

The context dependence of non-consumptive predator effects

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Abstract

Non-consumptive predator effects (NCEs) are now widely recognized for their capacity to shape ecosystem structure and function. Yet, forecasting the propagation of these predator-induced trait changes through particular communities remains a challenge, in part because we lack a predictive framework that accounts for environmental and species context. Accordingly, focusing on plasticity in prey anti-predator behaviors, we conceptualize the multi-stage process by which predators trigger direct and indirect NCEs, review and then distill potential drivers of NCE contingencies into three key categories (properties of the prey, predator, and setting), and conduct a meta-analysis to quantify the extent to which prey behavioral plasticity in response to predation risk hinges on a well-studied driver – prey energetic state. Our synthesis underscores the myriad factors that can generate NCE contingencies while guiding how research might better anticipate and account for them. We highlight two key knowledge gaps that continue to hinder development of a comprehensive framework for exploring non-consumptive predator-prey interactions. These are insufficient exploration of 1) context-dependent indirect NCEs and 2) the ways in which direct and indirect NCEs are shaped interactively by multiple drivers of context dependence.

REVIEW AND SYNTHESIS

The context dependence of non-consumptive predator effects

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Running head : Context dependence of NCEs

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Abstract. – Non-consumptive predator effects (NCEs) are now widely recognized for their capacity to shape ecosystem structure and function. Yet, forecasting the propagation of these predator-induced trait changes through particular communities remains a challenge, in part because we lack a predictive framework that accounts for environmental and species context. Accordingly, focusing on plasticity in prey anti-predator behaviors, we conceptualize the multi-stage process by which predators trigger direct and indirect NCEs, review and then distill potential drivers of NCE contingencies into three key categories (properties of the prey, predator, and setting), and conduct a meta-analysis to quantify the extent to which prey behavioral plasticity in response to predation risk hinges on a well-studied driver – prey energetic state. Our synthesis underscores the myriad factors that can generate NCE contingencies while guiding how research might better anticipate and account for them. We highlight two key knowledge gaps that continue to hinder development of a comprehensive framework for exploring non-consumptive predator-prey interactions. These are insufficient exploration of 1) context-dependent indirect NCEs and 2) the ways in which direct and indirect NCEs are shaped interactively by multiple drivers of context dependence.

Introduction

The idea that predators might influence prey non-consumptively by eliciting trait changes has a long history. Indeed, Darwin (1839) hypothesized that prey escape responses cost time and energy to maintain and, consequently, should attenuate in the absence of predators. Today, these predator-induced trait changes, or non-consumptive effects (NCEs), have a strong conceptual basis (Charnov *et al.* . 1976; Lima & Dill 1990; Lima 1998, Creel & Christianson 2008) and are thought to rival or even exceed direct predation in terms of their impacts on prey populations and ecosystems (Kotler & Holt 1989; Peacor & Werner 2001; Werner & Peacor 2003; Schmitz *et al.* . 2004; Preisser *et al.* . 2007). Once the purview of laboratory and short-term field experiments involving small-bodied taxa (Kotler 1984; Preisser *et al.* . 2005; Weissburg *et al.* . 2014), NCEs and their broader consequences are increasingly being explored in large vertebrate systems (e.g., Dill *et al.* . 2003; Willems & Hill 2009; Burkholder *et al.* . 2013; Middleton *et al.* . 2013; Basille *et al.* . 2015; Moll *et al.* . 2016; Le Roux *et al.* . 2018; Courbinet *et al.* . 2019; Smith *et al.* . 2019; Valeix *et al.* . 2019). This expansion has shed new light on the extent to which NCEs scale up to communities of larger-bodied species. Yet, it has also drawn more attention to contingencies in NCEs. Such contingencies currently defy a coherent explanation, underscoring the need for standardized methodology for evaluating these phenomena across species and environmental contexts (Ford & Goheen 2015; Prugh *et al.* . 2019) and conceptual clarity (Schmitz *et al.* . 2017a; Gaynor *et al.* . 2019) to guide research.

A growing literature suggests that contingency in NCEs hinges on key properties of the organisms involved as well as the environments in which they interact (Preisser *et al.* . 2007; Heithaus *et al.* . 2009; Wirsing *et al.* . 2010; Creel 2011; Schmitz & Trussell 2016). Accordingly, there have been several recent calls for these properties to be characterized and incorporated into a general framework for predicting the nature and consequences of NCEs within ecological communities (e.g., Cresswell 2008; Heithaus *et al.* . 2009; Creel 2011; Moll *et al.* . 2017). Here, to facilitate the development of such a framework, we (i) conceptualize the multi-stage process by which predators may trigger direct and indirect NCEs; (ii) review key drivers of context dependence in NCEs; and (iii) quantify the extent to which prey trait plasticity in response to predation risk hinges on prey energetic state to demonstrate how considerations of contingency are critical

to understanding the role of NCEs in complex communities. We then (iv) conclude with a synthesis and prospectus for future work. Our review spans aquatic and terrestrial ecosystems, addresses invertebrates and vertebrates, and focuses on a prevalent form of prey trait plasticity that is often implicated in the transmission of NCEs, *anti-predator behaviors*. We emphasize, however, that many of the sources of context dependencies that we address likely also apply to other forms of predator-induced trait modification (e.g., prey development, morphology, and physiology).

Propagation of NCEs in communities

Predation risk is typically defined as the probability of an individual becoming prey within a given place and time (Lima & Dill 1990). However, predation risk could just as easily be conceptualized as the probability of an individual becoming prey at a given place and time assuming no, or some set amount of, anti-predator investment (Lank & Ydenberg 2003). Predation risk under the former definition is more intuitive, given its direct link to observable patterns of mortality, and therefore lends itself to estimation via the combination of spatiotemporal probabilities of encountering and being killed by predators (Lima & Dill 1990; Lima 1992). Estimates of risk based on this definition reflect inherent properties of the location and time of interest and dynamic properties of the predator (e.g., decisions about whether to attack in response to prey behavior) and the prey (e.g., defensive investment). Accordingly, we view them as measures of *realized predation risk*. By contrast, predation risk under the latter definition, termed *intrinsic predation risk* or *danger*, is harder to measure because it is an abstract construct (Lank & Ydenberg 2003). Nevertheless, this latter conceptualization importantly decomposes the process by which prey individuals experience and respond to the threat of predation into a series of steps beginning with exposure to risk stimuli and ending with changes to prey numbers and traits (e.g., behavior) that may affect additional species within the community (**Fig. 1**). Consequently, it provides a clearer mechanistic basis for understanding when and how various sources of contingency might direct the propagation of NCEs through communities than does the former definition. Hence, while acknowledging the validity of both approaches to defining predation risk, we focus on intrinsic risk for the remainder of our review.

Propagation of NCEs consists of three phases (**Fig. 1**) within a context of intrinsic risk. Every point in space and time is characterized by some value of intrinsic predation risk, which includes spatial properties of the situation that influence the likelihood of predator-induced mortality but that prey cannot easily modify through behavioral changes. These properties include availability of refuges, presence of escape impediments, dilution of risk by conspecifics and by other species, and the abundance of predators and species that might inhibit predator effectiveness (Lank & Ydenberg 2003). Collectively, they are often viewed as determinants of the background pattern of risk for a given location. Areas with elevated background risk are sometimes called *risky places* (Creel *et al.* 2008). Intrinsic risk is also influenced temporally by whether predators, and other species or environmental conditions (e.g., moonlight) that might influence the predator's efficacy, are currently present at a location. Periods when the presence of predators or conditions heighten prey vulnerability are considered to be *risky times* (Creel *et al.* 2008).

Within the setting of intrinsic risk, phase one concerns whether the forager perceives any cues related to the current level of intrinsic risk. Prey may either detect spatiotemporal cues that reflect intrinsic predation risk (including an attack itself), setting up the possibility of NCEs, or fail to detect appropriate risk stimuli, in which case no NCEs will result (from the cue in question) and mortality from the predator will be more likely. Thus, factors influencing prey detection of intrinsic risk cues may operate as key sources of context dependencies in NCEs.

Foragers that perceive intrinsic cues can then respond to them in phase two. Perceived danger may or may not elicit a prey response of sufficient magnitude to precipitate a NCE. In response to background risk and risky times, prey individuals may manage this risk proactively. In response to immediate threats (including attacks), prey may respond reactively through behavioral countermeasures (Creel 2018). The energetic, reproductive, and opportunity costs that ensue from these adjustments determine the magnitude of any associated risk effects (Creel & Christianson 2008). Thus, the type of anti-predator behavior exhibited by a prey individual in any situation is crucial to whether and to what extent it will experience fitness penalties.

Prey individuals that perceive danger may also experience stress, which may affect fitness (Clinchy *et al.* 2013) and thereby precipitate risk effects either alone or in concert with other (e.g., lost opportunity) costs of anti-predator behaviors. Accordingly, during phase two, factors that influence the strength of responses to perceived risk, the form of anti-predator behaviors, and the amount of associated stress could act as important drivers of contingency in associated predator risk effects experienced directly by prey and ensuing propagation of NCEs.

In phase three, the responses of the forager to intrinsic risk can give rise to indirect effects on other species. Risk effects from predator-induced risk management and stress can reduce prey population size (Creel & Christianson 2008) and thereby trigger indirect interactions if prey abundance drops enough to affect other community members. Moreover, the nature of prey risk management can determine whether and how other species in the community are affected indirectly. Some behavioral adjustments may only affect the prey species that responds to perceived risk, potentially leading to direct risk effects, whereas others may further (or exclusively) influence third parties and thereby propagate through ecological communities as indirect interactions. Therefore, any factor that modulates the impacts of perceived risk on prey population size and anti-predator behaviors also has the potential to shape indirect NCEs.

Potential drivers of context dependence in NCEs

Properties of the prey

Within prey guilds, species employ various means to detect (Weissburg *et al.* 2014), evade (Moore & Biewener 2015), and resist (Creel 2011) predators. Modes of detection (acoustic, chemical, olfactory, visual, tactile) enable prey to identify risky places, for example by quantifying spatial variation in the intensity of persistent predator cues; and risky times, as when a predator's approach is observed (Creel *et al.* 2008). Sensory modalities for perceiving and responding to risk are a critical source of contingency during phase one (**Fig. 1**). Prey species may lack the capacity to detect persistent evidence of a predator's presence and thus to prepare for encounters, or instances when predator-prey spatial overlap is such that detection of one by the other is possible (Lima & Dill 1990). Alternatively, their preparation for encounters may be continuous and generalized, leading to high fitness costs and reduced efficacy (Creel *et al.* 2008; Creel 2018). Similarly, inability to sense the approach of a predator limits reactive responses to those triggered by an attack (e.g., physical resistance; Creel 2018). In sum, then, consideration of sensory biology should aid in predicting which members of prey guilds are least likely to be subject to non-consumptive (versus consumptive) effects of a predator, and which kinds of risk stimuli (background versus immediate) are most likely to induce defensive responses by a given prey species.

The kinds of sensory modalities used to perceive predation risk should also shape the propagation of NCEs during phases two and three (**Fig. 1**). First, different sensory modalities may mediate the type and intensity of information transferred from a risk cue to prey (Weissburg *et al.* 2014). Thus, sympatric prey species that use different senses to detect the same predator may respond with divergent intensity and/or specificity depending upon the pathway through which they receive and process the information (Weissburg *et al.* 2014). The threat level and predator identity perceived by a given prey species could influence its response and any associated risk effects (including from stress) during phase two, as well as any indirect interactions precipitating during phase three. Second, prey with multiple sensory modalities may be better able to detect predators and have an anti-predatory advantage (Munoz & Blumstein 2012). For example, access to both visual and chemical cues allowed for more accurate detection and appropriate responses to predators by mosquito fish (*Gambusia holbrooki*) (Ward & Mehner 2010). Thus, members of prey guilds with multiple sensory modalities may exhibit more striking and appropriate anti-predator responses, higher vulnerability to risk effects, and greater capacity to transmit indirect NCEs to other community members than sympatric heterospecifics relying on a single means of detection.

Although some may double as routine safeguards, tactics for evading and resisting predator attacks are typically reactive countermeasures triggered by encounters with predators (Creel 2018). Thus, these 'escape behaviors' (Heithaus *et al.* 2009; Wirsing *et al.* 2010) usually act as drivers of contingency during the

latter two phases of non-consumptive interactions, after risk is perceived. Evasive behaviors are diverse and include altered activity (Schmitz 2007), body part autotomy (Maginnis 2006), dynamic flash coloration (Murali 2018), feigning death (Humphreys & Ruxton 2018), fleeing (Moore & Biewener 2015), grouping (to confuse predators or dilute risk; Lehtonen & Jaatinen 2016), hiding/crypsis (Caro 2014), and seeking a refuge (Sih 1987). Their efficacy can be prey- and predator-specific and hinge on environmental features (Heithaus *et al.* 2009; Wirsing *et al.* 2010; Schmitz 2017; Creel 2018). The effectiveness of flash coloration as a means of visually confusing predators, for example, can depend on visual obstructions, light levels, and background colors (Murali 2018). To the extent that prey have scope to modify the effectiveness of their escape tactics, interspecific variation in evasive behaviors may lead to differences in anti-predator responses to the same risk stimuli during phase two. For example, sympatric prey species that flee predators with disparate means of locomotion may respond divergently to a shared predator by proactively seeking areas that suit their respective movement styles in preparation for an encounter or reactively shifting to these areas after an encounter has occurred. Consistent with this expectation, mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) exhibited divergent proactive shifts to terrain suiting their respective running gaits (bounding and galloping) when exposed to gray wolves (*Canis lupus*) (Dellinger *et al.* 2019; **Fig. 2**). A similar scenario characterizes NCEs of tiger sharks (*Galeocerdo cuvier*) on a community of vertebrates in the seagrass ecosystem of Shark Bay, Australia (Heithaus *et al.* 2012; **Fig. 3**). By implication, during phase three, a predator targeting more than one sympatric prey species could impose multiple indirect effects on other community members (e.g., basal resources for the different prey species) that occur because of prey-specific forms of evasion with divergent consequences for distribution (Wirsing & Ripple 2011). This possibility has not been tested.

Forms of prey resistance may discourage predators prior to an attack or repel an attacker. Resistance may include cooperative defense (Lehtonen & Jaatinen 2016), induced chemical defense (Mukherjee & Heithaus 2013), fighting back (Mukherjee & Heithaus 2013), and honest (e.g., aposematism, pursuit deterrence; Harvey & Paxton 1981; Caro 1995) and deceptive signaling (e.g., actions that make an individual seem more difficult to capture such as increases in apparent size, mimicry; Caro 2014). As with evasion, the efficacy of resistance may be predator- and setting-specific (Mukherjee & Heithaus 2013). Chemical defenses of herbivorous insects, for example, are more effective against vertebrate than invertebrate predators, perhaps because of the latter group's enhanced capacity to develop adaptations to tolerate or overcome prey defenses (Zvereva & Kozlov 2016). Unlike evasive behaviors, however, resistance usually manifests after the predator detects the prey, and often after an attack has been initiated. Rough-skinned newts (*Tarichia granulosa*), for instance, show little behavioral response to predators (Murray *et al.* 2004) save to honestly signal by displaying the bright coloration of their underbelly when accosted by a would-be attacker. Hence, these countermeasures are less likely than evasion to result in either costly risk effects (e.g., diminished condition after prolonged foraging disruption) or in changes to prey activity budgets and distributions during phase two (e.g., displacement) that could indirectly affect other species during phase three. For example, adult moose (*Alces alces*), which can fight back effectively against wolves (*C. lupus*), show little spatial response to wolf presence (Nicholson *et al.* 2014). Not surprisingly, observed indirect effects of wolves on the plants that moose consume appear to be transmitted primarily by the numerical effects of direct predation rather than NCEs (Post *et al.* 1999). By implication, prey species relying on resistance should respond differently to predation risk, and to be less likely to be vectors of indirect NCEs, than those depending on evasive behaviors. There are studies supporting the former expectation (e.g., Lingle & Pellis 2002) but it has not been addressed broadly. The latter expectation remains unexplored.

Within populations, prey state may shape individual responses to predation risk and, consequently, propagation of NCEs (Sih *et al.* 2015; Schmitz 2017). States can be relatively stable (e.g., sex, behavioral type, and epigenetically or genetically derived morphs) or dynamic (e.g., age/developmental stage, current behavior, disease state, learning, nutritional condition, residual reproductive value, and stress level). An individual's state can influence its risk taking behaviors in any of three ways. First, an individual's capacity to recognize danger may be state-dependent, as when prey acquire the capacity to detect and respond appropriately to cues via development/growth and learning (Kavaliers & Choleris 2001). For example, large bumblebees

(*Bombus terrestris*) are more sensitive to spider risk while visiting inflorescences, likely (at least in part) because they possess eyes with greater visual acuity than smaller conspecifics (Gavini *et al.* 2019). Working with fathead minnows (*Pimephales promelas*), Ferrari *et al.* (2006) showed that individuals learned to recognize northern pike (*Esox lucius*) as predators from a paired exposure to conspecific alarm pheromones and pike odor. Once learned, a minnow's fear response increased with the concentration of pike odor alone. Not surprisingly, therefore, naïve individuals often differ markedly from experienced conspecifics in terms of whether (phase one) and how (phase two) they respond to predation risk (Sih *et al.* 2010). This form of experience-driven contingency in defensive behaviors could give rise to differences in the extent to which individuals (and populations) with divergent amounts of prior predator conditioning transmit indirect NCEs (phase three).

Second, prey state may affect vulnerability, as when individuals in different growth stages are differentially able to outpace (Diamond *et al.* 2019) or resist (Schmitz 2017) predators. Thus, against any predator, individuals in less susceptible states should have reduced need to invest in countermeasures and, consequently, respond differently to perceived risk than more vulnerable conspecifics during phase two. For example, Christensen (1996) observed that juvenile roach (*Rutilus rutilus*) that were beyond the gape limits of their predators invested less in defense (time spent near the surface and jumping out of the water when at risk) than smaller (ingestible) conspecifics. Similarly, Dannock *et al.* (2019) found that blue wildebeest (*Connochaetes taurinus*) eschewed chewing while being vigilant following lion (*Panthera leo*) playbacks, presumably because mastication hampers predator detection. Thus, the overall pattern of anti-predator behavior characterizing a prey population during phase two, and the degree to which it transmits indirect NCEs during phase three, could hinge on the distribution of states manifested by its constituents. Indeed, where prey switch ontogenetically from being the prey to being the predator of another species (Ferrari *et al.* 2010), relative abundance of different developmental stages within a population could mediate the extent to which it experiences and transmits versus initiates NCEs. These hypotheses have yet to be evaluated systematically.

Third, a prey's state may influence its willingness to respond to perceived risk, as when individuals with risk-prone behavioral types are less likely to invest in anti-predator behavior (Michalko & Řežucha 2018) or those with compromised energetic state are more willing to expose themselves to danger to avoid starvation (Clark 1994). The former mechanism is gaining support in the literature (Réale *et al.* 2007; Mittlebach *et al.* 2012; Sih *et al.* 2015; Moran *et al.* 2017). The latter, known as state-dependent risk taking, has long been recognized and is thoroughly explored in a range of taxa (e.g., **Box 1**). Both have consequences for levels of anti-predator investment and subsequent predation rates experienced by prey during phase two. For example, bold mud crabs (*Panopeus sapidus*) exhibit lower refuging times relative to shyer conspecifics following exposure to predator cues, and consequently experience higher predation from blue crabs (*Callinectes sapidus*) (Belgrad & Griffen 2016). Rainbow trout (*Onchorhynchus mykiss*) with reduced access to food take greater risks to achieve growth and, consequently, suffered increased predation mortality (Biro *et al.* 2005). Thus, the extent to which any prey population is subject to consumptive versus non-consumptive predator effects may depend on its average behavioral type (Sih *et al.* 2004; Moran *et al.* 2017) or its mean energetic state (Anholt & Werner 1995; Heithaus *et al.* 2008; Matassa & Trussell 2014). These scenarios have only rarely been assessed under large-scale field conditions (e.g., Sinclair & Arcese 1995). The additional inference that mean temperamental or energetic states should influence the transmission of indirect NCEs in communities has, to our knowledge, not been addressed.

Finally, prey may possess constitutive (permanent) defenses that influence risk-taking behavior including armor, harmful morphology (e.g., spines), toxicity/unpalatability, and honest or deceptive advertisements of similarity to toxic/unpalatable heterospecifics (Tollrian & Harvell 1999). In theory, the effectiveness of these defenses should be inversely proportional to the need for anti-predator behavior (Dewitt *et al.* 1999). Freshwater snails (*Physa gyrina*) with vulnerable shell shapes, for instance, exhibited greater behavioral responses (refuging, avoidance) than harder-to-kill conspecifics when confronted by cues from crayfish (*Orconectes rusticus*) (Dewitt *et al.* 1999). By implication, taxa that are well defended constitutively should exhibit weaker anti-predator responses than other community members with less effective constitutive defen-

ses during phase two, whether or not cues are detected in phase one, and be less likely to transmit indirect NCEs during phase three. However, the effectiveness of any constitutive defense is, itself, context dependent. For example, Pokallus & Pauli (2016) observed that, despite possessing a well-developed predator deterrent (quills), porcupines (*Erethizon dorsatum*) altered their movements to reduce risk from fishers (*Pekania pennanti*), a specialized porcupine predator. Hence, even prey with generally effective constitutive protections may react to and transmit indirect NCEs elicited by predators that can, under some circumstances, breach their defenses.

Properties of the predator

The means by which predators capture their prey, or their hunting modes, are a pervasive driver of context dependence in NCEs (Preisser *et al.* 2007). Hunting predators, and their prey, are also characterized by a habitat domain, or the spatial extent over which individuals move while foraging (Schmitz 2005; Schmitz *et al.* 2017a). Together, these properties form the ‘hunting mode-habitat domain concept’, which aims to explain spatiotemporal contingency in the nature of predator-prey interactions. It can predict how foraging predators and prey should interact during the three phases as a consequence of contingencies in their spatial movement and overlap, the nature of which depends on how prey respond to the threat of predation across space.

Habitat domain size appears to be consistent among predators with similar hunting modes (Miller *et al.* 2014). At one extreme of a continuum, actively roaming/coursing predators typically have large habitat domains; at the other, sit-and-wait/ambush predators usually exhibit smaller domains. Notably, predators may switch hunting modes (Helfman 1990; Olson & Eklov 2005; Donihue 2016), which can change space use, habitat domain size, and contingency in the nature of interactions. Smaller prey may forage locally, whereas larger prey may roam widely depending on their forage requirements in relation to the distribution of plant (or other resource) quality and productivity (Haskell *et al.* 2002), creating contingency in prey movement and habitat domain size. Further contingencies could arise if prey have different habitat domain sizes as they adjust their movement behaviours to the type of predator they face (Fischhoff *et al.* 2007; Merrillet *et al.* 2010; Miller *et al.* 2014).

The spatiotemporal nature of predator-prey movement and overlap may determine prey perception of predation risk (phase one). Sit-and-wait predators, by remaining sedentary in fixed locations, create a continuous presence within a narrow habitat domain (Schmitz 2007; Schmitz *et al.* 2017a). Consequently, prey facing sit-and-wait predators may have a heightened perception of risk because of the persistent point-source cue of predator presence. Actively hunting predators roam widely and thereby often produce diffused, moderate cues in any given location within their broad habitat domain, resulting in lower perception of risk by prey (Schmitz 2007). Consistent with this framework, Murie & Bourdeau (2019) observed that herbivorous snails (*Tegula funebris*) altered their distribution in an intertidal ecosystem in response to the purple sea star *Pisaster ochraceus*, which moves slowly within a narrow domain producing an acute and spatially localized acute risk signature. These snails did not alter their distribution when exposed to crab and octopus predators that hunt actively within larger domains and generate diffuse risk profiles. Hence, relative to sedentary predators occupying narrow habitat domains, active predators with large domains may be less likely to initiate direct and indirect NCEs that play out during phases two and three (e.g., Schmitz 2008).

Prey responding to predator cues (phase two) must weigh potentially considerable opportunity costs, in terms of energy and nutrient intake (up to 25% of daily energy expenditure: Schmitz [2005]) and survival, of remaining continuously vigilant given the likelihood of encountering and being captured by a predator. Thus, prey occupying landscapes with sit-and-wait predators may accept those costs and respond with chronically heightened apprehension. This response could involve heightened vigilance at the expense of reduced foraging, or seeking safety in refuges, or both, depending on the sizes of their habitat domain relative to their predator’s (Schmitz 2005). Alternatively, prey facing active hunting predators may encounter predators infrequently. Under these circumstances the prey should not be chronically apprehensive and incur a large energetic penalty. Rather, prey under these conditions should react acutely to imminent risk by simply evading predators upon encounter (Schmitz 2005). There is evidence that these divergent phase two

scenarios can govern the nature of indirect NCEs in phase three. For example, Schmitz *et al.* (2017b) found that chronic avoidance of sit-and-wait spider predators by grasshoppers increased plant diversity while decreasing soil carbon retention, whereas a predator guild dominated by actively-hunting spiders failed to elicit grasshopper anti-predator behavior and, consequently, did not indirectly affect plant composition and soil carbon via a non-consumptive pathway.

Whether or not a predator-prey interaction during phase two is largely consumptive or non-consumptive will depend on the relative habitat domain sizes of predators and prey (Schmitz *et al.* 2004; Schmitz 2005). There are at least four contingencies that can arise, with non-consumptive effects being predominant in three of the four. Whenever prey and predator have overlapping, narrow habitat domains, prey will respond with chronic vigilance. Prey with narrow habitat domains that face widely roaming predators with broad habitat domains will likewise be chronically vigilant. Prey with broad habitat domains should seek refuge by shifting habitat use when facing predators with a narrow habitat domain. Finally, when prey and predators both have broad habitat domains, prey are less prone to exhibit habitat shifts or chronic vigilance, in which case consumptive effects (phase two) and their indirect consequences (phase three) should predominate (Schmitz *et al.* 2004; 2017a).

Predator state is also a factor that can shape NCEs. State variation can drive differences in a predator's detectability (Scherer & Smee 2016) and motivation to seek (i.e., its activity and, consequently, spatiotemporal pattern of cue generation) and/or successfully attack (i.e., its lethality) prey (Brown & Kotler 2004; Brown *et al.* 2016). This variation can range from being highly dynamic, as when predator hunger elicits increased foraging activity (Hooten *et al.* 2019), to persistent, as when aggressive behavioral types are more likely to attack prey given an encounter (e.g., Michalko & Řežucha 2018). During phase one, dynamic changes to a predator's feeding states can change how detectable it is to prey that rely on cues from depredated conspecifics as signals of danger. For instance, mud crabs (*Panopeus herbstii*) detected and responded to predatory blue crabs (*Callinectes sapidus*) that had recently been fed a mud crab diet at a greater distance than food-restricted blue crabs (Weissburg & Beauvais 2015). By implication, predator populations that rely on such prey species may be more likely to initiate NCEs that cascade through to phase three. In the Weissburg & Beauvais (2015) study, blue crabs that had fed recently on mud crabs indirectly reduced consumption of a basal resource (oysters) by mud crabs to a greater degree than their hungry counterparts.

During phase two, dynamic predator state changes can influence the strength of anti-predator responses by prey over short intervals (e.g., when hungry predators are perceived as more threatening; **Box 1**). Thus, prevalence of certain states within predator populations (e.g., compromised energetic state) could drive changes to overall prey risk taking that are large enough to affect propagation of indirect NCEs during phase three. More persistent differences in predator state can give rise to marked inter-individual variation in the anti-predator behavior induced by predators during phase two (Sih *et al.* 2012). For example, Winandy & Denoël (2015) found that goldfish (*Carassius auratus*) with aggressive temperaments elicited greater reduction in newt (*Lissotriton helveticus*) foraging than less aggressive conspecifics. By implication, the temperamental mix of predator populations could influence the nature of prey defenses during phase two and the likelihood of cascading NCEs in phase three.

Properties of the setting

Both prey and predator traits crucially predict the outcome of their non-consumptive interactions. Additionally, the propagation of NCEs depends also on the setting in which the interaction takes place. During phase one, changes to the environment may impair prey detection of predator cues by disrupting acoustic (e.g., owing to anthropogenic noise; Chan *et al.* 2010), chemosensory (e.g., because of pollution; Lüring & Scheffer 2007), or visual (e.g., via increased turbidity; Abrahams & Kattenfield 1997) systems. These environmental changes may reduce the likelihood of, or even preclude, anti-predator behavior. For example, predator avoidance by freshwater snails (*Physa acuta*, *Helisoma trivolvis*) disappeared when eutrophication of their outdoor mesocosms led to chemosensory impairment (Turner & Chislock 2010). Environmental features that impede predator detection may themselves be recognized as risk cues by prey and thereby result in elevated defensive investment. For example, Embar *et al.* (2011) demonstrated that gerbils (*Gerbillus*

andersoni allenbyi) reduced their foraging activity (measured by GUDs) when landscape features blocked sightlines that were necessary for anti-predator vigilance. In general, then, environmental heterogeneity with respect to properties that influence predator detection may mediate substantial inter-individual and population variation in the degree to which prey recognize predation danger and subsequently experience and transmit NCEs.

During phase two, properties of the setting may influence the scope for prey anti-predator behavior in several ways. First, predator and prey habitat domains are shaped in part by environmental context (e.g., thermal conditions, vegetative structure; Schmitz & Barton 2014). Accordingly, environmental factors constraining prey movement or the amount of predator-free space could dictate whether prey manifest chronic anti-predator vigilance, use refugia, or experience consumptive effects under the four contingent scenarios described above. Barton & Schmitz (2009) showed, for example, that experimental warming created enemy-free space by shifting the environment from one where two spider predators were spatially complementary to overlapping. This led to a strictly non-consumptive interaction whereby grasshoppers avoided predators rather than a composite scenario where they avoided the sit-and-wait predator but experienced consumptive effects of the active hunter.

Second, even when predator and prey domains are unaffected by the setting, landscape features can shape NCEs by modifying the efficacy of prey escape behavior. The ability of an individual to escape a predator following an encounter can depend on environmental factors that influence mobility (e.g., terrain) or visibility (e.g., when the background affects prey camouflage) (Wirsing *et al.* 2010). Thus, areas with properties that render prey escape tactic(s) less effective are likely to be avoided, at least when predators are present, or to elicit other countermeasures that enhance the probability of early predator detection (e.g., vigilance). For instance, reef habitat complexity enhanced and dampened anti-predator behaviors of large and small fishes, respectively, likely because large-bodied fish are less able to flee from predators through obstacle-rich reefs than their smaller counterparts (Catano *et al.* 2016).

Third, food quantity or quality at the landscape scale can shape NCEs by influencing the mean energetic state of prey populations (Heithaus *et al.* 2008; Wirsing & Ripple 2011). In depauperate landscapes, average energetic states will be depressed and the overwhelming necessity of food should drive foraging decisions (Chesson & Kuang 2008), whereas anti-predator investments should increase when resources are plentiful and prey have nutritional reserves (Hopcraft *et al.* 2010; Matassa & Trussell 2014). For example, Matassa *et al.* (2016) found that elevated resource (barnacle, *Semibalanus balanoides*) density strengthened anti-predator investment (refuge use) by sub-adult snails (*Nucella lapillus*) exposed to risk cues from predatory crabs (*Carcinus maenas*), presumably by augmenting prey state.

Fourth, interacting predator-prey pairs are unlikely to do so in isolation from other species, which may alter the focal prey species' responses to perceived risk. For instance, dwarf mongooses (*Helogale parvula*) displayed lower rates of anti-predator vigilance when in the presence of an avian co-forager, the drongo (*Dicrurus adsimilis*) (Sharpe *et al.* 2010). The presence of other predators may also affect the transmission of NCEs if prey species with conflicting predator-specific responses consequently reduce their investment in defense (Sih *et al.* 1998). In accord with predator facilitation (Charnov *et al.* 1976; Kotler *et al.* 1992; Korpimäki *et al.* 1996), for example, Meadows *et al.* (2017) showed that larval mosquitoes (*Culex pipiens*) abandoned diving behavior normally deployed to escape surface-hunting insect mesopredators when also exposed to a benthic predator (dragonfly naiads, *Aeshna* spp.).

Lastly, landscape properties may mediate how prey are affected by temporal variation in predation risk (**Box 2**). Many nocturnal animals, for example, decrease their activity on moonlit nights because of their increased exposure to visually-orienting predators, and this trend is accentuated in areas dominated by open habitats (Prugh & Golden 2014). Therefore, moonlight exacerbation of NCEs experienced by nocturnal prey species is likely to be inversely proportional to landscape cover availability. Landscapes also may influence temporal patterns of predation risk, and thus NCEs, over longer intervals. Seasonal variation in snow accumulation, for example, can give prey a temporary refuge or heighten vulnerability to predation by restricting mobility (Gorini *et al.* 2011). Not surprisingly, snow depth has been linked to prey risk taking (e.g., yarding in deer;

Nelson & Mech 1991).

Any of these environmental attributes, alone or in concert, can influence the kinds of anti-predator behaviors that manifest during phase two and that precipitate as indirect NCEs during phase three (Heithaus *et al.* 2009; Wirsing & Ripple 2011). Thus, direct and indirect non-consumptive relationships between the same suites of interacting predator and prey species may differ markedly as a function of landscape type. Trussell *et al.* (2006) determined, for example, that habitat type (availability of refugia) shaped how risk from crabs (*Carcinus maenas*) altered the foraging intensity of a snail (*Nucella lapillus*) and, consequently, the levels of consumption of the snails' resource (*S. balanoides*).

The magnitude of contingency

To quantify strength of contingency in NCEs, we conducted a meta-analysis of the relationship between four types of prey risk taking and a key hypothesized driver of context dependence: prey energetic state (Kotler *et al.* 2004; Schmitz & Trussell 2016; see **Box 3** for methods). Reduced energetic state resulted in significantly elevated prey risk taking in each behavioral dimension (**Fig. 4**). When in a compromised energetic state, prey subjected to predation risk tended to be more active ($d = 0.73$, $\pm 95\%$ CI = 0.32-1.14; $\ln RR = 0.34$, $\pm 95\%$ CI = 0.17-0.51), spend less time in refugia ($d = 0.95$, $\pm 95\%$ CI = 0.74-1.16; $\ln RR = 0.58$, $\pm 95\%$ CI = 0.46-0.71), invest more in foraging versus apprehension ($d = 0.84$, $\pm 95\%$ CI = 0.50-1.19; $\ln RR = 0.49$, $\pm 95\%$ CI = 0.22-0.77), and be more isolated from other group members ($d = 0.86$, $\pm 95\%$ CI = 0.29-1.42; $\ln RR = 0.42$, $\pm 95\%$ CI = 0.19-0.65) than conspecifics in better nutritional condition. The mean estimates of d suggest a medium/strong effect of reduced energetic state on prey activity, and strong effects on exposure, foraging investment, and isolation. We detected significant heterogeneity among studies exploring each risk-taking dimension: activity ($d : Q_{33} = 178.39$, $p < 0.001$; $\ln RR : Q_{33} = 88.04$, $p < 0.001$); exposure ($d : Q_{70} = 213.60$, $p < 0.001$; $\ln RR : Q_{70} = 369.66$, $p < 0.001$); foraging investment ($d : Q_{40} = 186.19$, $p < 0.001$; $\ln RR : Q_{40} = 924.42$, $p < 0.001$); isolation ($d : Q_9 = 34.85$, $p < 0.001$; $\ln RR : Q_9 = 57.06$, $p < 0.001$).

These results underscore the marked differences that can characterize risk taking by prey individuals with divergent energetic states, and by extension the pivotal role that prey condition plays as a mediator of direct NCEs in communities. Most of the studies included in this analysis examined small-bodied taxa in laboratory or small-scale mesocosm settings (Appendix S1 in Supporting Information), and we found few investigations of the indirect community consequences of state-mediated variation in prey risk taking. Accordingly, there remains need for studies quantifying the influence of energetic state on risk taking under field conditions, especially with larger-bodied species, and the degree to which disparate responses of prey in divergent nutritional states shape indirect predator NCEs. Furthermore, prey state was the only potential driver of contingency in prey anti-predator behavior subject to enough empirical investigation to support meta-analysis. Thus, we also encourage further work addressing other potential drivers of context dependent NCEs.

Our findings also revealed considerable variability in the magnitude and direction of the effect of prey condition on anti-predator behavior. Some studies in each of the four behavioral categories showed effects opposite the majority of studies. In these studies, anti-predator behavior increased with decreasing body condition or state of the prey (7 of 34 studies of activity; 7 of 71 for exposure; 5 of 41 for foraging investment; 1 of 10 for isolation). This variability may, in part, stem from the myriad means by, and circumstances under, which the experiments of the meta-analyses were conducted. The variability in results is also consistent with the idea that, during phase two, anti-predator behavior and the way it is shaped by context (including prey state) hinge on the relative safety benefits conferred by different behavioral options available to the prey species. Either increased or decreased activity, for example, can serve as effective anti-predator tactics depending on the hunting mode of the predator against which they are deployed (Schmitz 2007). Furthermore, if individuals in a low state are more vulnerable to predation, then they may adopt a higher level of antipredator investment (Raveh *et al.* 2011; Makon *et al. in press*). It is not surprising, then, that some studies we assessed found that sated prey exposed to predation risk became more active, and that food restriction diminished rather than exacerbated this response (e.g., Hossie & Murray 2011). Though beyond the scope

of this review, meta-regressions with covariates potentially influencing the efficacy of different anti-predator behaviors (e.g., predator type) would likely reduce some of the uncertainty characterizing our findings.

Conclusions and future directions

In a recent review of context-dependent species relationships, Chamberlain *et al.* (2014) called for increased scrutiny of the factors contributing to, and the ecological and evolutionary consequences of, variation in interaction outcomes. Focusing on non-consumptive predator-prey interactions, we address both of these knowledge gaps. First, we present new insights into NCEs by showing when and how contingency can arise from properties of the prey, the predator, and the setting as these effects unfold across three phases (prey risk perception; prey responses to perceived risk; impacts of these responses on other species). Second, while recognizing that there is more work to be done, we help to unravel the consequences of contingency by quantifying the extent to which prey energetic state drives differences in anti-predator behavior, and by spotlighting cases where variation in the outcome of non-consumptive predator-prey interaction has shaped the indirect NCEs experienced by other community members. Our synthesis also highlights two knowledge deficiencies – insufficient exploration of context-dependent indirect NCEs during phase three and the ways in which direct and indirect NCEs are shaped simultaneously, or even interactively, by multiple drivers of context dependence – that must be remedied if we are to develop a coherent framework for predicting NCEs.

Drawing from a broad literature spanning diverse taxa and ecosystems, our review reveals how contingencies in NCEs can arise as a result of many factors. It is hardly surprising, then, that studies have revealed so much variation with respect to whether, and in what way, NCEs manifest in communities (Moll *et al.* 2016; Schmitz 2017; Gaynor *et al.* 2019; Prugh *et al.* 2019). We clarify these factors by grouping them into three broad categories: (1) prey properties that influence detection of and responses to risk; (2) predator properties shaping their detectability and lethality; and (3) properties of the setting that influence the prey's scope for predator detection and countermeasures. We also emphasize that there is great potential for interplay among them. For example, divergent responses to predators with disparate hunting modes could disappear if declining food supply limits prey capacity for defensive investment. Similarly, because prey often have multiple defenses whose efficacies are context-specific (Britton *et al.* 2007; Wirsing *et al.* 2010; Wirsing & Ripple 2011; Schmitz 2017; Creel 2018), sympatric prey may respond divergently to a shared predator in one setting but similarly in another, depending on the availability of landscape features that facilitate particular responses (e.g., refuge space). Moreover, the latter two give rise to an emergent fourth driver, (4) the timing of predation risk, and prey properties then determine how individuals respond to this temporal dimension of danger (**Box 2**). By implication, predictions based on a single driver of contingency may provide an incomplete picture of the impacts of predation risk on prey populations and communities. Rather, examination of NCEs requires thorough consideration of the functional properties of interacting predator and prey species, as well as the circumstances under which these interactions occur (Heithaus *et al.* 2009; Wirsing *et al.* 2010; Creel 2011; Schmitz 2017). Fortunately, many of these natural history or environmental details are available or attainable (Wirsing *et al.* 2010), especially given new approaches (e.g., animal-borne video, camera traps, drones) that facilitate placing behavioral data in context (Moll *et al.* 2007; Wirsing & Heithaus 2014).

Our review also highlights the staged manner in which NCE contingencies can manifest. Namely, prey anti-predator investment may vary intra- and inter-specifically as a function of differences in sensory perception (phase one) and the form of any deployed countermeasures (phase two); contingent outcomes during either of the first two phases then determine if, and in what way, indirect NCEs emerge during phase three. Identifying the phase(s) in which context dependence arises is therefore crucial to predicting how the outcome of non-consumptive predator-prey interactions will respond to perturbation. For example, landscape changes that constrain prey habitat domains and raise the frequency of encounters with predators may elicit increased anti-predator defense during phase two (Schmitz *et al.* 2004; 2017a) and thereby elevate the potential for indirect NCEs in phase three. However, such changes would be expected to have minimal non-consumptive impact on prey species lacking the ability to detect risk cues during phase one, unless they also reshape the sensory environment. Thus, studies exploring the phase-specific mechanisms by which prey, predator,

and landscape properties shape anti-predator investment will strengthen a general framework for forecasting NCEs in a changing world.

Recent syntheses have quantified the degree to which NCEs vary as a function of resource competition (Bolnick & Preisser 2005), predator hunting mode and habitat domain (Preisser *et al.* 2007), resource dynamics (Preisser *et al.* 2009), and refuge availability (Orrock *et al.* 2013). The results of our meta-analysis add prey energetic state to the growing list of drivers whose strong impact on the outcomes of NCEs has been quantified across systems and taxa. Notably, our findings differ somewhat from those listed above because we addressed multiple forms of antipredator behavior and only chose experiments explicitly contrasting responses of prey individuals with different energetic states to risk. Hence, we offer novel insights into the manifold ways in which energetic state can shape patterns of anti-predator investment under conditions where the potentially confounding effects of differing environments and other prey traits have been minimized. Our findings also highlight the varied ways by which state-dependent variation in anti-predator behaviors might influence the manifestation of indirect NCEs during phase three – for example via differences in vigilance or space use – though these hypothetical scenarios remain to be evaluated empirically.

Our survey revealed two knowledge gaps that represent fruitful directions for future research. First, whereas there is ample evidence for context dependence during phases one and two, few studies have rigorously examined contingency in the propagation of indirect NCEs. There are notable examples, including the role of predator hunting mode in shaping indirect NCEs of spiders on plant and soil properties (Schmitz *et al.* 2017b), and the impact of the presence or absence of prey refugia on indirect non-consumptive relationships between crabs and barnacles (Trussell *et al.* 2006). These studies offer a template for expanded scrutiny of contingencies in NCEs during phase three, which will improve our understanding of when and how predators initiate indirect effects by altering prey traits.

Second, a growing literature underscores the importance of simultaneously considering multiple drivers of contingency in NCEs. For example, anti-predator investment by mud crabs varied with their personality (bold versus shy) and predator hunting mode (actively hunting blue crabs versus sit-and-wait toadfish, *Opsanus tau*) (Belgrad & Griffen 2016). Working in a large vertebrate system, Thaker *et al.* (2011) showed that small members of an African ungulate guild avoided all predators whereas their larger counterparts avoided sit-and-pursue but not active hunters. More work is needed, however, particularly on the importance of three-way interactions among factors drawn from the aforementioned groups.

There are also studies suggesting that interactive impacts of multiple contingent drivers may act collectively to shape indirect NCEs during phase three. For example, Murie & Bourdeau (2019) speculated that, compared to the strong effects initiated by slow-moving sea stars, the absence of direct and indirect non-consumptive effects of crabs and octopuses on snail grazing and kelp, respectively, might owe to the inability of snails to escape these vagile predators. By inference, more mobile prey species with greater scope for avoidance may have responded equivalently to all three predators, yielding similar rather than predator-specific cascades of NCEs. The possibility that interactions between context dependent factors might modify cascading NCEs has yet to be tested empirically, however, and thus remains as an exciting research frontier.

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Figure Legends

Fig. 1 . Flow chart, adapted from Figure 1 in Lima & Dill (1990), conceptualizing the process by which direct and indirect non-consumptive predator effects (NCEs) may manifest. (a) Phase one. Each point in space and time is characterized by some value of intrinsic predation risk, or danger, defined after Lank & Ydenberg (2003) as the inherent probability that an individual will become a prey item given no, or a standard amount of, anti-predator investment. Danger may or may not be perceived; in the latter case, no NCE will precipitate from the danger cue in question. (b) Phase two. Given that the forager perceives risk cues, does it respond? Danger that is perceived may nevertheless fail to elicit a response of sufficient magnitude to trigger a NCE. Though not the focus of this review, prey individuals that do respond to perceived danger may experience stress, which may in turn affect fitness and consequently lead to risk effects. Furthermore, prey individuals that perceive danger may seek to manage their risk of predation through behavioral modifications, whose costs in terms of time and energy determine the magnitude of any associated risk effects. (c) Phase three. Given that the forager responds to the cues, does the response induce an indirect interaction? Risk effects flowing from predator-induced stress and risk management can reduce prey population size and, in turn, trigger indirect interactions if changes to prey abundance affect other members of the community. The nature and strength of predator-induced risk management by prey can also determine whether and how other species in the community are affected indirectly; namely, if additional species are impacted by prey risk management, then NCEs can propagate through communities in the form of indirect interactions that are transmitted by prey behavior.

Fig. 2 . Observed (solid arrows) and hypothesized (dashed arrows) relationships between gray wolves (*Canis lupus*) and two sympatric ungulates – mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) – in areas of eastern Washington, USA, located outside (a, c) and inside (b, d) wolf pack territories. Non-consumptive effects of wolves on prey behavior (relative to wolf-free sites; a) are depicted in b, whereas c and d display baseline and wolf-influenced tropic relationships between the herbivores and the plants they target, respectively. Increasing effect size corresponds with arrow thickness. Mule and white-tailed deer are morphologically similar but have different running gaits (Lingle 1993). When threatened, mule deer flee by stotting, a bounding gait that limits speed on flat ground but facilitates navigation of uneven terrain and obstacles. White-tailed deer flee danger by galloping, a swift means of moving over gentle terrain that is less effective where the ground is more sloped or broken. This disparity explains differences in the space use of these two deer species that emerge when they are exposed to the risk from wolf predation during phase two (b versus a). Working in a system in eastern Washington, USA, Dellinger *et al.* (2019) found that wolf presence elicited elevated use of sloped terrain by mule deer (b; heavy arrow), presumably because the uneven ground characterizing these uplands confers an advantage to bounding prey seeking to escape coursing wolves. White-tailed deer space use differed comparatively little as a function of wolf presence, with individuals exposed to wolf risk manifesting small-scale shifts within their home ranges toward flat ground and roads that actually led to increased overlap with wolves (b; thin arrow). By inference, white-tailed deer were able to manage risk ‘in place’ because of spatial synchrony between the effectiveness of their galloping means of escape and the space use pattern of their coursing predator. Notably, this form of risk management is expected whenever the safety benefits of matching predator distribution that accrue from escape facilitation outweigh the costs associated with elevated encounter probability (Lima 1992). These divergent anti-predator responses raise the possibility of recolonizing wolves triggering prey-specific indirect NCEs on plants during phase three (c versus d). In this ecosystem, mule and white-tailed deer exhibit considerable dietary overlap, though mule deer rely more heavily on upland shrubs (e.g., serviceberry; *Amelanchier* spp), and white-tailed deer exploit lowland riparian vegetation (e.g., willow; *Salix* spp.) to a greater degree (A. Craig, *unpublished*

data). Given that they elicit broad-scale spatial shifts by mule deer, wolves may dampen the impact of mule deer on lowland plant species (*d*; thin dashed arrow) while strengthening this species' effects on upland plants growing in areas with steeper slopes (*d*; thick dashed arrow). By contrast, the absence of a strong spatial response by white-tailed deer in areas occupied by wolf packs suggests that wolves may have modest and localized (i.e., within existing home ranges) indirect effects on the plants exploited by this deer species (similarity in the thickness of the solid and dashed arrows in *c* and *d*).

Fig. 3. Observed (solid arrows) and hypothesized (dashed arrows) relationships between tiger sharks (*Galeocerdo cuvier*), their air-breathing prey – dugongs (*Dugong dugon*), dolphins (*Tursiops* cf. *aduncus*), green turtles (*Chelonia mydas*), sea snakes (*Disteria major*; not pictured), pied cormorants (*Phalacrocorax varius*) – omnivorous fish (*Pelates octolineatus*), and seagrasses within shallow (<4.5m water depth) habitats in Shark Bay, Western Australia. Species interactions are depicted during times when tiger sharks are present and absent from the bay, and interaction effect sizes correspond with arrow thickness. When tiger sharks are present, they preferentially spend time over shallow banks (Heithaus *et al.* 2002). Within these shallow habitats, they spend more time over bank edges compared to interior areas of banks (Heithaus *et al.* 2006). Non-consumptive direct effects of sharks on prey behavior (phase two) are black lines, whereas indirect relationships between tiger shark prey and lower trophic levels are gray lines (phase three). Dugongs (Wirsing *et al.* 2007), cormorants (Heithaus *et al.* 2009), dolphins (Heithaus & Dill 2006), and sea snakes (Wirsing & Heithaus 2009) distribute themselves between edge and interior portions (microhabitats) of shallow banks roughly proportional to food abundance when tiger sharks are absent. When sharks are present, by contrast, these species, along with green turtles (Heithaus *et al.* 2007), shift among the two microhabitats to enhance safety. Their spatial shifts during phase two, however, are based on species-specific escape tactics. Green turtles, dugongs, and dolphins escape through sub-surface flight and rely on maneuverability that is constrained over interior portions of banks. Accordingly, these species move into bank edges when tiger sharks are present to facilitate escape even at the cost of higher encounter rates with sharks (Heithaus *et al.* 2009). Conversely, sea snakes, which are unlikely to escape a tiger shark, and cormorants, which escape by flying away, shift toward interior areas of banks where shark encounters are minimized. For green turtles, habitat use is state-dependent with turtles in better condition selecting safer areas of banks with less food (Heithaus *et al.* 2007). Experimental studies of herbivory (Burkholder *et al.* 2013; Bessey *et al.* 2016) show that these spatial shifts cascade to seagrass communities during phase three.

Fig. 4. Results of meta-analyses using two effect size metrics, Hedges' *d* (black boxes) and log response ratios (gray boxes), to examine relationships between compromised energetic state and four dimensions of risk taking by prey under threat of predation: activity (*n* = 30 studies making 34 species-specific contrasts); exposure (versus use of a refuge; *n* = 68 studies making 71 contrasts); foraging investment (versus apprehension; *n* = 37 studies making 41 contrasts); isolation (versus grouping/shoaling; *n* = 10 studies presenting 10 contrasts). For each dimension, positive effect size values quantify the extent to which risk taking by energetically compromised prey individuals subjected to a predation threat exceeded that of conspecifics in better condition. Mean effect sizes and accompanying 95% confidence intervals were calculated using random effects models in *OpenMEE*; confidence intervals not overlapping zero were considered to indicate significant effects.

Fig. 1

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Fig. 2

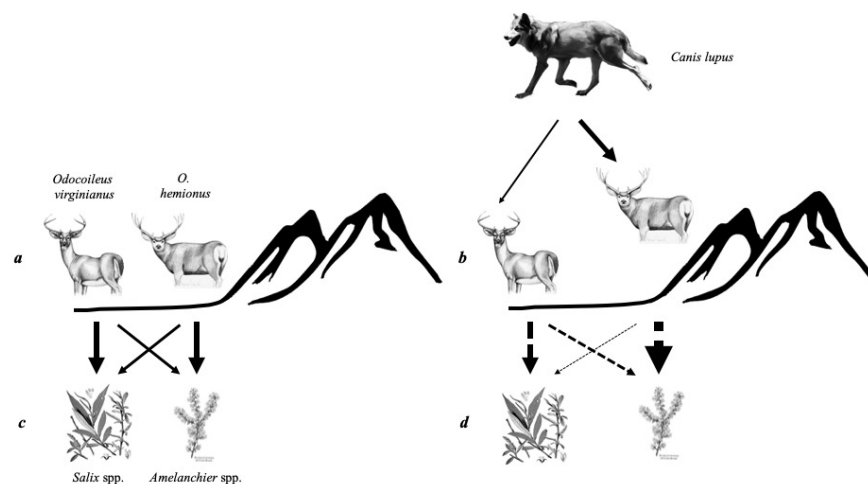
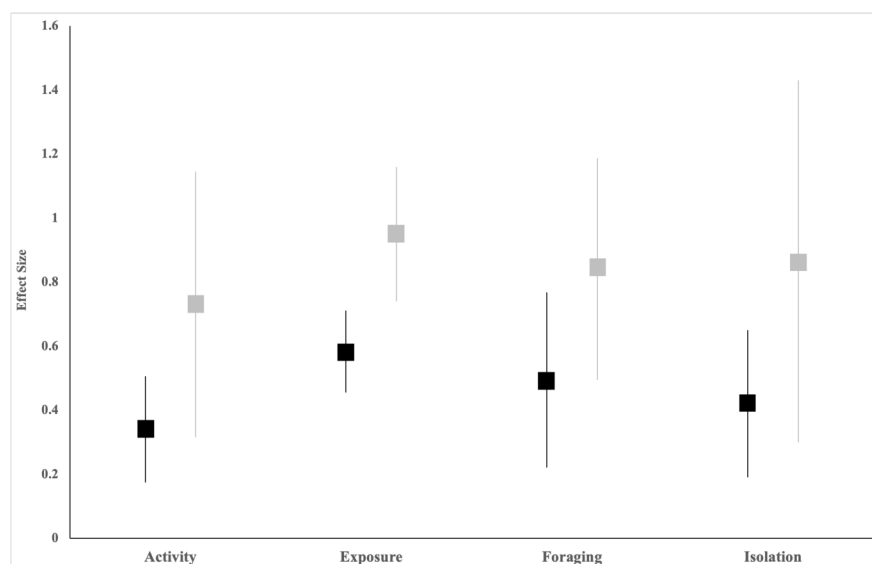


Fig. 3

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Fig. 4



Box 1 : State dependent foraging games between gerbil prey and owl predators

The interaction of predator and prey is a state-dependent foraging game where the prey must manage risk using time allocation and vigilance (Brown 1999), and the predators must manage fear: as prey become more afraid, they become less catchable. The predator's tools include time allocation and derring-do; a more daring predator is more willing to risk injury in order to capture its prey (Brown *et al.* 2016). Here we focus on Allenby's gerbil (*Gerbillus andersoni allenbyi*), a nocturnal rodent of sand dunes in the Middle East, and its barn owl (*Tyto alba*) predator. Within an outdoor vivarium (17 x 34 x 4.5 m), it is possible to

manipulate the energetic states, and subsequently quantify the foraging behavior, of both gerbils and owls (Kotler *et al.* . 2004).

In theory, a forager should exploit depletable resource patches until the benefits of its harvest rate no longer exceed the sum of energetic, predation, and missed opportunity costs of foraging (Brown 1988). The food density at which this occurs is called the giving-up density (GUD) and is a behavioral indicator of foraging costs for that context. Energetic costs of foraging and risk factors should all lead to higher GUDs, and do so in gerbils (Kotler *et al.* . 1991; Kotler *et al.* . 1993). The predation cost is highly state-dependent as it equals predation risk multiplied by the survivor's fitness divided by the marginal value of the food. Hungry animals and those in a low state or with poor prospects should be less fearful and have lower GUDs.

In vivarium experiments, gerbils that received supplemental food, relative to those that did not, used food patches less intensively, had higher GUDs, and avoided risky open microhabitat (Kotler 1997; Kotler *et al.* . 2004). These effects carried over into the subsequent night when no gerbils received supplemental food. Gerbils that had received supplemental food previously responded more strongly to owls than those that did not (Kotler 1997). These results show how a higher energetic state acts to magnify foraging costs and alter behaviors, ultimately leading to diminished risk taking during phase two.

Tracking gerbil foraging over the course of lunar cycles revealed the dynamic nature of risk management and feedbacks with state (Kotler *et al.* . 2010). Starting at new moon, as the moon waxes, gerbils increased vigilance to counter the greater ease of predator encounter, and reduced their time allocation to limit their exposure to predators; they sacrificed state to buy safety. By full moon, the gerbils upped vigilance even more, but increased time foraging; they defended state to guard against starvation. As the moon waned, gerbils decreased vigilance and increased foraging time to rebuild state. By new moon, vigilance was at a minimum, and foraging time began to decline; state had been rebuilt in time for another cycle (Kotler *et al.* . 2010).

Prey foraging behavior also depends on the interaction between the state of the prey and that of predator. Using vivarium experiments, Berger-Tal & Kotler (2010) showed that hungry barn owls (*Tyto alba*) were 4-7 times more active than their satiated counterparts. Gerbils responded to this increase in predator activity by visiting fewer patches and leaving them at higher GUDs, but only when in high energetic state (Berger-Tal *et al.* . 2010).

Predators, too, consider their state as well as that of their prey. Hungry owls, for example, showed derring-do by performing dangerous attack maneuvers (plunging into areas with stiff, spikey experimental shrubs) more than twice as often as well-fed conspecifics (Embar *et al.* . 2014a). Moreover, owls choose between well-fed and hungry gerbils (Embar *et al.* . 2014b). In spring when gerbils were reproductive, owls favored well-fed gerbils; in the summer when they were months away from breeding, owls favored hungry gerbils. That may seem odd, but well-fed gerbils are more active in spring when energy supports offspring, and hungry gerbils are more active than well-fed gerbils in summer when survivorship to the next reproductive season is paramount. Owls, when given the choice between gerbils with fleas and gerbils without, chose the more active flea-free gerbils (Raveh 2018). In all cases, then, owls sought more active prey.

In summary, foraging games between gerbils and their predators are contingent on environmental factors such as microhabitat and moon phase and biotic factors such as the energetic states of predators and prey. Prey manage risk, predators manage fear, and these actions feed back between the players and the environment throughout each night (Kotler *et al.* . 2002), across moon phases (Kotler *et al.* . 2002, 2010), and over the seasons (Kotler *et al.* . 2004).

Box 2 : The timing of predation risk as an emergent driver of contingency in NCEs

How prey invest in defense at any given time during phase two (prey response to perceived risk) may depend on the temporal pattern of intrinsic predation risk. Namely, according to the risk allocation hypothesis, defensive investment should be greatest in response to transient pulses of high risk against a background of relative safety (given that periods during which safe feeding can occur should soon return), and reduced when

pulses of safety occur against a background of elevated danger (Lima & Bednekoff 1999). By implication, prey in systems where predation danger is highly punctuated may be able to compensate for heavy anti-predator investment when predators are most active (and/or lethal) by feeding during periods of predator inactivity. For example, vicuñas (*Vicugna vicugna*) exploit puma (*Puma concolor*) downtimes (during the day) to utilize their feeding grounds but avoid these densely-vegetated areas when low light levels and ample stalking cover combine to enhance puma lethality (Smith *et al.* 2019). Under these circumstances, demographic risk effects experienced by prey populations and the potential for prey to transmit indirect NCEs during phase three may be limited (Kohl *et al.* 2018).

To date, empirical support for the risk allocation hypothesis has been mixed (Ferrari *et al.* 2009), perhaps in part because prey condition in some assessments has been high enough to allow for continuous anti-predator investment even when risk is chronic (Matassa & Trussell 2014), or because some focal prey species were not given sufficient time to learn the risk regime (Moll *et al.* 2017). Our review offers an additional, non-mutually exclusive explanation. Namely, the temporal pattern of intrinsic risk experienced by a prey individual is an emergent outcome of the interaction between the properties (e.g., activity) of the predator(s) by which it is threatened and setting in which an encounter might take place. Moreover, as outlined earlier, the response of any prey individual/species to perceived intrinsic danger cues during phase two hinges on its own properties (e.g., escape tactics). Thus, proper quantification of the temporal pattern of risk and how prey should respond to perceived stimuli in any situation requires explicit consideration of each of these drivers of context dependence, as well as their interplay. It is possible that, lacking the capacity to be this comprehensive, some prior tests of the risk allocation hypothesis may have misrepresented the temporal pattern of risk. We view studies exploring this possibility as a fruitful line of inquiry. In the meantime, a recent investigation by Dröge *et al.* (2018) offers a path forward, at least in terms of accounting for predator properties. Namely, their ability to explain vigilance responses by African ungulates was greatest when immediate risk stimuli (predator proximity) were considered in relation to patterns of long-term risk associated specifically with the approaching predator species rather than the predator guild overall.

Box 3 : Methodology for the meta-analysis exploring contingent relationships between prey energetic state and risk taking

As the basis for our meta-analysis, we searched the literature using the bibliographic sources BIOSIS Previews, Google Scholar, and Web of Science using search terms for each engine were ‘predator’ OR ‘predation’ AND ‘prey’ AND ‘risk taking’ OR ‘behavior’ AND ‘state’ OR ‘condition’ OR ‘hunger’ OR ‘nutrition’ OR ‘food’. We then screened all resulting studies to ensure that they (i) manipulated prey state directly (e.g., via starvation or nutritional supplementation of individuals) or indirectly (e.g., by contrasting behavior of individuals in environments offering different amounts of food); (ii) exposed prey to direct (e.g., live or model predators) or indirect (different amounts of cover) predation risk cues; (iii) presented comparisons of some form of risk-taking behavior by prey individuals with divergent energetic states that were not confounded by differences with respect to development, experience/learning, parasite load, personality/temperament, reproductive state, sex, or size; and (iv) included means, measures of variance, and sample sizes required for calculating effect sizes. Separate experiments addressing different species within the same study were considered to be independent.

After filtering, our review of the literature yielded a total of 145 studies spanning a broad range of taxa and presenting 156 unambiguous, species-specific contrasts of risk-taking behavior manifested by prey individuals with disparate energetic states (see Appendix S1 in Supporting Information). The risk-taking behaviors addressed by these studies clustered into four categories, which we analyzed separately: activity ($n = 30$ studies making 34 species-specific contrasts); exposure ($n = 68$ studies making 71 contrasts); foraging investment (at the expense of apprehension; $n = 37$ studies making 41 contrasts); and isolation (versus grouping/shoaling; $n = 10$ studies presenting 10 contrasts). For the studies quantifying prey activity (movement), response metrics included time spent active or latency to resume activity after exposure to a predation risk cue for individuals, as well as the proportion of individuals in a group engaged in activity. Risk-taking responses addressed by studies of exposure were either time spent or the proportion of individuals not hiding, outside

of a refuge, or in a dangerous versus safe area/patch. Studies addressing foraging investment quantified several feeding behaviors expected to influence vulnerability to predation: namely, feeding motivation (attack distance or latency to feed), feeding time, giving-up densities (GUDS; with greater amounts of food consumed corresponding to heightened foraging activity), and the proportion of individuals feeding. Studies of isolation quantified risk taking in terms of group cohesion (e.g., nearest neighbor distance) or size. For each of these four dimensions of risk taking, we first scaled all measures such that higher values corresponded with increased risk taking. Then, we assessed the across-study effects of prey energetic state on risk taking using two effect size metrics: Hedges' d (Hedges & Olkin 1985) and log response ratios (lnRR, Hedges *et al.* 1999). For Hedges' d , we interpreted effect sizes of 0.2 to be “small”, 0.5 to be “medium”, 0.8 to be “large”, and any exceeding 1 to be “very large” (Gurevitch & Hedges 1993). Estimates of both effect sizes were considered to be statistically significant if their 95% confidence intervals did not overlap zero. For each of the four dimensions of risk taking, we calculated mean effect sizes for each effect size metric using random effects models in *OpenMEE* (Wallace *et al.* 2017). We also tested for publication bias with Spearman's rank-order correlations; no test was significant (all p [?] 0.076), so we did not use funnel plots to remove outliers from any of our four sub-analyses (Begg & Mazumdar 1994). Finally, our meta-analyses of activity, exposure, and foraging investment included a few papers presented behavioral contrasts of more than one species. Given that these contrasts may not have been independent (Gurevitch & Hedges 1999), we conducted truncated meta-analyses for the three aforementioned risk-taking dimensions that included only one randomly-selected contrast from each study addressing multiple species. Owing to close agreement between our full and truncated analyses, we only present results from the full analyses below.