Predator-prey interactions in the Anthropocene: reconciling multiple aspects of novelty

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Highlights

- Human activities have modified many habitats and ecological communities on earth, and will continue to do so throughout the Anthropocene. Consequently, predator-prey interactions will increasingly occur in settings characterized by novel abiotic and biotic conditions that differ from historical conditions.
- We identify multiple ways by which novelty may alter predator-prey interactions, illustrating the inherent complexity of predation in novel habitats.
- We provide a framework to organize data describing novelty in predator-prey interactions based on a series of events (the "predation sequence") common to all predator-prey interactions.
- The predation sequence provides a way to link well-developed areas of predator-prey theory, providing insight into possible outcomes of novel predator-prey interactions and highlighting hypotheses to guide future research on Anthropocene predator-prey interactions.

Glossary

Antipredator behavior: Actions taken by prey to reduce the likelihood of being captured and/or consumed by other organisms.

Baseline: Abiotic and biotic conditions within a specified evolutionary range of variability. Baseline systems can be used as a comparison to potentially novel interactions between predators and prey, and can be described using historical data or contemporary ecosystems characterized by lower novelty.

Dimension: An aspect of predator-prey interactions that is altered by abiotic or biotic novelty.

Form of novelty: A factor causing abiotic or biotic novelty (e.g., shifts in temperature or introduction of a new predator species).

Novel ecosystem: A highly-modified environment that may be difficult to restore to baseline conditions.

Novelty: Dissimilarity between contemporary (or future) and historic conditions (typically characterized by a baseline system) that can influence the outcomes of predator-prey interactions. Novelty is not simply synonymous with change; it implies conditions outside the range of variability found throughout relevant evolutionary history.

Predation: A relationship where one species (a predator) kills and consumes another (a prey).

Predation sequence: A common set of steps that can unfold as part of an interaction between predators and prey.

Abstract

Ecological novelty, when conditions deviate from a historical baseline, is increasingly common as humans modify habitats and communities across the globe. Our ability to anticipate how novelty changes predator-prey interactions will likely hinge upon the explicit evaluation of multiple forms of novelty, rather than a focus on single forms of novelty (e.g., invasive predators or climate change). We provide a framework to assess how multiple forms of novelty can act, alone or in concert, on components shared by all predator-prey interactions (the predation sequence). Considering how novelty acts throughout the predation sequence could improve our

understanding of predator-prey interactions in an increasingly novel world, identify important knowledge gaps, and guide conservation decisions in the Anthropocene.

Key words: Antipredator behavior, novel ecosystem, predation sequence, species interaction

Causes and consequences of ecological novelty in species interactions

Ecosystems are inherently dynamic, but due to rapid anthropogenic environmental change many species now inhabit highly-modified “**novel ecosystems**” (see Glossary). Novel ecosystems are characterized by new biotic interactions in warming, fragmented, and polluted habitats outside the range of conditions experienced in evolutionary history [1–3]. Predicting which species will persist in novel habitats remains difficult, despite more than a decade of research and debate [3–6]. While multiple definitions of “novel ecosystems” have been described [5], one recent description of ecological **novelty** (see Glossary) as a quantifiable, continuous dissimilarity between current and **baseline** (see Glossary) conditions provides clarity to explore variation among novel ecosystems [2]. This definition suggests that while almost all ecosystems experience some degree of novelty, the magnitude of individual **forms of novelty** (see Glossary) vary in space and time [2,7]. While this quantitative definition of novelty provides a powerful tool to compare the strength of different forms of novelty, it remains difficult to predict the consequences of novelty, such as changes in the type or strength of species interactions that may disrupt ecosystem function and community diversity [8–10]. Without accounting for the effect of novelty on species interactions, it may remain difficult to predict human-mediated changes in species distribution and abundance [11], highlighting the need to understand the complex effects of novelty on species interactions.

Predation (see Glossary) is a ubiquitous species interaction that can shape predator and prey behavior, population dynamics, and evolution [12], transform ecosystems [9], and influence human society (e.g., disease transmission) [13]. However, we currently do not have a basis for predicting where and when novelty intensifies (or dampens) the strength of predation [e.g., 14,15]. Our perspective is that novel predator-prey interactions remain difficult to understand because we lack a guiding set of principles to inform and organize data collection and make predictions about how multiple forms of novelty should modify predator-prey interactions [16]. Studies of predation in novel ecosystems often focus on the effect of one form of novelty on one **dimension** (see Glossary) of predator-prey interactions. Here, we highlight multiple ways by which novelty can change the outcome of predator-prey interactions. We then show that many diverse predator-prey interactions share a common series of component events (the **predation sequence** [17], see Glossary), and illustrate how novelty influences each step in this sequence. We then discuss the implications of novelty throughout the predation sequence, and provide recommendations and hypotheses for future studies.

Common forms of novelty and their effects on predator-prey interactions

Many forms of novelty can change predator-prey interactions (Figure 1), but novelty often falls into one of two categories: novelty in the environment ("novel stages") and novelty in the identity or function of organisms ("novel actors"). Examples of novel stages changing predation include shifts in predator or prey phenology due to climate change (e.g., seasonal migration or torpor) [14], cues of predators degraded by pollution [18], and reduced availability of prey refugia following habitat fragmentation [19]. Examples of novel actors altering predation include increased mesopredator activity following apex predator extirpation [20], naivete of native prey to introduced predators [21], and decreased hunting efficiency due to declines in social predator population sizes [22]. Because multiple forms of novelty may act on different dimensions of predator-prey interactions (Figure 1), they are often studied in isolation with little consideration of how one form of novelty may constrain responses to subsequent forms of novelty. While these examples are not exhaustive, they illustrate the scope of the challenge posed by the Anthropocene: predicting outcomes of novel predator-prey interactions will require integrating data and theory describing how several forms of novelty may act in concert to alter predation.

The predation sequence: a unifying model of predator-prey interactions

Predator-prey interactions consist of a series of sequential steps; as an interaction escalates, the risk of prey being consumed increases [17,23]. Here, we simplify the predation sequence (also known as the encounter sequence [17] or predatory sequence [23]) into three component steps: 1) activity of predators and prey overlap in space and time (overlap), 2) prey attempt to detect and avoid hunting predators, (avoidance), and 3) prey respond to predator attacks (escape). As this sequence progresses, the spatial and temporal scales at which interactions occur also change: predator-prey overlap is set at broad scales (kilometers, days), avoidance takes place at intermediate scales (hectares, hours) and escape occurs at fine scales (meters, minutes). To avoid being consumed, prey can use **antipredator behavior** (see Glossary) to break off the predation sequence at any of these steps [17]. While we consider the predation sequence primarily from the perspective of prey, this framework could easily be extended to assess how novelty changes predator success.

Step 1: Overlap

Before predators can kill prey, predators and prey must first have the potential to occupy the same space at the same time [17]. Empirical methods of assessing overlap between predator and prey activity at broad scales include comparisons of geographic ranges [24], space use [25–28], migration [29], and phenology [30] (Box 1). Habitat domain theory, which describes overlap in predator and prey space use while foraging [25], may be particularly useful in anticipating changes in the potential for encounter as predator species are lost or introduced. Recent observational studies also highlight the importance of activity timing in predator-prey interactions [14,31], suggesting that analogous concepts of temporal overlap between predators and prey (i.e., "temporal domains") are needed to fully understand encounter probability.

Step 2: Avoid

When the potential for encounter exists, prey can end the predation sequence by avoiding spatiotemporal hotspots of predation risk in the "landscape of fear" [17,32-34]. Successful avoidance may require prey to collect information about the risk of an encounter (direct or indirect cues of risk [34,35]), distinguish between informative and non-informative stimuli, and weigh the costs and benefits of a particular action [36]. For example, prey that detect predator urine must be able to identify the urine as a cue of risk, determine whether the strength of the cue suggests imminent attack, and evaluate if the cost of responding is too great given the information at hand [1,37]. However, informed animals may not always respond to predators due to other constraints (e.g., energy state). Expected utility theory [38] and signal detection theory [1,39], among other approaches [40], provide a theoretical approach to predict how prey react to such ambiguity (Box 1).

Step 3: Escape

If prey fail to avoid an encounter with predators, prey must resist or escape an attack in order to survive [17]. Prey exhibit morphological defenses (e.g., crypsis or poisonous chemicals) and behavioral defenses (e.g., group defense) that represent adaptations to traits of historical predators (e.g., predator attack mode) [41]. Prey can also flee to a refuge when attacked. Because the decision to flee integrates information about prey defenses and the perceived danger of predators, economic models of flight [42] can be used to understand mismatches between predator attack and prey defense in novel habitats, which may be measured empirically with flight initiation distance [40,43] (Box 1).

Ecological novelty and the predation sequence

Although many predator-prey studies demonstrate that a single form of novelty can increase [44], decrease [14], or not change [45] the probability that the predation sequence escalates, predator-prey interactions increasingly occur in situations characterized by multiple forms of novelty that act independently on different steps of the predation sequence (Figure 1). Systematically considering the role of novelty in all steps of the predation sequence (Box 1), might improve ecologists' understanding of why the outcome of novel predator-prey interactions can vary over space and time (Box 2). The effect of each form of novelty can be described as a continuous measure of dissimilarity from baseline conditions [2] along two dimensions in each step of the predation sequence (discussed below, Figure 2).

Effects of novelty on prey overlap with predators

Novelty can change spatial and temporal overlap between predators and prey at broad scales (Figure 1), forming two important dimensions for considering novelty. Many of the most dramatic changes in predation pressure in the Anthropocene hinge on shifts in predator or prey space use [10]. The movement of predators and prey can be either suppressed or enhanced in novel stages, such as habitats characterized by fragmentation [10,46] or light pollution [47]. Simultaneously, novel actors may introduce new spatial dynamics, because adding or removing predator species may alter the overlap between predator and prey habitat domains [25,48] (Figure 2). Even introduced prey species may shift space use of native predators, leading to hyperpredation of native animals [49]. However, it remains unknown whether novel stages that influence predator activity (e.g., climate-mediated shifts in predator space use [50,51]) could also fundamentally change predator habitat domains (Box 1).

Novelty can also affect the timing of predator and prey activity. Warmer or wetter climates may create seasonal mismatches in the activity of predators and prey, such as migration [14,29,30]. Similarly, introduced predators may be active at different times than native predators (e.g., crepuscular versus nocturnal activity), eliminating an important temporal refuge for native prey [48]. Alternatively, invasive plants might decrease the potential for overlap between predators and prey because many predators avoid dense habitats, where moonlight cannot be used to locate prey [52]. Because the overlap of predator and prey activity frames subsequent steps in the predation sequence, resolving the direction of effects of ecological novelty on encounter probability will be necessary to understand net changes in predation in novel habitats.

Effects of novelty on prey avoidance of predators

At finer scales, prey may fail to avoid predators for two general reasons (Figure 1): prey cannot detect predators, or the costs of avoiding predators outweigh the benefits. Important cues of predators might degrade or attenuate quickly in novel stages (e.g., decreased wind speed [53] or light pollution [54]), decreasing the likelihood that prey detect predators. Differences in sensory acuity among species [55] may therefore partly explain differences in species' ability to detect predators in novel habitats. Prey may also fail to recognize novel actors, such as introduced predators representing entirely new taxonomic groups [1] or archetypes [56] (Figure 2), or historical predators eliciting novel chemical cues (due to consumption of anthropogenic food subsidies [57]). Alternatively, prey can over-respond to cues of benign stimuli (e.g., running from eco-tourists), and such novel situations that are "safe but appear dangerous" may have detrimental effects on prey survival [58]. Learning, cultural transmission, and transgenerational plasticity may therefore be important mechanisms promoting persistence when prey populations confront changing conditions (Box 1) [1,56].

Novelty might also change the relative costs and benefits of avoiding predators. Prey commonly face a tradeoff between foraging and antipredator behavior, but animals may opt to forego antipredator behavior when faced with stress caused by novel climatic conditions, such as drought or extreme heat [33,59]. Anthropogenic food subsidies may relax resource constraints on urban prey, providing flexibility to avoid predators [60]. Additionally, because human activity [31], artificial light pollution [47], and warmer night-time temperatures [61] can constrain prey activity timing, they may also increase costs of avoiding predators. Optimal decision-making models (Box 1) can help predict when prey behavioral responses to the uncertainty posed by novelty may be adaptive or maladaptive [36,39,40]. These or similar models may also help highlight situations where avoidance does not occur because prey cannot perceive risk (e.g., a novel predator that prey do not recognize) [21] or because novelty modifies the costs and benefits of avoidance (e.g., prey that have access to food subsidies) [38].

Effects of novelty on prey escape from predators

Antipredator defenses represent diverse adaptations to coevolutionary arms races [62], but novelty can create mismatches in predator and prey tactics by changing the efficacy of predator attacks (e.g., “novel weapons”) and the efficacy of prey defenses (e.g., access to refuge habitat). For example, climate change may affect the speed of predator movement [63,64], or predators may learn to exploit changes in habitat structure by trapping prey against human-made structures [63]. Resource subsidies [22] or climate change [65] might also alter the pack sizes of social carnivores, changing their ability to coordinate against prey [50,66].

Prey defenses that are adaptive in baseline environments may function poorly or impose new costs in novel environments. For example, seasonal camouflage in snowshoe hares provides crypsis in snowy habitats, but makes hares conspicuous in warmer winters with little to no snow [67]. Even without specific defenses, prey may escape predator attacks by fleeing to refuge, but the likelihood of flight can be altered by multiple forms of novelty, such as land-use changes increasing high-risk matrix habitat [19] (Figure 2), warmer water temperatures bleaching important coral refuge [68], or invasive plants providing dense cover from predators [27]. Species with plastic behavioral defenses, such as an ability to hide effectively, may be less vulnerable to novelty than species that rely entirely on morphological defenses [1]. Economic models of flight provide theoretical expectations about when prey should pay the cost of seeking refuge [42,69], which may be complemented by empirical measurements of flight initiation distances [43] (Box 1). Current efforts to link flight initiation distances to specific neurological circuits [70] may provide valuable insight into cognitive limitations of prey responses to novel predator-prey interactions.

Implications of novelty in the predation sequence

Considering how multiple forms of novelty simultaneously alter each step of the predation sequence leads to two important implications that may guide future research. First, experiments studying predator-prey interactions may be most informative when they consider the effect of novelty on multiple steps of the predation sequence. Additionally, multiple forms of novelty could have unexpected synergistic effects on novel predator-prey interactions. We explore these ideas in more detail below.

The predation sequence illustrates how empirical studies of novel predator-prey interactions occur within a larger context. For example, salmon fisheries may be concerned that juvenile salmon cannot detect cues of introduced bass [21], but fully understanding the importance of this naivete for salmon survival requires data describing changes in predator and prey space use or activity timing (overlap step) and refuge availability or gape limitation (escape step). Experiments that collect data describing novelty at all three steps promise to be particularly informative, but at minimum ecologists should qualitatively consider the effects of novelty at other predation sequence steps when interpreting their data. Because very different predator-prey interactions can be described using the same set of steps (Box 2), the predation sequence may also facilitate meta-analysis or coordinated continental-scale replicated studies to identify general patterns in species' responses to novelty [2]. Ideally, the net effects of novelty on predator-prey interactions could be represented as the change in conditional probability that prey fail to end each step of the predation sequence in novel versus baseline habitats (i.e., using information-theoretic approaches [1,40,58]).

Species responses to ecological novelty are often unpredictable [71], and empirical studies that examine multiple forms of novelty in predator-prey interactions sometimes report synergistic effects [16]. Synergistic effects may be most likely in scenarios where novelty in one step of the predation sequence is positively associated with novelty in another step. For example, invasive plants may simultaneously increase predator-prey overlap (e.g., providing resource subsidies [72]) and decrease the efficacy of prey defenses (e.g., robins nest closer to the ground in invasive shrubs [73]). Using the predation sequence to anticipate synergistic effects among different forms of novelty could help ecologists identify worst- and best-case scenarios that can guide conservation planning [71].

Concluding Remarks

Both novel actors and novel stages influence the probability of prey overlapping with, avoiding, and escaping predators. Although it is not always documented, novelty is likely increasingly pervasive in many predator-prey interactions around the globe. Without accounting for both novel actors and novel stages in each step of the predation sequence, studies of novel predator-prey interactions likely underestimate the effect of novelty on predation (see Outstanding Questions). While our framework focuses on prey survival in novel predator-prey interactions, novelty may also impose sublethal effects on prey fitness that should be integrated into the predation sequence. As prey face escalating encounters with predators, prey reproduction may be limited by increasing stress hormones (including trans-generational effects [74]) or constraining foraging opportunities [58,75]. Moreover, we demonstrate the importance of the predation sequence for predator-prey interactions, but similar sequential approaches could be used to model pathogen-host [13,76,77] or plant-consumer interactions [14]. Because contemporary ecology increasingly studies highly-modified, novel systems [2], embracing the complexity of novel actors on novel stages will be essential for anticipating shifts in the strength of species interactions in the Anthropocene.

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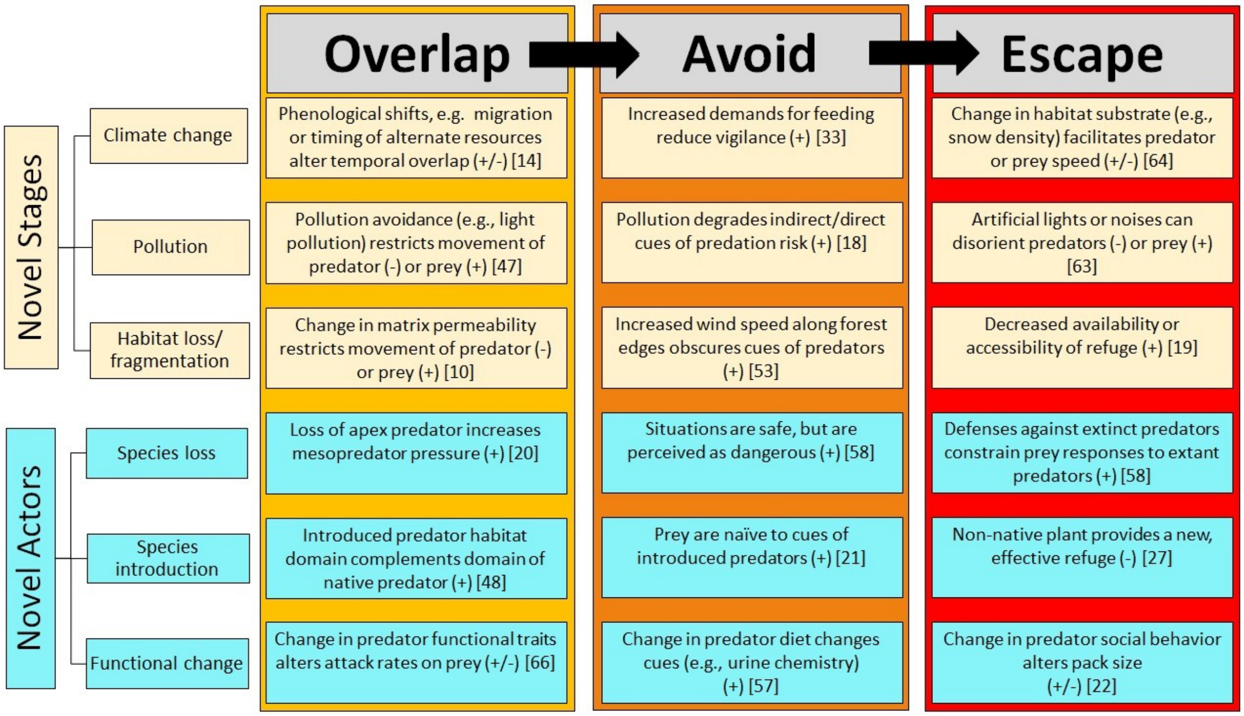
Figure legends

Figure 1: Six common forms of novelty (three novel stages and three novel actors) that may influence the three steps of the predation sequence. Novelty may change the likelihood that prey overlap, avoid, and escape predators (plus (+): increases the likelihood that the predation sequence proceeds, minus (-): decreases the likelihood that the predation sequence proceeds). Text boxes within a column describe changes in the corresponding step of the predation sequence (Overlap, Avoid, Escape), while text boxes within a row describe consequences of the corresponding form of novelty (climate change, pollution, etc.). See Figure 2 for additional information and examples regarding the steps of the predation sequence.

Figure 2: a) We consider a simplified, hypothetical historic landscape, with an ambush predator (a snake) that is more likely to attack the prey (a squirrel) in grassland habitat. b) Predator-prey interactions in the historic landscape consist of three sequential steps: predators and prey overlap in space and time, prey detect and avoid predators, and prey attempt to escape predator attacks. c) In the contemporary landscape, both novel actors and novel stages introduce dissimilarity between the historic and contemporary predator-prey interaction. Habitat degradation and the introduction of a novel predator (a canid) increase the spatial and temporal overlap of predators and prey. The novel predator elicits unfamiliar cues, and prey are less vigilant due to energetic constraints. Prey flight is less effective against the novel cursorial predator, but light pollution provides a novel predation refuge from the introduced predator. d) The probability that each step of this predator-prey interaction proceeds to a more dangerous step in the predation sequence can be increased or decreased by novelty. The effect of novelty on predator-prey interactions can be measured as continuous dissimilarity from the historic landscape along two dimensions (for more details, see "The predation sequence: a unifying model of predator-prey interactions" in the main text). These dimensions capture changes in the spatial and temporal scale of predator-prey interactions as the predation sequence proceeds. Within each step of the predation sequence, the origin represents the baseline predator-prey interaction and the novel predator-prey interaction is shown as the relative change from this baseline. Predator-prey interactions pushed into the upper-right corner of each step of the predation sequence are more likely to proceed to the next step; in the case of the attack step, this means capture and possibly death for the prey.



		Overlap	Avoid	Escape
Novel Stages	Climate change	Phenological shifts, e.g. migration or timing of alternate resources alter temporal overlap (+/-) [14]	Increased demands for feeding reduce vigilance (+) [33]	Change in habitat substrate (e.g., snow density) facilitates predator or prey speed (+/-) [64]
	Pollution	Pollution avoidance (e.g., light pollution) restricts movement of predator (-) or prey (+) [47]	Pollution degrades indirect/direct cues of predation risk (+) [18]	Artificial lights or noises can disorient predators (-) or prey (+) [63]
	Habitat loss/ fragmentation	Change in matrix permeability restricts movement of predator (-) or prey (+) [10]	Increased wind speed along forest edges obscures cues of predators (+) [53]	Decreased availability or accessibility of refuge (+) [19]
Novel Actors	Species loss	Loss of apex predator increases mesopredator pressure (+) [20]	Situations are safe, but are perceived as dangerous (+) [58]	Defenses against extinct predators constrain prey responses to extant predators (+) [58]
	Species introduction	Introduced predator habitat domain complements domain of native predator (+) [48]	Prey are naïve to cues of introduced predators (+) [21]	Non-native plant provides a new, effective refuge (-) [27]
	Functional change	Change in predator functional traits alters attack rates on prey (+/-) [66]	Change in predator diet changes cues (e.g., urine chemistry) (+) [57]	Change in predator social behavior alters pack size (+/-) [22]

Figure 1

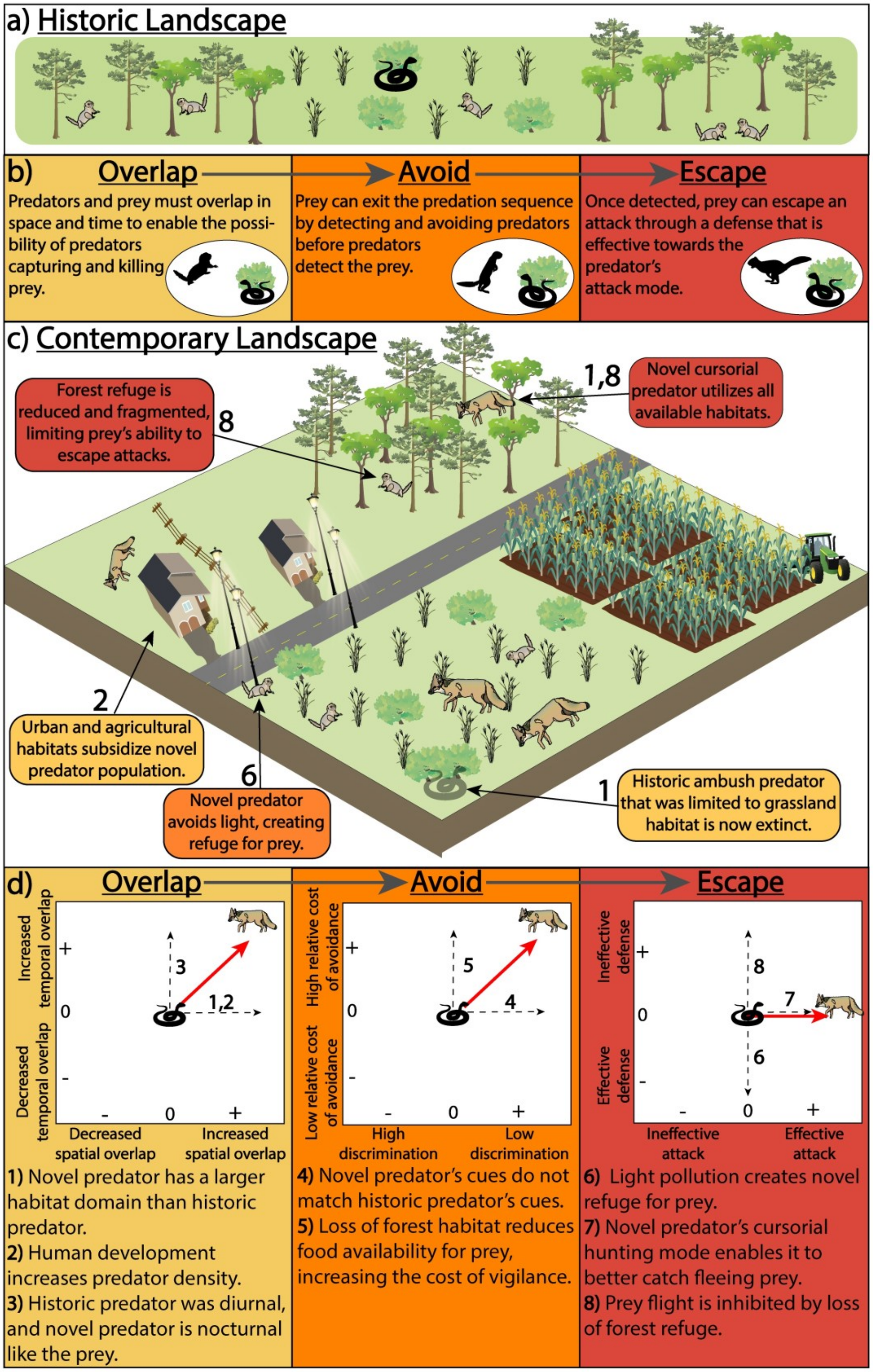

a) Historic Landscape
b) Overlap
Avoid
Escape
Predators and prey must overlap in space and time to enable the possibility of predators capturing and killing prey.
Prey can exit the predation sequence by detecting and avoiding predators before predators detect the prey.
Once detected, prey can escape an attack through a defense that is effective towards the predator's attack mode.
c) Contemporary Landscape
Forest refuge is reduced and fragmented, limiting prey's ability to escape attacks.
8
1,8
Novel cursorial predator utilizes all available habitats.
2
Urban and agricultural habitats subsidize novel predator population.
6
Novel predator avoids light, creating refuge for prey.
1
Historic ambush predator that was limited to grassland habitat is now extinct.
d) Overlap
Avoid
Escape
Increased temporal overlap
Decreased temporal overlap
+
0
-
3
1,2
- 0 +
Decreased spatial overlap
Increased spatial overlap
High relative cost of avoidance
Low relative cost of avoidance
5
4
High discrimination
Low discrimination
Ineffective defense
Effective defense
8
7
6
Ineffective attack
Effective attack
1) Novel predator has a larger habitat domain than historic predator.
2) Human development increases predator density.
3) Historic predator was diurnal, and novel predator is nocturnal like the prey.
4) Novel predator's cues do not match historic predator's cues.
5) Loss of forest habitat reduces food availability for prey, increasing the cost of vigilance.
6) Light pollution creates novel refuge for prey.
7) Novel predator's cursorial hunting mode enables it to better catch fleeing prey.
8) Prey flight is inhibited by loss of forest refuge.

Figure 2

Box 1: Empirical and theoretical tools for assessing novel predator-prey interactions

Quantifying novelty requires measurements of dissimilarity between baseline and contemporary conditions. Evaluating novelty across the three steps of the predation sequence is greatly simplified by existing empirical and theoretical tools that address individual steps of the predation sequence.

Quantifying overlap

A variety of techniques exist to quantify the spatiotemporal distribution of activity (e.g., GPS-tracking or camera traps), which can be used to asses synchrony between predator and prey activity patterns. However, predators may only use part of their total home range to forage (habitat domain), and thus may only be dangerous in this subset of their range [25]. Habitat domain theory [78] provides a theoretical tool to evaluate activity patterns (Figure I). One key prediction of habitat domain theory is that adding predators with complementary activity patterns enhances risk [25].

Quantifying avoidance

Evolutionary history is central to understanding organisms' ability to recognize novel stimuli. Cues that differ from those experienced throughout eco-evolutionary history are least likely to be accurately identified as dangerous [1,56]. Signal detection theory provides one way to predict how organisms discriminate between risky and safe cues, and may explain why organisms seemingly make inappropriate choices when given imperfect information (Figure I) [1]. Expected utility theory provides a means to incorporate costs and benefits of prey actions when faced with uncertainty, demonstrating how selection can produce decision rules to consistently err on the side of safety or risk (error-management theory). These approaches can be extended by models that allow animals to make repeated choices [58]. Many empirical tools also exist to quantify prey avoidance of predation risk, including giving-up-density experiments that determine the costs prey are willing to accept to avoid predators [37,79]. Future studies assessing the interplay of novel actors (e.g., cues of novel predators) and novel stages (e.g., anthropogenic resource subsidies) will be particularly important in understanding how prey avoid predators in novel habitats.

Quantifying escape

While prey employ a diverse suite of morphological and behavioral antipredator defenses [75], many prey ultimately rely on reaching a predator-free refuge. Economic models of flight [42] suggest that even if prey detect predators, they may not attempt escape immediately given costs associated with flight (e.g., reduced foraging [80]). Decisions about when to attempt flight often integrate information about prey morphological defenses (e.g., crypsis), as well as prey experience with predators and the distance to refuge [43]. Comparing flight-initiation distance between novel and baseline habitats [81] may help ecologists identify mismatches between novel predator and prey tactics.

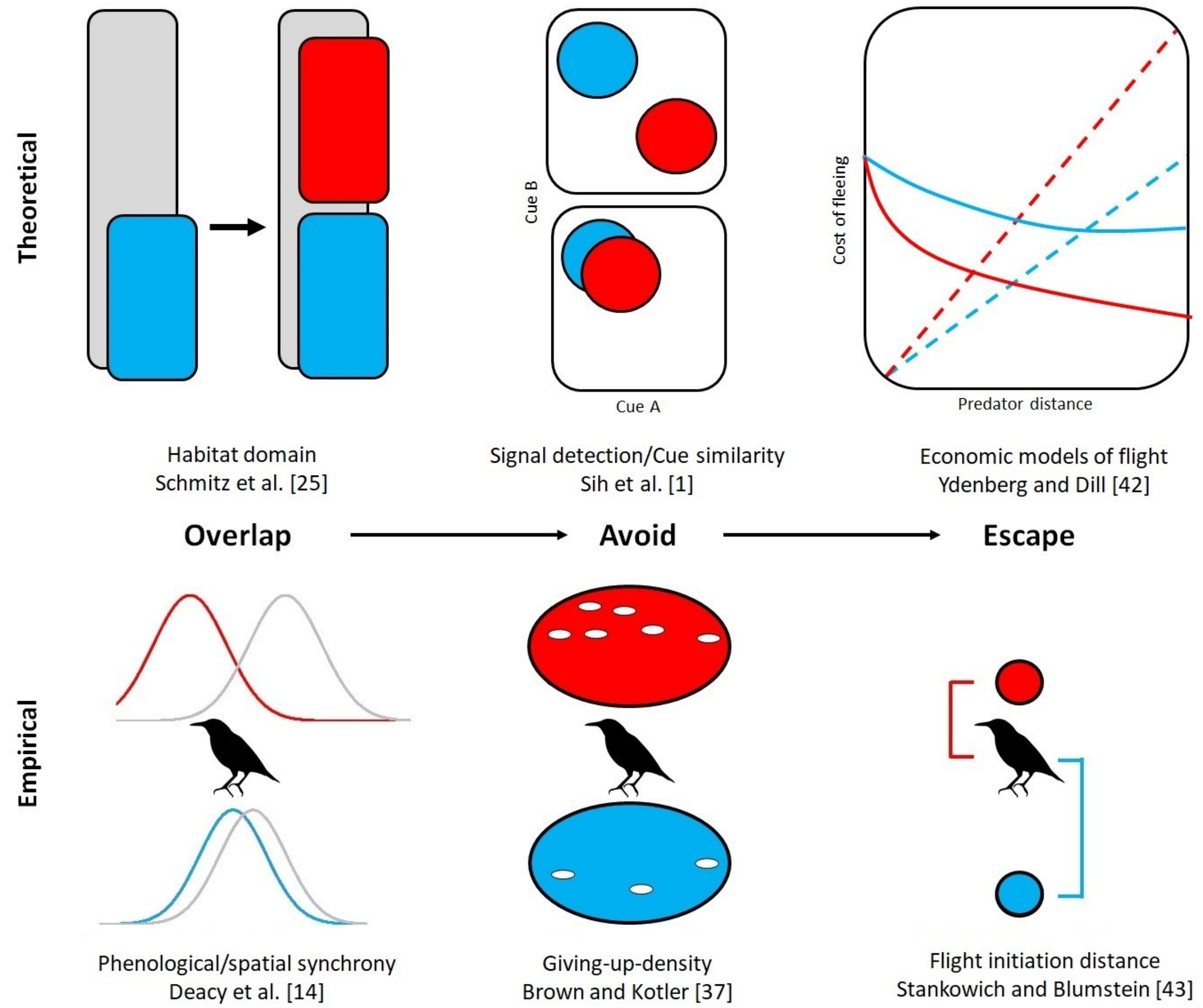


Figure I: Theoretical (top) and empirical (bottom) approaches to understand changes in the strength of predation in novel (red) and baseline (blue) habitats at in each step of the predation sequence for a generic prey (starling silhouette). In the overlap step, habitat domain theory provides predictions about changes in predator (blue, red) and prey (grey) space use, which might be used to interpret broad patterns of spatial or temporal overlap between prey and its novel and historical predators. In the avoidance step, the similarity between novel and baseline cues (cue similarity hypothesis) might predict the ability of prey to detect predators, and giving-up-density can be calculated to determine how much food (white) prey sacrifice for safety in novel and baseline foraging patches. In the escape step, economic models of flight can help anticipate how prey balance costs (dashed lines) and benefits (solid lines) associated with seeking refuge, and flight initiation distance provides a convenient way to integrate prey perceptions about defenses, safety, and predator danger.

Box 2: Case studies of novelty in the predation sequence

We used the predation sequence to build hypotheses about several novel predator-prey interactions from the perspective of prey. Figure I shows how novelty can increase or decrease the probability that the predation sequence proceeds to the next step; ellipses indicate variation in the effects of novelty. Regardless of the specific assumptions made (Supplemental Information), the predation sequence provides a tool to synthesize disparate elements of predator-prey ecology.

Brown Tree Snake (Boiga irregularis)

This introduced snake decimated Guam's avian community [82], yet not all prey species declined. Snakes avoid urban areas, providing refuge for urban-dwelling prey. Forest-dwelling prey with arboreal nests experienced more overlap with snakes, exacerbated by the snake's narrow habitat domain and nocturnal habit (both of which are novel to Guam's forest). Because Guam has no native predatory snakes [48], prey were naïve to the danger posed by snakes. Brown tree snakes are Guam's only ambush predator [48], and its arboreal habit implies that trees no longer provide refuge for avian prey. The predation sequence illustrates how species responses to novelty may either increase or decrease predation, explaining why some bird species were extirpated following the introduction of the brown tree snake, while others persist today (Figure I).

Pacific lionfish (Pterois volitans)

Lionfish have drastically altered Caribbean reef ecosystems. Space use data suggest lionfish have a broader habitat domain than native predators [83]. Lionfish are unlikely to be detected due to their novel crypsis [84], and prey may take greater risks in warm or acidic waters due to metabolic stress [59]. Native fish defenses are ineffective against lionfish [84], who deploy novel tactics (herding) and weapons (venom) to subdue prey [85]. The predation sequence illustrates why lionfish may be a particularly problematic invasive predator (Figure I). As lionfish expand into new habitats (e.g., estuaries [86]), the predation sequence could identify important knowledge gaps (e.g., comparing habitat domain between lionfish and native predators).

Cougar (Puma concolor)

Not all novel predator-prey interactions involve introduced species, as cougars are surprisingly well-adapted to some novel habitats. Cougars that select urban habitats overlap with synanthropic prey, but not wild prey [87,88]. Anthropogenic food subsidies [87] may produce novel chemical signatures in cougar urine, making it difficult for prey to detect cougars. Avoidance of cougars may be costly given strong constraints on diel activity timing in urban areas [31]. Artificial light may provide an effective refuge from cougars [47], but asocial urban prey lack a group defense against cougar ambushes [15]. Using the predation sequence to generate hypotheses about cougar use of novel habitats may help reduce human-wildlife conflicts by helping to anticipate where and when such conflicts are likely to arise.

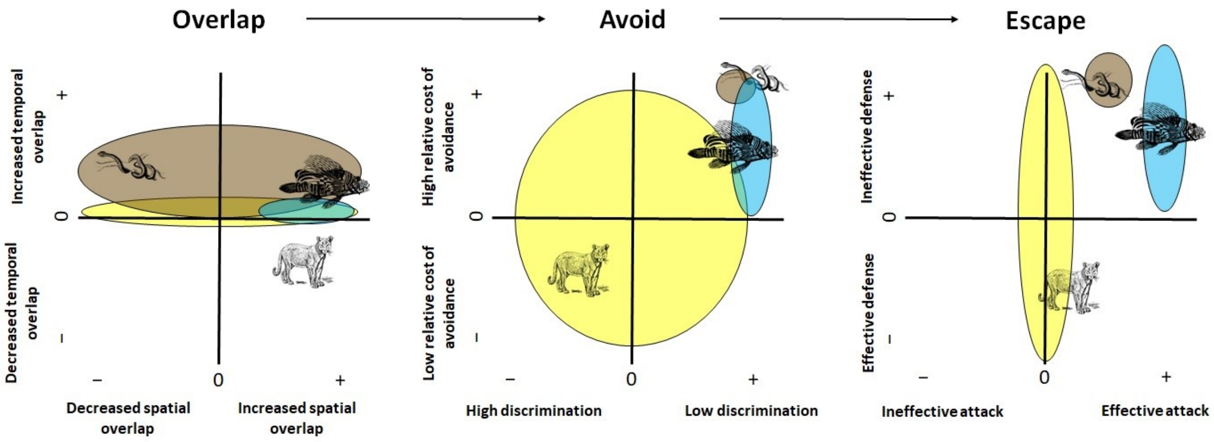


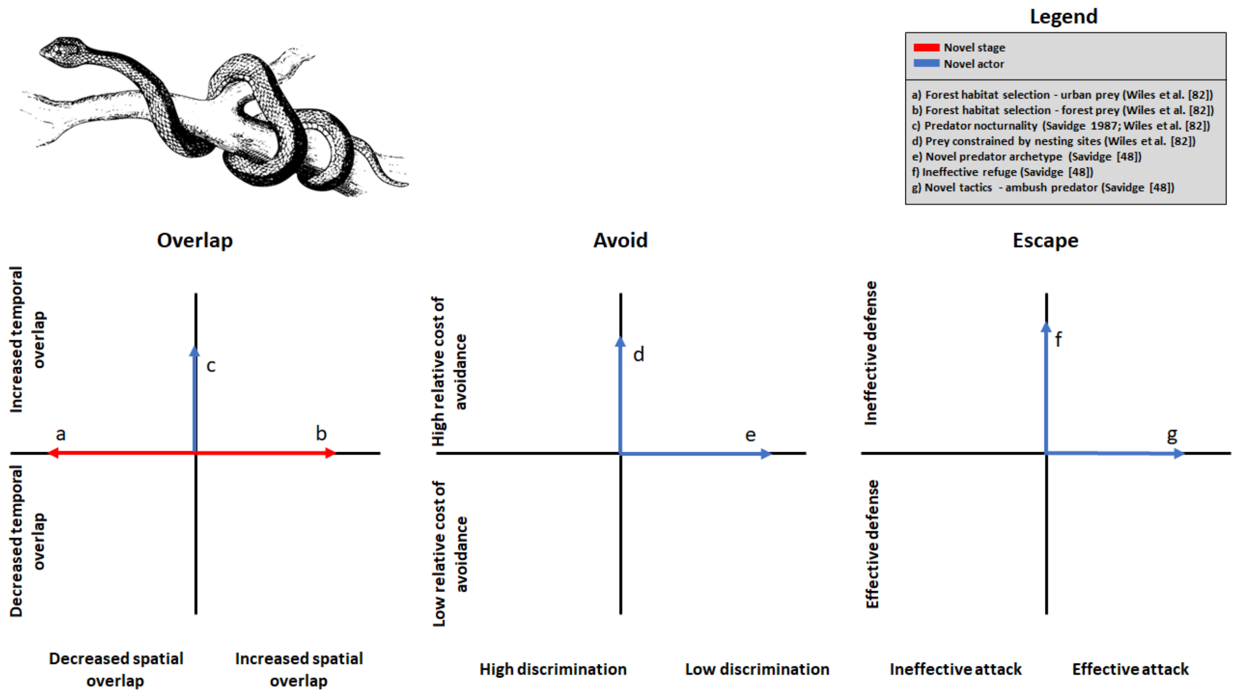
Figure I: The predation sequence can be used to generate hypotheses about novel predator-prey interactions in a diverse suite of predators, including invasive predators (brown tree snake, brown; lionfish, blue) and native predators (cougars, yellow). Each axis represents a dimension of predator-prey interactions that can be altered by novelty, but the magnitude and direction of the effects of novelty on predator-prey interactions can differ in space and time. The intersection of the axes represents baseline (historical) conditions. Positive values (+) indicate that the interaction is increasingly likely to proceed to the next, more dangerous step of the predation sequence, while negative values indicate that the predation sequence is more likely to end. Ellipses illustrate the range of potential outcomes in novel habitats, which is determined by local context (e.g., broad ellipses represent more uncertainty in the magnitude and/or direction of the consequences of novelty for predator-prey interactions). Predator-prey interactions pushed into the upper-right corner of each step of the predation sequence are most likely to proceed to the next step; in the case of the attack step, this means capture and possibly death for the prey.

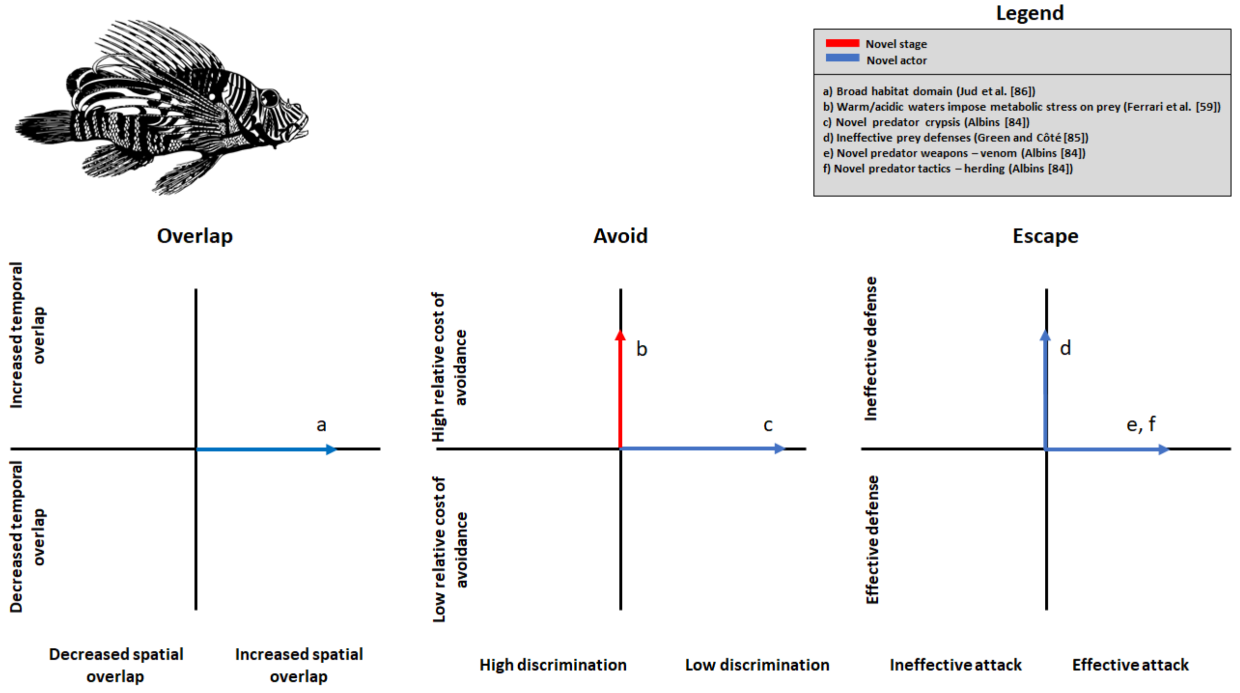
Outstanding Questions

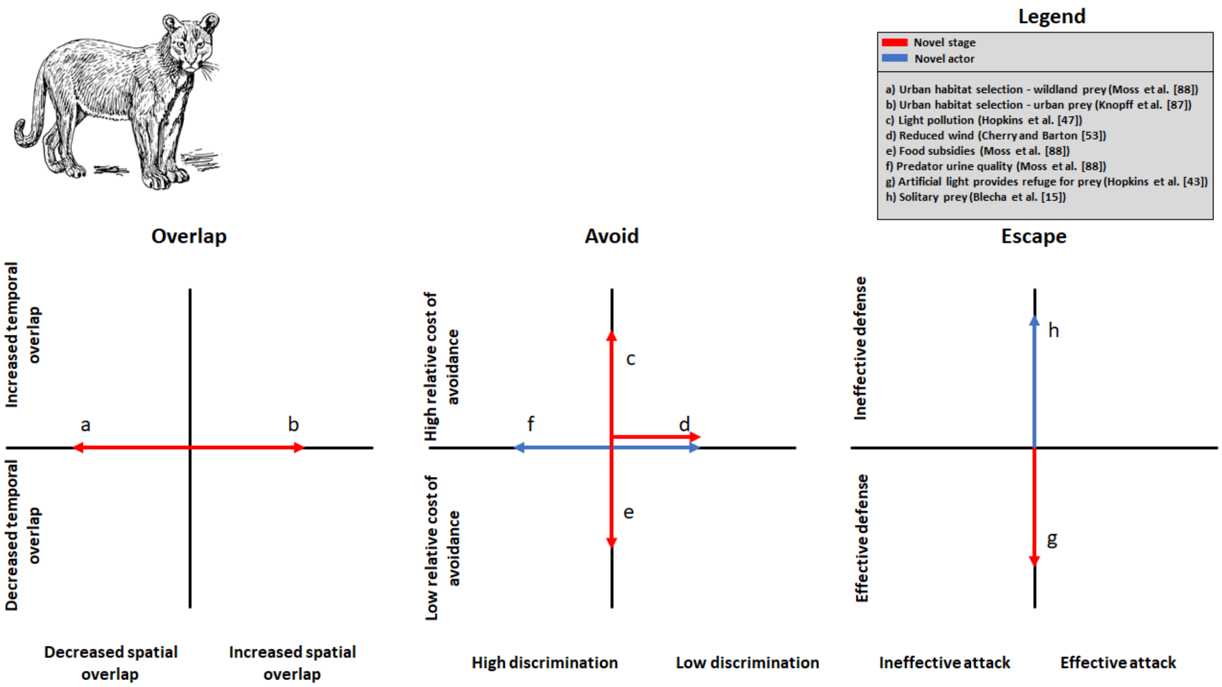
- Which steps of the predation sequence are most strongly affected by novelty, and do the effects of novelty on each step vary predictably over large spatial gradients?

- What is the capacity for predators and prey to adapt to novel actors and novel stages, and how will adaptation change the outcome of predator-prey interactions?
- Can specific traits or habitat conditions reliably predict increases or decreases in the probability that the predation sequence proceeds to more dangerous steps?
- While the causes of novelty can be readily mapped over large spatial scales, how might the consequence of novelty for species interactions be similarly mapped?
- How often do multiple forms of novelty exhibit synergistic effects?
- Is novelty more likely to change the lethal or non-lethal effects of predation?
- How readily can new technologies (e.g., using Next Generation Sequencing to reconstruct animal diets) and continental/global databases (e.g., Global Biodiversity Information Facility distribution data) be used to quantify novelty in species interactions?
- Can the predation sequence be used to develop strategies that mitigate the effect of novelty on predator-prey interactions?

Supplemental Information: Assumptions for Box 2, Figure I


Legend
Novel stage
Novel actor
a) Forest habitat selection - urban prey (Wiles et al. [82])
b) Forest habitat selection - forest prey (Wiles et al. [82])
c) Predator nocturnality (Savidge 1987; Wiles et al. [82])
d) Prey constrained by nesting sites (Wiles et al. [82])
e) Novel predator archetype (Savidge [48])
f) Ineffective refuge (Savidge [48])
g) Novel tactics - ambush predator (Savidge [48])
Overlap
Increased temporal overlap
Decreased temporal overlap
Decreased spatial overlap
Increased spatial overlap
a
b
c
Avoid
High relative cost of avoidance
Low relative cost of avoidance
High discrimination
Low discrimination
d
e
Escape
Ineffective defense
Effective defense
Ineffective attack
Effective attack
f
g


Legend
Novel stage
Novel actor
a) Broad habitat domain (Jud et al. [86])
b) Warm/acidic waters impose metabolic stress on prey (Ferrari et al. [59])
c) Novel predator crypsis (Albins [84])
d) Ineffective prey defenses (Green and Côté [85])
e) Novel predator weapons – venom (Albins [84])
f) Novel predator tactics – herding (Albins [84])
Overlap
Increased temporal overlap
Decreased temporal overlap
Decreased spatial overlap
Increased spatial overlap
a
Avoid
High relative cost of avoidance
Low relative cost of avoidance
High discrimination
Low discrimination
b
c
Escape
Ineffective defense
Effective defense
Ineffective attack
Effective attack
d
e, f


Legend
🟥 Novel stage
🟦 Novel actor
a) Urban habitat selection - wildland prey (Moss et al. [88])
b) Urban habitat selection - urban prey (Knopff et al. [87])
c) Light pollution (Hopkins et al. [47])
d) Reduced wind (Cherry and Barton [53])
e) Food subsidies (Moss et al. [88])
f) Predator urine quality (Moss et al. [88])
g) Artificial light provides refuge for prey (Hopkins et al. [43])
h) Solitary prey (Blecha et al. [15])
Overlap
Increased temporal overlap
Decreased temporal overlap
a
b
Decreased spatial overlap
Increased spatial overlap
Avoid
High relative cost of avoidance
Low relative cost of avoidance
c
d
e
f
High discrimination
Low discrimination
Escape
Ineffective defense
Effective defense
h
g
Ineffective attack
Effective attack