely to avoid humans when the costs of avoidance are low [50]. Conversely, when the past or recent costs of avoidance are high, animals are less likely to over-avoid nonlethal humans (e.g., when the animals are engaged in a beneficial activity [54,55], when visits from ecotourists are frequent [56,57], or during seasonal dips in resource availability [58]). The three-option view emphasizes that when the opportunity costs of avoidance are high, animals might not just avoid or ignore danger, they might approach situations even when they appear dangerous (e.g., [59]).

With regard to the threshold to accept versus ignore resources, organisms should be more selective (have a lower 'acceptance threshold') if the cost of erroneously accepting 'neutral' or even poor options was high compared to the cost of erroneously ignoring a good option (i.e., adopt a least-cost strategy [20]). Selective animals are less susceptible to being trapped, but more likely to miss an undervalued resource. For example, herbivores should be less likely to adopt novel plants if they perform poorly on native plants that are outside of their normal diet. The observation that specialists rarely adopt valuable novel plants, like crops, is consistent with this prediction [60]. The three-option view adds that when past costs of erroneously consuming low value foods was very high, animals should not just ignore (but perhaps occasionally incidentally sample) novel foods, they should actively avoid them.

III. Past prevalence of options

SDT predicts that organisms should be more susceptible to novel dangers if, in the past, danger was either very rare or very common. Prey that evolved with very few predators should be bold, since most situations they encounter are not dangerous [61]. For example, since aquatic predator-prey interactions are often size-dependent [62], prey in habitats where most large fish are non-predatory should be more vulnerable to a novel large predatory fish compared to prey from habitats where most large native fish are predators. Theory adds that, perhaps counter-intuitively, organisms should be bold if they evolved with a high prevalence of dangerous situations, because waiting for or searching for a safe situation is futile (e.g., the ‘risk allocation hypothesis’, [23,63–65]). For example, if organisms evolved in environments where most sites were risky and there is sufficient uncertainty about danger, they should be willing to settle in a site even if it appears moderately dangerous [66].

The prediction that prey that evolved with low predation risk should be highly susceptible to novel predators is supported by the high vulnerability of naïve prey to exotic predators on isolated islands (i.e, those with few predators) [36,67–69]. For instance, native bird populations on Guam have been decimated by introduced snakes [70], while mainland-derived birds on the island continue to persist [71]. Understanding the importance of previous experience with danger in setting thresholds for predator avoidance can help control native pests [72] and protect at-risk populations facing novel predators [73–75]. Further work on factors, including behavioral type [76], that facilitate learning to escape evolutionary traps will be valuable to help researchers protect at-risk individuals [13].

From a three-option view, the prevalence of options that emit safety cues [77] should also matter. If safe situations are either very common or very rare, animals should be more likely to be attracted to them, which would make those animals more susceptible to being trapped by situations that appear safe but are dangerous. The study of safety cues is a new field where predictions remain largely untested.

Similarly, animals should be more susceptible to mismatch if historically risky options (i.e., those that should be ignored) were rare. This prediction might help explain the consumption of plastic debris by many marine species. Prior to the plastic revolution of the past half century, risky food options that resembled nutritious options were rare in marine habitats. Plastic appeared rapidly in the late 20th century, emanating cues that resembled nutritious options [78]. High-quality foraging opportunities are limited in the open ocean and often co-occur with plastic [79]. Bypassing feeding opportunities in a patchy landscape is energetically risky, shaping cue-response systems that accept plastic readily as a food option.

SDT also predicts that the past prevalence of danger should influence over-avoidance of neutral or safe situations [9]. Numerous studies have quantified flight initiation distances (FIDs) in response to a harmless scientist's approach. A meta-analysis revealed that for birds, FIDs vary with regional estimates of predation risk (including hunting pressure) [80]. However, the converse also applies: a high prevalence of repeated contact with safe humans associated with domestication, captivity, urbanization, and ecotourism can lead to a rapid reduction of anti-predator responses to other predatory stimuli [81,82]. Thus, the increase in prevalence of humans in safe situation may increase the susceptibly of animals to future novel dangers, like introduced predators.

IV. Past ease of discriminability

An intuitive idea is that animals with a greater ability to distinguish between beneficial and deleterious options should be less susceptible to mis-evaluating novel options. Some species with high cognitive capacity [83] can differentiate between safe and dangerous humans [84], and indeed, interactions with humans may drive selection on animals' cognitive abilities [85].

For a given level of cognitive capacity, however, SDT predicts that if, in the past, dangerous versus safe situations were easy to discriminate, organisms should be more likely to erroneously ignore novel costly situations. If they were difficult to discriminate, organisms should evolve to 'play it safe' by avoiding situations that appear even moderately risky, and should thus respond better to novel predators, but be more likely to miss an undervalued resource. In contrast, if organisms evolved in conditions where high risk was associated with a precise, narrow range of cues (e.g., prey should only flee when potential predators initiate a specific attack sequence), these organisms will be more likely to incorrectly assess dangers that fail to fit this specific profile (e.g., the 'danger discriminability hypothesis' [23]). In essence, when organisms are more certain about what is good versus bad versus neutral, they are more susceptible to novel mismatches.

Discriminability between safe and dangerous situations can be reduced if the distributions of safe versus danger cues (or both) are very broad and thus overlapping. Ease of discriminability can also be reduced if the background environment is ‘noisy’ (e.g., acoustically, visually, or chemically) or if it does not transmit cues well (e.g., low light, turbid water) [86,87]. Indeed, studies suggest that environmental “noise” affects learning and predator recognition [88–90]. Importantly, HIREC can affect multiple aspects of novelty, and increased environmental noise and pollution can change cue discriminability, subsequently influencing cue-response thresholds [6].

Concluding remarks

Tinbergen’s Four Approaches [91,92] can help identify sources of variation in response to evolutionary mismatches that would benefit from further study. Here we focused on the proximate mechanisms (approach 1) underlying maladaptive behaviors (i.e., mismatches in cue-response system). While the sensory portion of these cue-response systems has been well studied in some cases [31,93], many of the cues underlying mismatches are purely speculative and lack empirical testing. Furthermore, identifying variation in cognition could provide insights into why some individuals are more susceptible to certain mistakes. An animal that makes decisions quickly based on simple cues [94], might be more susceptible to accepting novel toxic foods but less likely to miss a novel nutritious food source compared to organisms that rely on multiple cues [95].

While our framework touches on the role of experience in shaping cue-response systems, additional insights could come from investigating the influence of ontogeny in shaping these behaviors (approach 2). Accurate cue-response systems need time to update based on experience, and age-class could be a critical predictor of likelihood of making a mistake [96]. Additional useful avenues of study include the role of transgenerational effects [97] and social learning in shaping maladaptive responses [98–100]; yet, the role of social environment variation on susceptibility to evolutionary mismatches remains relatively unexplored (but see [101]).

The majority of trap research has focused on identifying the previously adaptive value (approach 3) of these behaviors. However, few studies directly measure costs and benefits [102–104], making distinguishing between evolutionary mismatches and a lack of beneficial options challenging [105]. While identifying potential areas of concern is an important first step, estimating fitness in these situations is critical for confirming which scenarios should be of management concern [106] (Box 3).

Lastly, while the role of evolutionary history (approach 4) in shaping current cue-response systems is a basic tenet of the evolutionary mismatch concept, few have applied a phylogenetic approach to see if certain clades are more susceptible to mismatches (but see [107]). Ultimately, identifying historical experience is paramount for developing predictions about which species are most susceptible to maladaptive behaviors in the Anthropocene (Outstanding Questions).

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Box 1. Ignore as an option

An animal's response to an ecologically-relevant stimulus involves a series of steps [108] that, in brief, include detection, judgment (discrimination, categorization, assessment, recognition) and then a decision (preference or choice) that produces a behavior (avoidance, attraction, or no action). Absence of action can be due to either lack of detection or an active judgment. Technically speaking, it can be difficult to be certain whether an animal not responding to a stimulus is due to lack of detection or an active choice (but see [109]). In some cases, the novel option (e.g., novel predator or food item) might actively seek to avoid detection (e.g., via hiding). We do not focus on those cases. Instead, we focus on the common situation where the object (e.g., novel predator, food, habitat) emits stimuli that are clearly within one or more sensory modalities, cue ranges, and intensities that the focal organism can detect. For example, when prey encounter a novel predator, we suggest that in most cases, there is little doubt that the prey sees (or smells or hears) the predator. When a consumer encounters a novel potential food item or habitat, there is typically little doubt that it detects the presence of that food item or habitat but may still choose to ignore it.

In more subtle cases, where it is unclear whether animals have detected a stimulus, within-taxon (or species or individual) variation in response to the stimulus can be informative. If some individuals clearly detect and respond to the stimulus, or if a given individual switches between responding or not, it suggests that lack of response by other individuals in similar contexts likely reflects ignoring the stimulus as opposed to not detecting it. Alternatively, emerging technologies can provide inroads. Gaze-tracking devices and visual-field reconstruction can provide evidence of detection of optical stimuli [110–112]. Biologging tags augmented with sensors to measure brain activity, heart rate, and other physiological parameters can be used to assess whether detection of a cue occurs [113–115]. Virtual or altered reality for experimental animals [116] coupled with the aforementioned technologies could provide insights through manipulative trials.

Even if ignoring may be difficult to determine, our framework is valuable for predicting the consequences of other slightly differing choices. That is, animals could vary in their extent to avoid or approach. For example, there is a difference between moving slightly in response to a predator and permanently leaving (i.e., multiple "avoid" options).

Box 2: Signal Detection Theory: the 3×3 abstraction

Standard signal detection theory (SDT; [16]) represents the environment as taking one of two conditions (e.g., safe vs dangerous) and assumes that there are two possible actions to choose between (e.g., approach or avoid) (Figure Ia). Organisms make decisions based on cues that contain imperfect information about the current condition. We expand standard SDT to consider three actions (approach, avoid or ignore) and a third class of objects that are of intermediate value, where an object's value is its benefit/cost ratio (e.g., growth/mortality rate) [117,118] (Figure Ib). Animals should often ignore intermediate stimuli because the associated costs outweigh the payoff.

We assume that each of the three object types produces a normal distribution of cues on a cue-axis where high value objects tend to emit high values on the cue-axis, and mediocre and poor objects tend to produce intermediate and low values respectively. Note that the cue-axis is not simply strength of cue, but a multi-dimensional indicator of the object's benefit/cost value. The key is that these distributions often partially overlap with each other, such that cues are not perfectly discriminable. As a result, animals will make errors. Before human induced rapid environmental change (HIREC), the probability of each type of object and the cost of potential errors determined two optimal cue-response thresholds. If the cue is above an upper threshold, animals should avoid the stimulus (i.e., it appears dangerous), if it below that threshold, the animal should ignore it. Only when the cue is below a second (lower) threshold, should the animal approach the object.

Following HIREC, we assume that individuals continue to use their previously evolved thresholds, but the probabilities, distributions and/or payoffs may have changed, thus changing error rates. The likelihood of these errors depends on the position of the previously evolved threshold and the similarity of the novel cue relative to previous distributions. For example, novel dangerous stimuli that more closely resemble historic safe options (Figure Ic) are more dangerous than ones that resembles historic neutral options (Figure Id), because individuals will approach the dangerous stimuli instead of just ignoring it. Distinguishing three behavioral options helps predict the severity of a trap: while an animal that fails to avoid a bad option if it appears good may be severely trapped, an animal that fails to avoid bad options that appear neutral may only be moderately trapped. See Supplemental Information for details.

Box 3: Considering 'ignore' decisions can facilitate management of traps

Animal decisions to ignore situations can sometimes translate to an intermediate outcome: neither the worst nor the best-case scenario for the individual to efficiently utilize resources and/or avoid dangers. In such instances, natural resource managers that consider not only what focal species naturally tend to approach or avoid in their environments, but also what they ignore, can use this knowledge as priors to formulate strategies to avoid least-desirable outcomes. Indeed, many conservation management decisions balance difficult tradeoffs [119–

121], and many decisions are not intended to achieve the most positive outcome for one particular species but, rather, to avoid the most negative outcomes for a range of species or for alternative ecosystem uses (e.g., recreational and/or industrial). Thus, by formally integrating animal decisions to ignore certain situations into our conceptual understanding of evolutionary traps, our framework offers management a finer suite of decisions and interventions to consider in the balancing act of keeping biodiversity/ecosystems intact and in the service of humankind [122,123].

Considering animals' options to behaviorally ignore cues allows us to predict the severity of traps, helping conservation managers to avoid the least-desirable outcomes (i.e., severe traps). Least-desirable outcomes include focal species of conservation concern readily approaching dangerous situations (e.g., novel but toxic food, novel predators) or avoiding beneficial ones (e.g., novel high-quality food), when, in either case, ignoring the situation would be a better option (probabilities of death via toxic food or a novel predator or of missing out on high-quality resource patches would be driven more by chance and could be reduced), even if avoiding or approaching, respectively, is the superior option. For example, if lethality is comparable between two invasive predators (or toxic resources) of a management-targeted prey species, but the prey tends to approach one of these predators (or resources) but ignore the other, it is the former on which population control efforts should be emphasized if such efforts are constrained by management tradeoffs.

Importantly, novel environments may be beneficial for some purposes but detrimental for others. For example, urban environments may provide greater availability of food and/or fewer predators, but are also associated with elevated concentrations of pollution and higher infection rates [124]. Similarly, novel plants may have noxious fruits but still be a beneficial source of nesting material or protection [125,126]. Management may need to consider these dual uses and appropriate responses for each in making conservation decisions.

Tables:

Optimal Choice	**Apparent Choice**	**Examples**
Approach	Ignore	Ignoring high fitness novel habitat (*farmland* [127]; *building* [128]) Ignoring new food sources (*crops* [129])
Approach	Avoid	Avoiding parks and restored habitats [130] Avoiding safe habitat *(antipredator behavior* [131])
Ignore	Approach	Using the wrong host (*parasitoid hosts* [132]; *toxic plants* [133]) Using new habitat with lower fitness (*urban* [134]; *farmland* [135]) Mating with suboptimal partner [136] Eating toxic/harmful food [137,138]
Ignore	Avoid	Avoiding innocuous threats (*ecotourists* [81])
Avoid	Approach	Approaching human harvesting traps [101,139] Using new habitat with higher mortality [100,140]
Avoid	Ignore	Using native habitat with higher mortality [141-143] Ignoring novel predators [144,145]

Table 1. Types of evolutionary mismatches organized within the 3x3 framework.

The citations in this table are only a subset of known examples (See Table S1 in Supplemental Information for a full list based on a systematic search of the literature from the previous five years).

Figures:

Figure 1. Summary of predictions.

We group predictions into four categories and suggest how specific factors influence cue-response thresholds and the likelihood of an evolutionary mismatch. For the first listed hypothesis in each category, we have included both a graphical representation and an illustration based on a hypothetical example—how a Western gull may respond to a novel plastic soda bottle. For all graphs, the x-axis represents environmental cues and the y-axis represents the frequency of those cues in the environment. Distributions of historic danger cues are red, historic safe cues are green, and novel dangerous cues are yellow. For ease, we have not included distributions of historic neutral cues. Dashed lines represent evolved thresholds between behavioral decisions. Predictions of behavioral responses are categorized as follows: (1) Cue similarity—if the water bottle more closely resembles historically edible items, the gull is more likely to fall for the trap and ingest the plastic. (2) Cue discriminability—if edible and nonedible items that the gull has interacted with are more similar, it should be less likely to fall for the trap. (3) Cost of errors—if inedible items were not just nutritious but toxic (like a puffer fish), the gull should be less likely to fall for a trap. (4) Prevalence of safe/dangerous items—if inedible items were historically very common, the gull should be more likely to fall for the trap. When inedible items are extremely common relative to edible items, animals must be willing to take some risks to avoid missing out on the comparatively harder-to-find edible items.

Glossary:

Cue: a biotic or abiotic feature that an organism uses to make a decision

Cue-Response System: the relationship between a specific level of a cue and action elicited, the threshold that a cue elicits a specific response

Ecological Trap: a specific type of evolutionary trap in which habitat choice and the associated cues lead an animal to making suboptimal decisions

Evolutionary Mismatch: a general term used to describe both evolutionary traps and undervalued resources; when the historic relationship between a cue and its fitness outcome is changed such that the cue no longer signifies a particular payoff

Evolutionary Trap: a suboptimal option that is either actively preferred or chosen as often as a higher fitness option due to a mismatch between a cue and its fitness outcome

Moderate Trap: a trap that negatively affects fitness but is less costly than a severe trap; caused by an animal ignoring something dangerous or approaching something neutral

Signal Detection Theory: a quantitative theory used to describe cue-response systems in which two options have associated cue distributions and the decision about whether a stimulus falls in either distribution depends on a response threshold

Severe Trap: a trap that will relatively quickly lead to extirpation because an animal actively approaches something it should avoid

Tinbergen's Four Questions: four levels of analysis that suggest that a full understanding of a behavior includes (1) evolutionary explanations, (2) phylogenetic history, (3) physiological mechanisms and (4) developmental history; named for Nikolaas Tinbergen who is often regarded as one of the founders of the modern study of animal behavior

Undervalued Resource: a high-quality option that is either actively avoided or chosen as often as a lower fitness option due to a mismatch between a cue and its fitness outcome

Factor Predicted to Lead to Evolutionary Mismatch	Change to Factor	Change to Threshold	Susceptibility to Evolutionary Traps	Susceptibility to Missing Underutilized Resources	
Novel Cue Similarity	Resemble historically safe options	No change	Increased	Decreased →	 Inedible and dissimilar from novel bad → Eat plastic bottle (fall for evolutionary trap)
	Resemble historically dangerous options	No change	Decreased	Increased	
Past Ease of Discriminability	Harder to discriminate	Avoid more	Decreased	Increased →	 Inedible but similar to edible options → Don't eat plastic bottle
	Easier to discriminate	Approach more	Increased	Decreased	
Past Cost of Errors	Dangerous options are highly costly	Avoid more	Decreased	Increased →	 Inedible and toxic → Don't eat plastic bottle
	Avoiding safe options is costly	Approach more	Increased	Decreased	
Past Prevalence of Safe versus Dangerous Options	Dangers are either very common or rare	Approach more	Increased	Decreased →	  Inedible and prevalent  → Eat plastic bottle (i.e., fall for evolutionary trap)
	Dangers are moderately common	Avoid more	Decreased	Increased	
	Safe options that look dangerous are common	Approach more	Increased	Decreased	