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Title: An integrated framework for unifying our understanding of nonconsumptive predation risk effects

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Open Research Statement: Empirical data were not used for this research. Code is available from Github: https://github.com/davidsonat/2026_Ecology_IREF_InPrep

Key words: ecology of fear; nonconsumptive; nonlethal; phenotypic plasticity; predation-risk; sublethal; trait-mediated; defensive traits

Abstract

Predation risk can induce risk-induced trait responses (RITRs) – changes in prey defensive traits including behavior, morphology, life history, and physiology – thought to have profound effects on prey fitness and population dynamics (termed ‘nonconsumptive effects’). Yet, predicting the magnitude of RITRs and their fitness consequences remains difficult because outcomes depend heavily on ecological context and processes that influence the costs and benefits of defensive trait changes costs, all of which vary greatly. To address this, we present the Integrated Risk-Effects Framework (IREF), an intuitive graphical framework that incorporates fitness components related to the benefits and costs of the RITR to identify the optimal trait value and costs to prey fitness (NCEs) and effects on predation mortality (termed ‘consumptive effects’, CEs). The IREF is designed with the objectives of 1) guiding researchers in explicitly and quantitatively describing the biology underlying risk effects; 2) helping generate process-based, theory-driven hypotheses about the occurrence and magnitude of risk effects; and 3) using standardized and intuitive structures and vocabulary to communicate and synthesize hypotheses about risk effects across systems.

Applying the framework to canonical cases (prey displacement and refuge use), we show that it recovers classic expectations (e.g., effects of predator hunting mode) while generating new, testable predictions. Specifically, we demonstrate that 1) the prey’s resource-processing rate shifts optimal defensive investment and the relative contribution of NCEs versus CEs to fitness outcomes; 2) prey satiation can transform predicted refuge use from boundary solutions to intermediate optima; 3) different factors that increase predation risk can move trait optima in opposite directions; and 4) in the same system, a predator density increase may lead to no, to large, to negligible increases in RITRs and NCEs, depending on initial predator density. By

unifying trait costs, predation risk, and fitness consequences within a common graphical structure, the IREF provides a transparent tool for synthesizing risk effects and generating mechanistic hypotheses across ecological contexts.

Introduction

Predators impact prey populations by consuming prey, but also by inducing changes in prey defensive traits (also known as anti-predator traits) that mitigate predation risk, hereafter referred to as *risk-induced trait responses* (RITRs). RITRs can manifest in prey behavior, morphology, physiology, and/or life history. The prevailing narrative in ecology is that prey RITRs can have profound effects on prey fitness and population dynamics (termed *nonconsumptive effects*, or NCEs), and the dynamics of species that those prey interact with (termed *trait-mediated indirect effects*, or TMIEs), rivaling or even exceeding the strength of direct consumption by predators (Werner & Peacor, 2003; Preisser et al., 2005; Sheriff et al., 2020). This narrative has led to an explosion of interest in risk effects (i.e., RITRs, NCEs, and TMIEs) over the past several decades, resulting in thousands of articles on the topic (Peacor et al., 2022), reinterpretation of classic studies (e.g., Peckarsky et al., 2008), and numerous reviews of the importance of risk effects in general (e.g., Werner and Peacor, 2003; Preisser et al., 2005; Wirsing et al., 2021), and in specific taxa or systems (e.g., Hermann & Landis, 2017; Mitchell & Harborne, 2020).

In stark contrast to this narrative, few studies have provided direct evidence of the influence of risk effects in nature by linking the processes underlying risk effects to patterns in natural prey populations or communities (Peers et al., 2018; Peacor et al., 2022). For example, Peacor et al. (2022), in a review of the literature from 1990 to 2018, found only three studies that examined the influence of risk effects on prey abundance in unmanipulated natural systems. Rather, the great majority of studies are experimental (Sheriff et al., 2020; Peacor et al., 2022) and thus most commonly conducted in simplified systems and over short periods of time. Therefore, it could be argued that risk effects research remains largely hypothetical, and that the discipline has not convincingly shown the need to consider their influence in natural systems, at least not routinely. Perhaps it is for these reasons that risk effects are rarely included in models of trophic population dynamics or species interactions (other than those that directly study risk effects) and are, to our knowledge, never considered in natural resource management.

Perhaps less obvious is the lack of generalized rules and predictive power concerning whether risk effects are expected, and if so, their relative strength (but see Creel, 2011; Schmitz et al., 2017; Wirsing et al., 2021). Several studies have made predictions concerning the effects of different factors, such as predator foraging mode (Schmitz et al., 2004; Schmitz, 2008) and competitor characteristics (Peacor & Werner, 2000), on the nature and magnitude of risk effects. Nevertheless, the great majority of studies on risk effects are not based on a common underlying theoretical framework, often relying on informal verbal models that lack a robust quantitative basis and clearly defined assumptions (Peckham et al., in review). Further, many studies that examine risk effects are founded on *a priori* knowledge or observations supporting the potential occurrence of NCEs within a given study system, without considering why they may or may not be present, and what environmental or species-level traits might explain their presence or absence.

What is more established is the difficulty in formulating predictions due to the complexity and highly context-dependent nature of risk effects. For example, experimental findings challenge even the intuitive prediction that more voracious predators (i.e., those that kill prey at a higher rate) will lead to larger risk effects (Creel & Christianson, 2008; Peacor et al., 2025). Further, there are no general relationships analogous to Hollings functional relationships (Holling, 1959; Holling, 1965) guiding the discipline, and yet such general relationships should be expected as risk effects are based on general principles that apply across diverse systems. For example, we might predict the functional relationship between fitness costs and the magnitude of trait responses to be similar for biologically different trait responses, which could lead to similar predictions of the magnitude of the optimal trait response and ensuing NCEs on prey fitness. Such categorization could help both in making predictions within particular systems and synthesizing across systems.

We are therefore limited in our ability to effectively synthesize and build on existing knowledge on risk effects. This limits the ability to address questions regarding whether risk effects are universally important and should be included in conservation and management models, and to examine their role in particular systems. We address these limitations by developing a graphical framework, termed the Integrated Risk Effects Framework (IREF). The main goal of the IREF is to provide an accessible and intuitive approach that enables empirical work to be based on a common theoretical framework. The IREF leverages existing classical theory describing the optimal strategy of fitness-maximizing prey and presents predictions in an intuitive graphical format (we hope akin to the theory of island biogeography, MacArthur & Wilson, 1963; Brown & Lomolino, 1989; or Holling's functional responses, Holling, 1959; Holling, 1965). The IREF translates mechanistically disparate, often context-dependent processes underlying different RITRs into a common language of fitness trade-offs faced by the prey. The IREF is developed with the following three objectives in mind:

1) to guide researchers in explicitly and quantitatively describing the biology of their systems, including addressing key underlying relationships, clarifying assumptions and abstractions made concerning predictions, and encouraging translation of that biology to quantitative representation;
2) to help generate process-based, theory-driven hypotheses about the occurrence and magnitude of risk effects and associated context dependences; and
3) to use standardized and intuitive structures and vocabulary that will facilitate communication of risk effect ecology (processes and underlying scenarios and assumptions), and thus facilitate effective and efficient peer review process, and synthesis across systems.

We illustrate the IREF, and how it addresses each objective, with case studies that explore risk effects across systems with different RITRs, predator traits, prey traits, and other environmental contexts. In so doing, our case studies accurately reproduce existing hypotheses (e.g., the effects of predator foraging mode) and also develop several novel ones including the effects of prey resource-processing rate and prey satiation. While informative in themselves, our main goal in developing the novel hypotheses is to illustrate how the IREF can foster hypothesis building.

The IREF: An Intuitive Graphical Model

The IREF is based on theoretical foundations provided by published models that share common properties and describe the RITR of fitness-maximizing prey (e.g., Mangel & Clark, 1986; McNamara & Houston, 1992; Houston et al., 1993; Lima & Bednekoff 1999). These models operate on the assumption that prey adjust the expression of plastic defensive traits (e.g., plasticity in behavior, morphology, etc.), as a function of the level of predation risk they experience, in a way that will maximize their fitness. These trait responses carry costs and benefits for fitness that can be explicitly defined. We hold that by relying on these fundamental relationships and a shared currency of fitness gains and losses, we can describe and compare risk effects across a broad range of system contexts despite the seemingly disparate biological mechanisms underlying them.

The IREF has three main elements: 1) describing the relationships between prey defensive trait expression and its costs and benefits to fitness, 2) using these relationships to calculate the level of trait expression that optimizes prey fitness, and 3) examining the relative strength of NCEs and CEs at that optimum. Here, we define "fitness" as the difference between prey per capita growth and mortality due to predation from the focal predator (Box 1) – thus, prey achieve "optimal" fitness by expressing RITRs in a way that maximizes this difference (though the IREF is flexible to other optimizing methods, see Discussion). Expressing a RITR carries costs to the prey's fitness, which may stem from a reduction in the prey's access to resources, changes to the parameters of the prey's functional response (e.g., reduced search rate or increased handling time), a reduction in resource conversion efficiency, and/or an increase in mortality from other factors, including other predators. Meanwhile, the benefit of the RITR stems from reduced predation from the focal predator – for example, due to a decrease in the prey's exposure to its predator and/or from changes to the predator's ability to effectively search for, capture, and handle prey (Prokopenko et al., 2023). Hence, using this framework, we can capture the fitness costs and benefits associated with prey expression of defensive trait by explicitly defining the relationships between expression of that trait and terms affecting prey growth and predation.

Each of the three elements serve at least one of the objectives of the IREF provided above. In Element 1, the process of describing the costs and benefits of the RITR quantitatively using trait curves (as described below) is vital to Objective 1 and a core part of translating risk effects into a shared and directly comparable language of fitness gains and losses, thus addressing Objective 3. In Element 2, determining the optimal RITR allows us to generate predictions about how different system contexts impact these interactions, serving Objective 2. In Element 3, deriving the relative strength of NCEs and CEs at the optimal RITR serves to further flesh out predictions about the effects of different system contexts on risk effects (in line with Objective 2), and more directly serves Objective 3 by framing these predator effects in a way that is directly comparable across different systems.

Quantitatively defining the relationships between prey defensive trait expression and the fitness components (i.e., growth and predation; Element 1) is central to risk-effects theory and the IREF (Fig. 1). We describe these relationships graphically using curves in which the fitness components (y-axis) are plotted as a function of trait expression (x-axis), and we denote these relationships as “fitness component-trait curves” (or “trait curves” for short), for which there is a predation-trait curve and a growth-trait curve (Fig. 1a; dotted red and solid blue line, respectively). The predation-trait curve describes the relationship between trait expression and the per capita rate (or probability) of predation by the focal predator. The growth-trait curve captures all other costs and benefits to the prey’s per capita growth rate; the fitness associated with expressing the trait, excluding direct predation by the focal predator. We chose the term “growth-trait curve” for lack of a better alternative, as it can include mortality factors, including predation-driven mortality by other predators. The y-intercept of both curves is the level of trait expression which provides the least protection from the focal predator (RITR = 0), whereas moving right (increased RITR) represents higher protection from predation. A major strength of the IREF lies in the ability to draw comparisons based on these functional forms – i.e., we expect that the trait curves of mechanistically different RITRs (e.g., behavioral vs. life history) may share the same general shape, allowing for potential generalization across systems (Objective 3).

The optimal level of prey trait expression is defined (Element 2) as the trait value where fitness is maximized. We define prey fitness (but see Discussion for alternatives) as:

$$fitness = growth - mortality \tag{1}$$

A fitness curve is this difference as a function of the trait value, with the optimal trait being at the maximum fitness level (Fig. 1b, dashed green line). After determining the optimal RITR, we can then determine the predator's CE and NCE at that optimum (Fig. 1c; Element 3). The CE is the value (height) of the predation-trait curve, whereas the NCE is the reduction in growth at the optimal trait value relative to its value at RITR = 0 (no risk response). These trait curves are fundamental (particularly to Objectives 1 and 3), because they make the costs and benefits associated with responding to risk quantitatively explicit. Thus, the researcher must carefully consider the biology of their systems (e.g., Table 1) when determining the shapes of the growth and predation-trait curves. We outline three general approaches to determining trait curves, while noting that the most powerful approach would be to combine all three.

One method for deriving trait curves is the use of verbal models (e.g., as in Abrams, 1984). For example, in the first set of case studies below, we consider a prey that reduces its displacement rate (representing foraging activity level) in response to predation risk. In this case, as we move along the x-axis in Fig. 1 from left to right, prey displacement rate decreases from a maximum (the baseline in the absence of risk response) to its minimum, which we assume is zero. At its simplest, we might assume that reducing displacement rate will lead to a linear decrease in predation risk at the cost of a corresponding linear decrease in growth, because prey will also encounter resources less frequently at lower displacement rates. However, this assumption may not accurately reflect the biological context of many ecosystems (see Table 1). For example, many animals require time to handle and digest their food (Jeschke et al. 2004), which may limit how much they benefit from increasing their displacement rate beyond a point. Rather than a linear growth-trait curve, this kind of system is best described using a concave-down curve (Fig. 1, more details follow).

A second method for deriving trait curves is to rely on formal theory. For example, in the above case, our verbal model lines up well with quantitative theory that formalizes this biological phenomenon – Holling's Type II Functional Response (Holling, 1959; Holling, 1965). There is a rich body of theoretical work built from Holling's functional responses that could be leveraged here to build predation-trait curves, describing how prey traits (e.g., activity rate, Werner & Anholt, 1993; defensive structures, Jeschke & Tollrian, 2000; body size, McCoy et al., 2011) influence their vulnerability to predation. Similarly, growth-trait curves could be parameterized using the language of functional responses if the RITR impacts the rate at which prey forage for and handle their own food resources. We encourage looking to theory to formalize the mathematical components underlying trait curves whenever possible.

A third method for deriving trait curves is to do so directly from empirical data. For example, increasing use of safer habitat patches (the trait) in sage grouse causes brood success (a component of growth) to decline sigmoidally (Sandford et al., 2017). In bison, deer, and elk, vigilance propensity (the trait) reduces predation risk but leads to a linear decline in foraging rate (a component of growth; Fortin et al., 2004; Ellsworth et al., 2024). Similarly, in salmon, foraging in larger groups (the trait) reduces predation risk, but foraging efficiency (a component of growth) decreases with group size in a decelerating fashion (Hintz & Lonzarich, 2018).

Case Studies

The case studies we describe below demonstrate the IREF, the process of applying its three main elements, and how it can be used to generate process-based, theory-driven hypotheses about the occurrence and magnitude of risk effects (e.g. optimal trait expression, CE and NCE strength, and overall predator effects on fitness) under different system contexts. Specifically, in Case 1, the prey's defensive trait is to reduce its displacement rate (leading to reduced encounter rates with both predators and resources). We describe the biology of this RITR with trait curves derived from first-principles theory (in line with Objective 1) and compare the effects of predator density, predator foraging mode, and prey resource-processing rate on the resulting optimal RITR and the strength of NCEs and CEs (in line with Objectives 2). Further, we demonstrate the IREF's ability to generate predictions about both the relative magnitude and occurrence of risk effects in line with Objective 2, and how the IREF can help us make comparisons across similar systems with different predator and prey traits in line with Objective 3. In Case 2, the prey's defensive trait is spending time in a refuge habitat, where predation risk is lower but conditions for growth are poorer due to a lower quality or quantity of resources. We illustrate the process of applying the IREF to this system, with the aim of exploring how the IREF can assist in explicitly describing the biology of the system. We demonstrate how our choice of trait curves can be shaped by our modeling assumptions (in line with Objective 1), and how that can lead to different predictions about the optimal RITR and the strength of NCEs and CEs (in line with Objective 2).

We chose these cases not to focus on the effect of these RITRs or system contexts in particular, but rather to demonstrate the IREF's application via its three main elements, as well as how its approach addresses the objectives provided above. We opted for different RITRs and system contexts, some of which are already well-known predictors of NCE and CE strength (i.e., predator density; predator foraging mode, e.g. Schmitz, 2008), which we reproduce using the IREF to highlight its ability to formalize and further explore these predictions. However, to our knowledge, no studies have explored how prey foraging characteristics, such as resource-processing rate, influence the relative strength of CEs and NCEs.

Case 1. Prey Displacement Rate: Exploring Context-Dependence in NCEs

In our first case, we consider a prey species that responds to predation risk by changing how active it is across the landscape, measured as displacement rate, s (Figs. 2-4). Below, we use the verbal model approach to predict trait-curves and then formalize and strengthen the predictions with quantitative theory (i.e., the second method described above). We then consider three instances where different system characteristics (i.e., contexts) change the prey's predicted optimal RITR and the strength of CEs and NCEs. Specifically, we explored how predator density (P; Eqn. 4, Fig. 2), predator foraging mode (v; Eqn. 3, Fig. 3), and prey resource-processing rate ($1/h$; Eqn. 2, Fig. 4) influence risk effects in this system. We chose these three characteristics because the former two are well-studied drivers of risk effects that we can use to demonstrate the IREF's operation, while the third is a novel characteristic that, to our knowledge, has not been explored in the context of risk effects. For each system characteristic, we derive the optimal RITR by calculating the point at which fitness is maximized, and we then observe the relative strength of NCEs and CEs at the optimum. While we could have manipulated other functional response parameters, or combinations of parameters, this study is not intended to be an exhaustive exploration of the parameter space – it is instead an illustrative guide to the IREF and its utility.

1a. Deriving Trait Curves

Prey that express a lower s (displacement rate) encounter predators less frequently. Therefore, moving along the x-axis from left to right, s is represented as *decreasing* from its y-intercept (1000 length/time; arbitrary magnitude), where prey exhibit no RITR and predation is thus at its highest (e.g., Fig. 2a), to lower s (i.e. higher defensive trait expression).

We can construct a verbal model of the growth-trait curve from first principles. At high s, prey frequently encounter resources, and hence growth would be limited by resource handling time, but at lower s, resource encounter rate becomes more limiting. We thus predict that a unit reduction in s should have a larger impact when s is already low (right-hand side of the x-axis), leading to a steeper growth-trait curve at low s. It is a simple matter to model this relationship (Fig. 2a, solid blue line) quantitatively by using a Type II functional response (Holling, 1959; Holling, 1965) as displayed by many animals (Jeschke et al., 2004):

$$f_C(R) = \frac{s \cdot d \cdot R}{1 + s \cdot d \cdot h \cdot R} \tag{2}$$

where d is the prey's resource-detection diameter (such that $s \cdot d$ is the search rate), R is prey resource density, and h is the prey's handling time of the resource. For simplicity, we assume that 'growth' is linearly proportional to resource-consumption rate and consider R and d to be constant in all of the following scenarios. This theoretical relationship (Eqn. 2) captures the biology of the system that we described verbally, yielding a decelerating growth-trait curve (e.g., Fig. 2a, solid blue line).

To determine the shape of the predation-trait curve, we consider the rate at which the prey and its predator encounter one another, as a function of s. First, consider a verbal model to derive the general shape from first principles. For predation to occur, the two species must first encounter one another, which will depend on both the predator and prey's displacement rates. For simplicity, we assume here that predation rate is proportional to encounter rate (i.e., predators exhibit a Type I functional response with handling time = 0; Holling, 1959; Holling, 1965). Encounters will thus increase with *s*, but the relative extent to which encounter rate increases will vary. When *s* is high relative to the predator's displacement rate, the encounter rate is governed primarily by *s*, and vice versa. This verbal model predicts a decreasing predation-trait curve that decelerates at low *s* (as in Fig. 2a; dotted red line).

It is also simple matter to derive the mortality curve based on theory. Many predator-prey models rely on ideal-gas law assumptions, which define encounter rate (and thus the CE) as linearly proportional to:

$$CE(s) = P \cdot k \cdot \sqrt{v^2 + s^2} \tag{3}$$

where *v* is the predator's displacement rate (Hutchinson & Waser, 2007, Avgar et al., 2011), *k* is a constant equal to the product of the predator's prey-detection diameter and the predator's lethality given an encounter, and *P* is predator density. We plot the relationship between *s* (x-axis) and the CE in Fig 2a (dotted red line). We see that this mathematical representation captures the intuitive shape of the mortality curve formulated in the verbal model (i.e. a decelerating decrease). With the trait curves in hand, we can derive the optimal RITR, and ensuing CE and NCE.

1b. Predator Density (P)

First, we examine how predator density influences risk effects. We show how predator density affects the shape of the trait curves (Element 1), which in turn changes the optimal RITR (Element 2) and the relative strength of NCEs and CEs (Element 3). To manipulate predator density, we double the density of predators (*P*) in Eqn. 3 (from Fig. 2a to 2b). This changes the trade-off prey face between securing resources and avoiding predation by changing the shape of the predation-trait curve in two key ways. First, because there are more predators present, risk is higher overall (i.e., even at the maximum RITR, $s = 0$, the predation-trait curve is still higher in Fig. 2a than in Fig. 2b). Second, by lowering s, prey receive proportionally higher protection from predation (i.e., the slope of the predation-trait curve is steeper; Fig. 2a-b), because s in this scenario contributes to how often they encounter twice as many predators. Because of this shift in the benefits associated with lowering s, the optimal strategy for prey at higher predator density is a higher RITR ($s*$ is further to the right; Fig. 2b). Because the optimal RITR is higher, prey growth is lower and NCEs are thus stronger. Meanwhile, because more predators are present, predation rates are higher overall. Thus, despite prey expressing a higher RITR to mitigate predation risk, there is still a net increase in the CE (Fig. 2b).

We can also use the IREF to consider how the occurrence and magnitude of risk effects change across gradients of environmental or biological factors. By plotting the optimal RITR across a gradient of predator densities (Fig. 2c), important patterns emerge at both extremes. First, there is a threshold level of risk below which it may be most adaptive for prey not to express the RITR (i.e., reduce their displacement rate) at all (visible at the far-left end of Fig. 2c, indicated by red arrow). The RITR thereafter increases monotonically until, at high predator densities (i.e., the far-right end of Fig. 2c), the RITR rate of increase decelerates. The latter pattern is because there are limits to how much prey can reduce s to avoid predation while still being able to acquire food (i.e., where the costs to growth greatly outpace any benefits; e.g., Fig. 2a where $s < 100$). This implies that there may be communities in nature where increasing predator density may not lead to a change in the optimal RITR (e.g., compare Fig. 2c where $P = 1.5$ to $P = 2.0$). Different functional forms and assumptions from the one we used here could yield qualitatively different results; a utility of the IREF is in providing the framework within which to explore these relationships.

Last, we provide an example of how the IREF can be used to explore different relationships between risk effects and environmental factors. We examine the relative contribution of NCEs to the total predator effect as a function of predator density (Fig. 2d). In this scenario, above the threshold at which a RITR is expressed, the relative NCE strength increases steeply as a function of predator density and then levels off (Fig. 2d). This prediction of leveling off occurs because at low predator density, the CE is relatively small and prey can easily offset it by increasing the RITR (thus increasing the NCE). However, at high predator density, the costs of offsetting the CE are prohibitively high (near point ‘b’ in Fig. 2d), and thus the increase in optimal RITR begins to decelerate (Fig. 2c) and the increase in the CE begins to slightly outpace the increase in the NCE (far-right end of Fig. 2d).

1c. Predator Foraging Mode (v)

Next, we apply the IREF to the well-studied question of how the predator’s foraging mode affects RITR expression. We can represent differences in foraging mode quantitatively by manipulating predator displacement rate (v in Eqn. 3). Specifically, we consider sit-and-wait and active predators to have a low and high displacement rate, respectively. Altering v leads to changes in the trade-off prey face via the predation-trait curve, as was the case for predator density. The encounter rate between predators and their prey depends on both predator and prey displacement rates (Eqn. 3); if the predator’s displacement rate is very low (e.g., $v \to 0$, which is the case for a sit-and-wait or ambush predator), the encounter rate is governed by the prey’s displacement rate (s). Thus, the predation-trait curve is predicted to be much shallower for sit-and-wait predators (modeled as $v_{sit\text{-}and\text{-}wait} = 0.2$) than for active predators (modeled as $v_{active} = 1$; Fig. 3a-b). In contrast with the example above (predator density), we held the y-intercept constant between foraging modes by multiplying the predation-trait curve by a scaling constant.

We did this to facilitate direct comparison between the shape of the predation-trait curves, as holding the y-intercept constant in this manner anchors the absolute magnitude of predator's CEs and NCEs when there is no trait change (s = 1000).

The IREF's predictions align well with those of Schmitz (2008) – sit-and-wait predators (Fig. 3a) induce higher optimal RITRs than active predators did (Fig. 3b). This occurs because, when predators have higher displacement rates (from Fig 3a to 3b; i.e., a more active predator is present in Fig. 3b), encounters between the predator and prey are less dependent on prey's displacement rate. Consequently, lowering displacement rate provides less protection for prey against predation (signified by a shallower predation-trait curve; Fig. 3b). Thus, with active predators, the optimal RITR is lower (i.e., further to the left; Fig. 3a-b). Because prey exhibit a lower response to active predators, they forage more actively and grow faster, causing NCEs to be weaker. Meanwhile, CEs are stronger due to a combination of the lower optimal RITR and stronger predation pressure exerted by more active predators (Fig. 3b). As in the previous scenario, we use the IREF to explore relationships between risk effects and environmental factors. The framework predicts that in the range of values we explored, the higher the predator's displacement rate, the lower the optimal RITR we expect (Fig. 3c), and the relative contribution of NCEs to the net predator effect falls to zero in a decelerating fashion (Fig. 3d).

1d. Prey Resource-Processing Rate (1/h)

Last, we will consider how prey resource-processing rate (inverse handling time, $1/h$) influences risk effects using the IREF. Prey naturally exhibit differences in the amount of time required to process food resources as they forage (represented as handling time, h in Eqn. 2) due to species- or population-level differences, ontogenetic stage, food type, or environmental factors (e.g., temperature in ectothermic prey; Brown et al., 2004; Englund et al., 2011). A lower resource-processing rate means a lower resource-consumption rate, regardless of resource abundance, but also differences in sensitivity to changes in the search rate (and hence the displacement rate). For example, at low displacement rates, prey growth is primarily limited by their encounter rate with resources, and thus lowering displacement rate is relatively costly. However, at high displacement rates, prey growth is primarily limited by the time required to handle food, so lowering displacement rate incurs lower relative costs. Consequently, and in contrast with the previous two scenarios, this change in the biology of the system leads to differences in the shape of the growth-trait curve (Fig. 4a-b, solid blue line). We show prey with a higher (Fig. 4a, $1/h = 1.0$) and lower (Fig. 4b, $1/h = 0.5$) resource-processing rate. First, prey with a lower resource-processing rate (Fig. 4b) acquire fewer resources per unit time spent foraging (and thus have lower growth and fitness) than those with higher resource-processing rates (Fig 4a); the absolute magnitude of the growth-trait curve (i.e., its height) is lower when $1/h = 0.5$ (Fig. 4b) than when $1/h = 1.0$ (Fig. 4a). Second, the growth-trait curve (growth as a function of displacement rate) is flatter for prey with lower resource-processing rates (Fig. 4b vs. Fig. 4a, solid blue line). Geometrically, this is simply a product of a reduction in the y-intercept (growth at the maximal search/displacement rate) when resource-processing rate is low, while the x-intercept remains constant (growth is 0 when search/displacement rate is 0, regardless of resource-processing rate). Consequently, when resource-processing rate is high, an increase in the expression of the RITR will lead to a proportionally larger growth penalty than the same increase when resource-processing rate is low. In other words, in comparison with fast resource-processing prey, slow resource-processing prey are more limited by their handling time than they are limited by their search rate at intermediate levels of s, and can hence tolerate (i.e. pay a smaller price in terms of growth reduction for) a greater reduction in their search rate than high resource-processing prey.

As a result, prey with lower resource-processing rates are predicted to have a higher optimal RITR (i.e., reducing displacement rate further, $s*$ is further to the right in Fig. 4b than Fig. 4a). This leads to stronger NCEs, due to the higher RITR, and weaker CEs, because encounters with predators are less frequent at the new higher optimum (i.e., further to the right in Fig. 4b). Fig. 4c illustrates that the prey's optimal RITR falls (i.e., the optimal displacement rate increases) nearly linearly as a function of the prey's resource-processing rate. The relative contribution of the NCE to the net predator effect decreases with increasing prey resource-processing rate as a consequence of decreases in the prey's optimal RITR (Fig. 4d, and compare 4a to 4b). Meanwhile, prey fitness also increases, as prey with higher resource-processing rates are able to collect more food per unit time than those with lower resource-processing rates (Fig. 4d).

Case 2. Prey Refuge Use: Elucidating Modeling Assumptions

A key strength of the IREF is its ability to clarify and make explicit the underlying assumptions that researchers make to generate, and the effect they have, on hypotheses (i.e., Objective 1). We demonstrate this strength in a second case exploring risk effects where prey respond to predation risk by making use of a refuge habitat in which risk is lower and there are fewer or poorer quality resources (i.e., similar to Schmitz, 2008). Prey can make use of two habitats: one habitat (hereafter, Habitat A) that carries considerable mortality risk due to predation, and a refuge habitat (hereafter, Habitat B) where prey face lower predation risk but there are fewer resources present. Biologically, predation risk could be lower in Habitat B for several reasons. Predators may simply be at very low density in Habitat B ($P(A) \gg P(B)$), because some other element of that habitat is not suitable for them. Alternatively, predators may have greater difficulty in locating, subduing, or capturing prey in Habitat B (e.g., due to greater habitat complexity or other factors resulting in shifts in one or more of the components of θ_P, Box 1). Habitat A's resources may be either of higher density or quality than Habitat B, but we approximate this by manipulating resource density (R) and will hereafter refer to Habitat A as having "higher resource density". The defensive trait, and thus the trait on the x-axis of our trait curves (Fig. 5), is the proportion of the time that prey are present in the refuge Habitat B. A higher RITR is thus higher use of Habitat B (i.e. higher safety in the refuge). We assume that the predation-trait curve is the sum of predation risk in Habitats A and B, weighted by the amount of time prey spent in either habitat. This results in a predation-trait curve that declines linearly with increasing time spent in the refuge Habitat B (Fig. 5a-c; red dashed line).

We examine how a property of prey growth, namely if prey experience diminishing returns on growth at higher resource levels, affects risk-effect predictions in a scenario with two habitats that vary as described above. This assumption of diminishing returns could result from, for example, processes that impact the ability of consumers to optimally gather resources. Consumers need time for other activities, like resting or searching for mates, or they may become satiated (if they are able to obtain enough food over a short enough time period). Consumer satiation can lead to lower foraging rates (via slower attack rates and/or longer handling times), leading to a saturating or step-wise relationship between growth and time spent foraging (see Jeschke et al., 2002; Jeschke, 2007; Li et al., 2018). Hereafter, we refer to prey that experience diminishing returns on growth at higher resource levels as becoming "satiated", for simplicity. We develop the growth curve using verbal models that reflect our understanding of the biology of the system, though quantitative models could also be used as in Case 1. We compare results between two contrasting assumptions concerning growth as a function of resource consumption, both of which are reasonable, and the importance of which may go unnoticed without explicit representation in a framework such as the IREF.

2a. Prey Do Not Experience Satiation

In the first instance, we assume that prey do not become satiated at higher resource levels, and thus growth is the linear sum of the number of resources the prey can gather in Habitats A and B, weighted by the time prey spend in each habitat. This results in a linearly decreasing growth-trait relationship (Fig. 5a-b) as a function of the proportion of time spent in the refuge (Habitat B).

In this instance, because both the growth-trait and predation-trait curves are linear (and thus proportional to one another), a change in trait value causes the same relative change in costs and benefits. The optimal behavior by prey is therefore to spend either all, or none, of their time in Habitat B, depending on which relationship has the steeper slope (Fig. 5a-b, Element 2; see also Peacor et al., 2013). If the predation-trait relationship is steeper than the growth-trait relationship, the relative costs of using Habitat B (reduced resources) do not outweigh its benefits (reduced predation), and thus prey should spend all of their time in Habitat B (Fig. 5a). However, if the growth-trait relationship is steeper than the predation-trait relationship, the relative benefits of using Habitat B (reduced predation) do not outweigh its costs (reduced resources), and it is optimal for prey to spend none of their time in Habitat B (Fig. 5b). Biologically, this means that there is a switch-point between using one habitat or the other, depending on their relative costs and benefits, resulting in a predator effect that is either all CE (if the optimal RITR is 0; Fig. 5b) or mostly NCE (if the optimal RITR is 1; Fig. 5a).

2b. Prey Experience Satiation

In the second instance (Fig. 5c), we assume that prey become satiated at higher resource levels, and hence growth decreases as an accelerating function of increasing time spent in the refuge (Habitat B). That is, a higher expression of the defensive trait (i.e. time in the refuge), and hence lower access to resources, will have a proportionally larger negative effect on growth when the prey are spending proportionally less time in the refuge (left hand side of Fig. 5c). We represent a simplified version of this case here by assuming that the growth-trait curve accelerates with increasing time spent in Habitat B (Fig. 5c).

The assumption of prey satiation leads to qualitatively different predictions than the previous scenario without it. Here, because prey become satiated at higher resource levels, the costs to growth associated with increasing refuge use are low at first (i.e., to the left in Fig. 4c), but increase with refuge use (i.e., to the right in Fig. 4c) in a saturating fashion. This leads to an optimal RITR where prey spend some intermediate amount of time in each habitat (Fig. 4c), rather than "all or nothing" as before (Fig. 4a-b). Unlike in the instance above where prey did not experience satiation, there is a range of trait expressions in which an increase in the defensive trait has a larger benefit (steeper mortality curve) than cost (steeper mortality than growth curve) until an optimal trait value is reached, above which the cost becomes greater than the benefit. This is further reflected by the predator effect being a more even blend of NCEs and CEs (i.e., Element 3; Fig. 4c), whereas when prey did not experience satiation, the predator effect was dominated either primarily by NCEs (Fig. 4a) or entirely by CEs (Fig. 4b). The different predictions stem from an underlying biological process – i.e., satiation leading to a change in the costs of additional time spent in the refuge (Habitat B) – that the IREF can help to describe and visualize the consequences of.

Discussion

While there has been considerable research in the past few decades surrounding predator risk effects (e.g., Werner & Peacor, 2003; Beschta & Ripple, 2013; Wirsing et al., 2021), there are major gaps in our understanding of the drivers of the occurrence and magnitude of RITRs and NCEs across different ecosystems. These issues stem in part from the highly "context-dependent" nature of risk effects, which greatly challenges our ability to effectively synthesize our knowledge (Wirsing et al., 2021; Peacor et al., 2022; Peckham et al., in Review). We believe that the IREF could be used to address this gap. We also stress that a key point about the IREF is that it is not intended as a replacement for quantitative predictions that may require more nuanced theoretical models – instead, it is a simple and intuitive "toy model" to generate hypotheses, consider how vastly mechanically different RITRs might operate in quantitatively similar ways, and test assumptions. While illustrating the use of the IREF, we further developed some risk-related hypotheses – some known to the literature, and some novel – which we summarize in Table 2.

Our first objective was to demonstrate how the use of the IREF can guide researchers in describing the biology of predator-prey systems in a quantitatively explicit fashion and help clarify the assumptions we make when generating predictions (i.e., Objective 1). In the first case study, we first described the system using a simple verbal model, which we then made quantitatively explicit using known theoretical relationships between the RITR, predation risk, and prey growth. In our second case study, we explored how our predictions changed depending on a fundamental assumption about prey foraging that likely reflects differences among real systems. In all instances, the IREF's trait curves were key to describing these relationships in a systematic manner.

A main advantage of the IREF lies in its use of trait curves as “building blocks” to quantitatively describe and compare the myriad ways in which prey respond to predation risk. They are the key relationships which underlie risk effects. We provided a few examples of the forms these curves can take and provided plausible mechanisms by which they may do so; we encourage others to consider how other traits beyond the scope of this study might behave similarly. We expect that most trait curves in nature are monotonic and conform to a set of five different general forms: linear (akin to Holling’s Type I curve); concave up or accelerating (e.g., the mortality curves in Figs. 2-4); concave down or decelerating (e.g., the growth-trait curves in Figs. 2-3; akin to Holling’s Type II curve); sigmoid (concave down and then up; akin to Holling’s Type III curve); and logit (concave up and then down). Further, we encourage the development of these trait curves from data whenever possible, whether that means experimentally deriving them or drawing on existing literature sources. In addition to studies that explicitly consider risk from either a theoretical (e.g., Abrams, 1984; McNamara & Houston, 1992; Prokopenko et al., 2023) or empirical (e.g., Ofstad et al., 2020; Sergeyev et al., 2020; Pays et al., 2021) standpoint, we suspect that studies that do not explicitly consider risk, such as those considering life-history tradeoffs, frequency-dependent selection, and environmental reaction norms (e,g., Davidowitz & Nijhout, 2004; de Mazancourt & Dieckmann, 2004; Sinervo & Calsbeek, 2006) may also be used to derive trait curves.

Our second objective was to illustrate how the IREF can be used to generate process-based, theory-driven hypotheses about how different ecological contexts impact risk effects (summarized in Table 2). We walked through the process of determining the growth and mortality curves based on the biology of the system and then showed how that led to different predictions concerning risk effects. This is perhaps best illustrated in Case 1c. We were interested in knowing the effect of prey resource-processing rate on risk effects but did not have a preconceived verbal hypothesis. The model predicted, somewhat counterintuitively, that prey with lower resource-processing rates would express a higher RITR. Unpacking this finding required delving into our understanding of the biology, which yielded an answer that was intuitive and reasonable, but that we were unlikely to come up with without the assistance of the framework. This ability of the IREF to guide users to an intuitive prediction in a complex problem is a power of models in general and could similarly be seen using mathematical equations.

We considered how two known drivers of risk effects (predator density and predator foraging mode) impacted risk effects in a system where prey avoid predation by reducing their displacement rates. We were able to recover classic expectations regarding these system characteristics. We also showed that higher predator density, which constitutes higher risk, should elicit a stronger RITR (i.e., a slower displacement rate) and stronger CEs and NCEs (Fig. 2a-b), but the effect eventually saturates (Fig. 2c). We showed that active predators elicited a weaker optimal RITR than sit-and-wait predators, leading to stronger CEs and weaker NCEs when active predators were present (Fig. 3; in agreement with predictions from a verbal model and subsequent empirical evidence from Schmitz, 2008). Our findings deviate from Schmitz's (2008) only in the biological complexity of the underlying mechanism. Whereas Schmitz's (2008) predictions assume that sit-and-wait predators provide less diffuse and "more reliable" risk cues, we did not need to invoke any such cognitive/behavioral mechanism, relying instead on the simple mechanics of ideal-gas interactions. In other words, we have used the IREF to show that the reliability of predator cues may be sufficient, but not necessary, to explain the relationship between the prey's optimal RITR and the predator's hunting mode.

We generated a series of novel predictions under the IREF (summarized in Table 2). In Case 1, we varied predator density and showed that there is a threshold under which prey should not respond to predation risk at all (Fig. 2d). This density-dependence analysis also revealed that the optimal RITR changes very little at high predator density, and thus there may be communities in nature where increases in risk do not lead to a change in the optimal RITR (e.g., compare Fig. 2c where $P = 1.5$ to $P = 2.0$). We also examined the impact of the prey's resource-processing rate on risk effects. We found that prey with faster resource-processing rates should exhibit weaker RITRs (i.e., faster displacement rates in our example), because as resource-processing rate increases, prey become more limited by their encounter rates with their resource. This in turn makes it relatively more costly for them to reduce their displacement rate in response to risk (Fig. 4). Last, we illustrated how prey satiation can be a driver of intermediate RITRs when prey use predation refuge habitats (Fig. 5). This may be common in natural systems, where prey might experience satiation or need to devote time to other activities like resting or searching for mates (Jeschke et al., 2002; Li et al., 2018).

Our third objective was highlighting the IREF's utility in facilitating communication of risk effects ecology, and comparisons and syntheses across systems (i.e., Objective 3). By using the same underlying structure (i.e., the trait curves) and currency of fitness gains and losses, we can make straightforward comparisons between the optimal trait response and NCE and CE strength in different systems. For example, we showed how two system characteristics that both increase predation risk (e.g., an increase in predator density, and an increase in predator displacement rate) can move the optimal RITR in opposite directions, because these system characteristics alter the trait curves – i.e. the relationships between the defensive trait level and fitness measures – differently (Figs. 2-3). Biologically, this finding stems from the fact that when predators are more abundant, reducing movement becomes more effective as a strategy for managing risk (Fig. 2a-c), whereas the more the predators move, the less effective it is for prey to reduce their own movement (Fig. 3a-c). Further in line with Objective 3, we captured different elements of the system's biology by manipulating parameters within the predator and prey's functional responses. In doing so, we hope to emphasize the generality of the IREF's approach, the potential applicability of its predictions and findings across systems, and the importance of looking to first-principles ecological theory (e.g., functional response models) to explore risk effects. For example, while we describe a predator with a higher displacement rate as being an "active" predator, as opposed to a "sit-and-wait" predator (Fig. 3), differences in foraging strategies between predators are only one potential source of variation in predator displacement rate. Temperature, for example, is a well-known driver of many functional response parameters in ectothermic organisms – in particular, higher temperatures often lead to higher search rates and faster handling times (Englund et al., 2011; Sentis et al., 2012; Dell et al., 2014). Thus, what we term a "more active" predator here could also be a predator in a system that has experienced warming, and what we consider two separate "contexts" might instead drive functionally similar risk effects. The same can apply to the example of prey with faster resource-processing rates (Fig. 4) – the differences in resource-processing rate could be for any number of differences either within or between different systems, including temperature, species-level differences, different resource types, etc.

The method for optimizing prey fitness used herein (Eqn. 1) is only one way of doing so – and choosing a method involves other assumptions that should be carefully considered. In particular, our approach is rooted in basic population models that are written using instantaneous rates of change (e.g., Abrams, 1984), which may not always be appropriate for the biology of every system. Alternative population-level ‘fitness functions’ include population size/biomass relative to population size/biomass at carrying capacity (in the absence of predation), discrete-time (e.g., annual) population growth rate, net-reproductive rate (R_0), and the ratio of mortality to growth (μ/g). Alternative, individual-level ‘fitness functions’ include annual reproductive success, lifetime reproductive success, and even multigeneration reproductive success (number of grandchildren). Whichever the chosen fitness function is, it reflects biological assumptions about the modelled system, and could have a qualitative effect on the results (see Appendix for an example using μ/g; Gilliam 1982, Werner and Gilliam 1984).

Despite the narrative that predator NCEs can have equal or greater impacts on ecological communities than predation itself (Werner & Peacor, 2003; Schmitz et al., 2004; Peckarsky et al., 2008), their influence on the structure and dynamics of natural communities remains ambiguous (Peers et al., 2018; Sheriff et al., 2020; Peacor et al., 2022). Further, many studies on risk effects are founded on either verbal models or quantitative models that are too system-specific to be broadly applicable, and many studies stop at simply describing risk effects as “context-dependent” due to differences in the ecology and/or life history of predator and/or prey species (e.g., Heithaus et al., 2009; Sheriff et al., 2020; Wirsing et al., 2021). Thus, in order to build on and synthesize our knowledge of risk effects, we hold that the use of a common framework such as the IREF will be necessary to 1) guide our intuition when designing studies of risk effects, 2) unify and formalize existing models and hypotheses surrounding risk effects, and 3) draw comparisons across systems with seemingly mechanically disparate risk effects. Further, we hope that this framework will help transfer insights and methodologies across ecological systems and promote advancement in a sub-field of ecology that has potentially significant applications to management and conservation challenges.

Acknowledgements: We thank Aaron Wirsing for providing comments on an earlier version of this manuscript. This research was supported by National Science Foundation Grant DEB 2342171. TA was financially supported by Biodiversity Pathways Ltd. SDP acknowledges support from AgBioResearch of Michigan State University.

Author Contributions: ATD wrote the original draft and participated in revising and editing subsequent drafts, assisted with conceptualization, scripted and implemented the models, and created the finalized figures and tables that appear in the manuscript. TA and SDP were instrumental in conceptualizing the study, revising and editing the manuscript, designing the model and graphical framework, supervising, and securing funding. DM assisted with conceptualization, editing and revisions, and securing funding.

Conflict of Interest Statement: The authors declare that there are no conflicts of interest with respect to the publication of this article.

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Boxes

Box 1. The IREF was initially developed to parallel classic models of consumer (prey) population growth (as in e.g., Abrams, 1984):

$$\frac{dC}{dt} = C \cdot [g \cdot f_c(R, C, \theta_C) - m] - P \cdot f_P(C, P, \theta_P) \quad (1)$$

where C and P are the densities of a consumer (which we refer to in the text as 'prey') and its predator, respectively. f_C and f_P are the functional responses of the consumer on its resource (with density R) and the predator on the consumer, respectively. g is the consumer's resource-conversion efficiency, and m is the consumer's background mortality rate. θ_C and θ_P are vectors of functional-response parameters (e.g., search rate or handling time) for the consumer and its predator, respectively. A RITR is, by definition, associated with a reduction in both the blue (which we term 'growth') and red (which we term 'predation') terms of Eqn. 1. A fitness-maximizing prey (consumer) is thus expected to express the trait such that it maximizes the difference between growth and predation.

Tables

Table 1. Candidate system characteristics (i.e., contexts) associated with the environment, prey species, or predator species that may shape trait curves and associated risk effects.

Environmental/System Characteristic	Prey	Predator
Resource quantity, quality, and spatiotemporal distribution	Density	Density
Refuge availability and quality	Foraging mode	Hunting mode
Alternative prey and its defensive traits	Reproductive state	Generalist/specialist
Additional predator species	Non-plastic defense level	Territoriality
Conditions (e.g., temperature affecting movement rate and metabolism, turbidity affecting detectability, nutrient concentration affecting morphological defenses)	Predation-independent cost/benefit of grouping	Diurnal and seasonal overlap with prey
	Age structure	
	Life history	
	Movement and habitat selection	

Table 2. A summary of the hypotheses generated using the IREF in this study, including the prey's RITR, the system characteristic manipulated, whether prior research has considered this system characteristic, and what the IREF predicted.

Prey RITR	System Characteristic	Prior Research	Hypotheses Generated
Displacement rate, *s*	Predator density, *P*	Novel	The RITR can show three phases as a function of predator density: no effect, monotonically increasing, or saturating.
	Predator displacement rate, *v*	Reinforces past studies*	Higher predator displacement rate (i.e., more active predators) leads to a lower RITR.
	Prey resource-processing rate, *1/h*	Novel	Higher prey resource-processing rate leads to a lower RITR.
Proportion of time spent in a refuge habitat, δ	Whether prey experience satiation at higher resource levels	Novel	The RITR can be either binary (δ = 0 or 1; in the linear case) or intermediate (in the saturating case) depending on prey satiation.

*Schmitz et al. 2004, Schmitz 2008.

Figure Legend:

Figure 1. Illustration of the Integrated Risk Effects Framework (IREF), representing the core three elements of the IREF. See text for explanation of mortality-trait curve (dotted red line) and growth-trait curve (solid blue line), which are the heart of the framework and used to derive changes in fitness (dashed green line in panel b) as a function of prey trait expression. The vertical dashed black line in panel b) shows the optimal trait response, where fitness is maximized. Values in panel c) reflect the relative strength of predator nonconsumptive effects (NCEs; calculated as the difference between the growth value with no trait change, i.e. 1.0, and at the trait optimum, depicted by the blue column), consumptive effects (CEs; mortality at the trait optimum, depicted by the red column), and resulting fitness (calculated as 1 – NCE – CE, depicted by the green column).

Figure 2. The effects of predator density (*P*) on risk effects when the prey defensive trait is displacement rate (*s*). Panels a-b) show predator densities of a) $P = 0.45$ and b) $P = 0.9$, which changes the predation-trait curve (dotted red line) but not the growth-trait curve (solid blue line). The different predator densities affect the optimal prey RITR (indicated by the position of the vertical column along the x-axis), prey fitness (indicated by the height of the green column) and CE and NCE strength (indicated by the height of the red and blue columns, respectively). Panels c-d) show the effects of predator density on c) the optimal RITR, and d) the relative contribution of NCEs to the net predator effect (note that the predator densities in c and d corresponding to those in a and b are marked as such). Red arrow indicates predator densities below which prey should exhibit no RITR.

Figure 3. The effect of predator displacement rate (*v*) on risk effects when the prey defensive trait is displacement rate (*s*). Panels a-b) show predator displacement rates of a) $v = 0.2$ and b) $v = 1.0$,

which changes the predation-trait curve (dotted red line) but not the growth-trait curve (solid blue line). The different predator displacement rates affect the optimal prey RITR (indicated by the position of the vertical column along the x-axis), prey fitness (indicated by the height of the green column) and CE and NCE strength (indicated by the height of the red and blue columns, respectively). Panels c-d) show the effects of predator displacement rate on c) the optimal RITR, and d) the relative contribution of NCEs to the net predator effect (note that the predator densities in c and d corresponding to those in a and b are marked as such).

Figure 4. The effect of prey resource-processing rate (*1/h*) on risk effects when the prey defensive trait is displacement rate (*s*). Panels a-b) show prey resource-processing rates of a) *1/h* = 1.0 and b) *1/h* = 0.5, which changes the growth-trait curve (solid blue line) but not the predation-trait curve (dotted red line). The lower prey resource-processing rate (b) leads to a higher optimal prey RITR (indicated by the position of the vertical column along the x-axis), lower prey fitness (indicated by the height of the green column), and lower CE and higher NCE strength (indicated by the height of the red and blue columns, respectively). Panels c-d) show the effects of prey resource-processing rate on c) the optimal RITR, and d) the relative contribution of NCEs to the net predator effect (note that the predator densities in c and d corresponding to those in a and b are marked as such).

Figure 5. The effect of different assumptions about prey growth on risk effects when the prey defensive trait is the proportion of time prey spend in a safer but resource-poorer refuge (Habitat B). In panels a-b) we assume that prey do not experience satiation at higher resource levels, and thus their growth is proportional to the amount of time they spend in Habitat B, resulting in a linear growth-trait curve. In panel c) we assume that prey experience satiation at higher resource levels (i.e., increasing time spent in Habitat B), resulting in a growth-trait curve that decreases in

an accelerating fashion. The different assumptions affect the shape of the growth curve (see text) and, in turn, the optimal prey RITR (indicated by the position of the vertical column along the x-axis), prey fitness (indicated by the height of the green column) and CE and NCE strength (indicated by the height of the red and blue columns, respectively).

Figure 1.

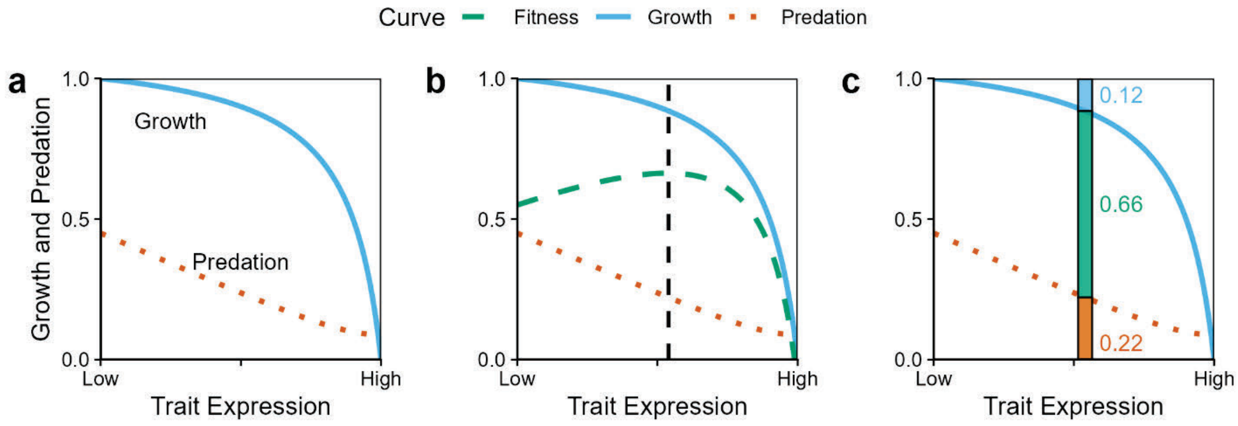
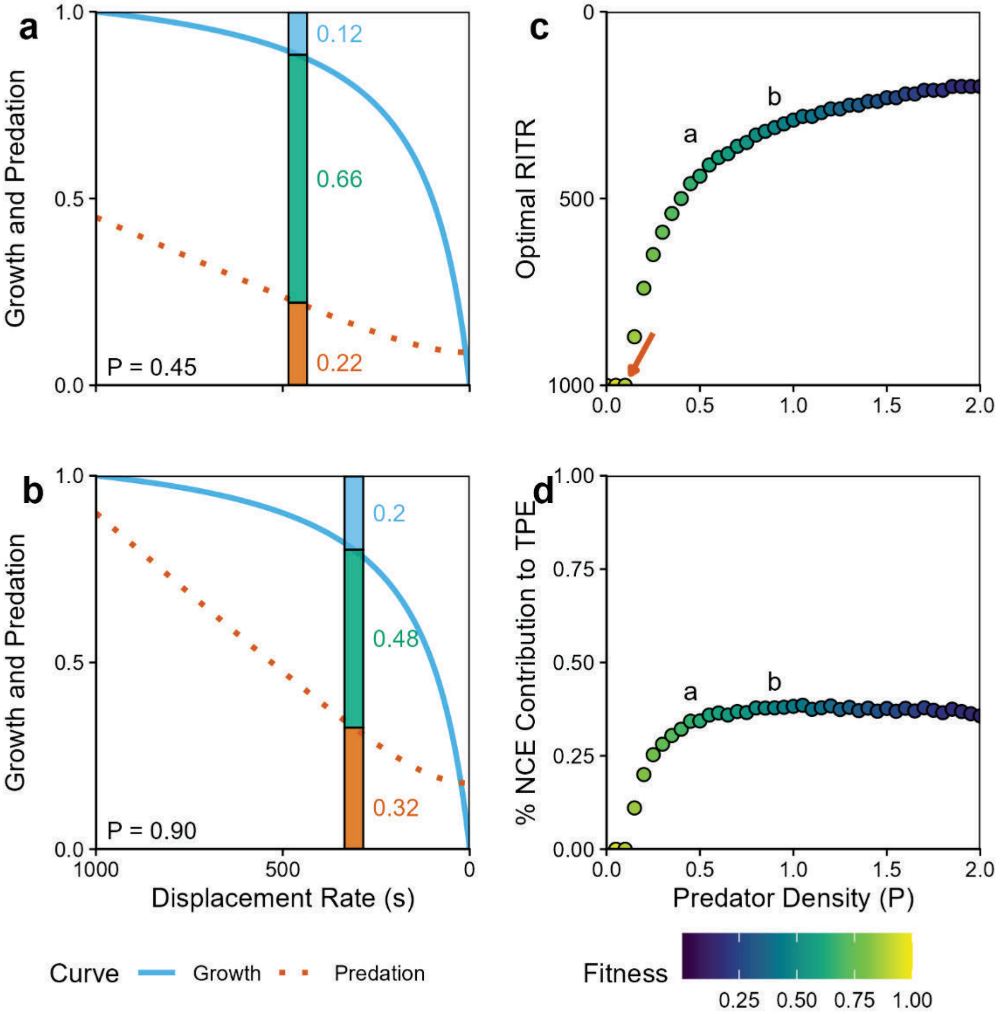
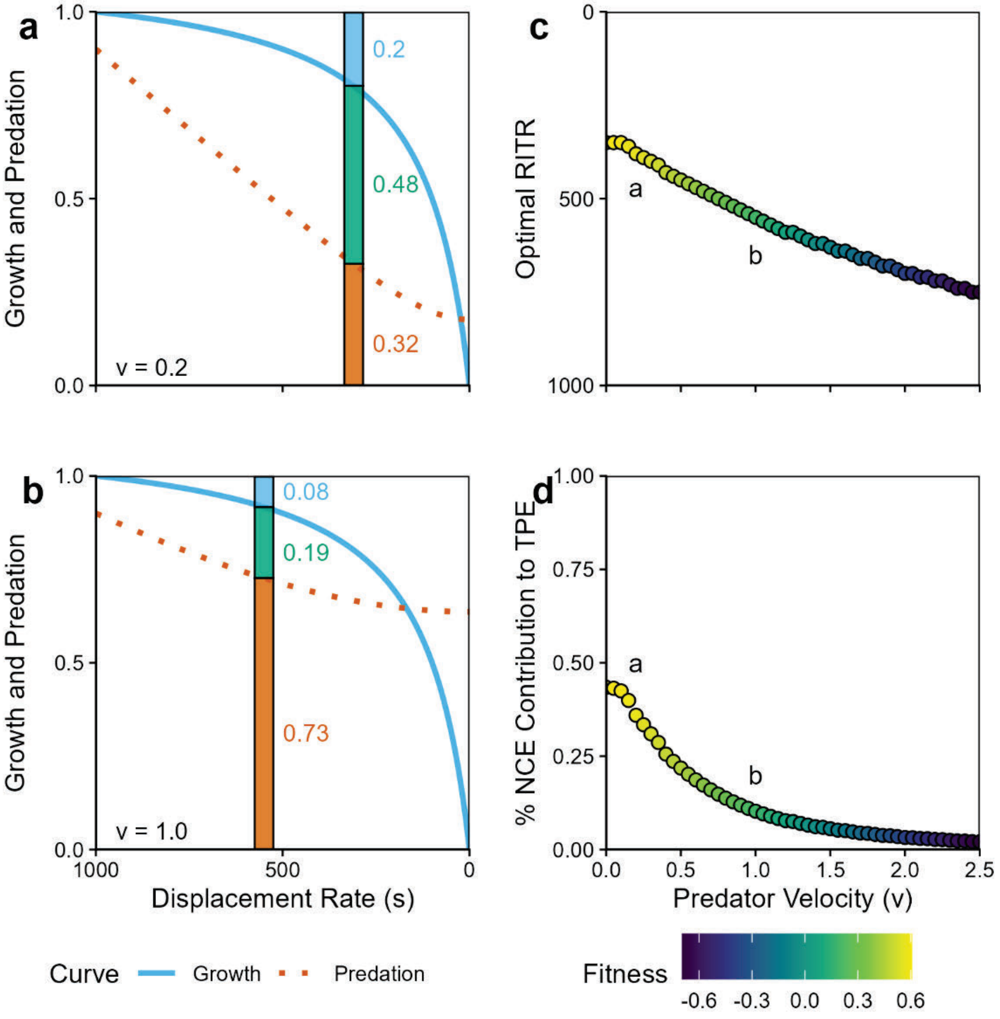

Curve
Fitness
Growth
Predation
a
b
c
Growth and Predation
1.0
0.5
0.0
Growth
Predation
Low
High
Trait Expression
0.12
0.66
0.22

Figure 2.


a
1.0
0.5
0.0
Growth and Predation
0.12
0.66
0.22
P = 0.45
b
1.0
0.5
0.0
Growth and Predation
0.2
0.48
0.32
P = 0.90
1000
500
0
Displacement Rate (s)
c
0
500
1000
Optimal RITR
a
b
0.0
0.5
1.0
1.5
2.0
d
1.00
0.75
0.50
0.25
0.00
% NCE Contribution to TPE
a
b
0.0
0.5
1.0
1.5
2.0
Predator Density (P)
Curve
Growth
Predation
Fitness
0.25
0.50
0.75
1.00

849 Figure 3.



850

Figure 4.

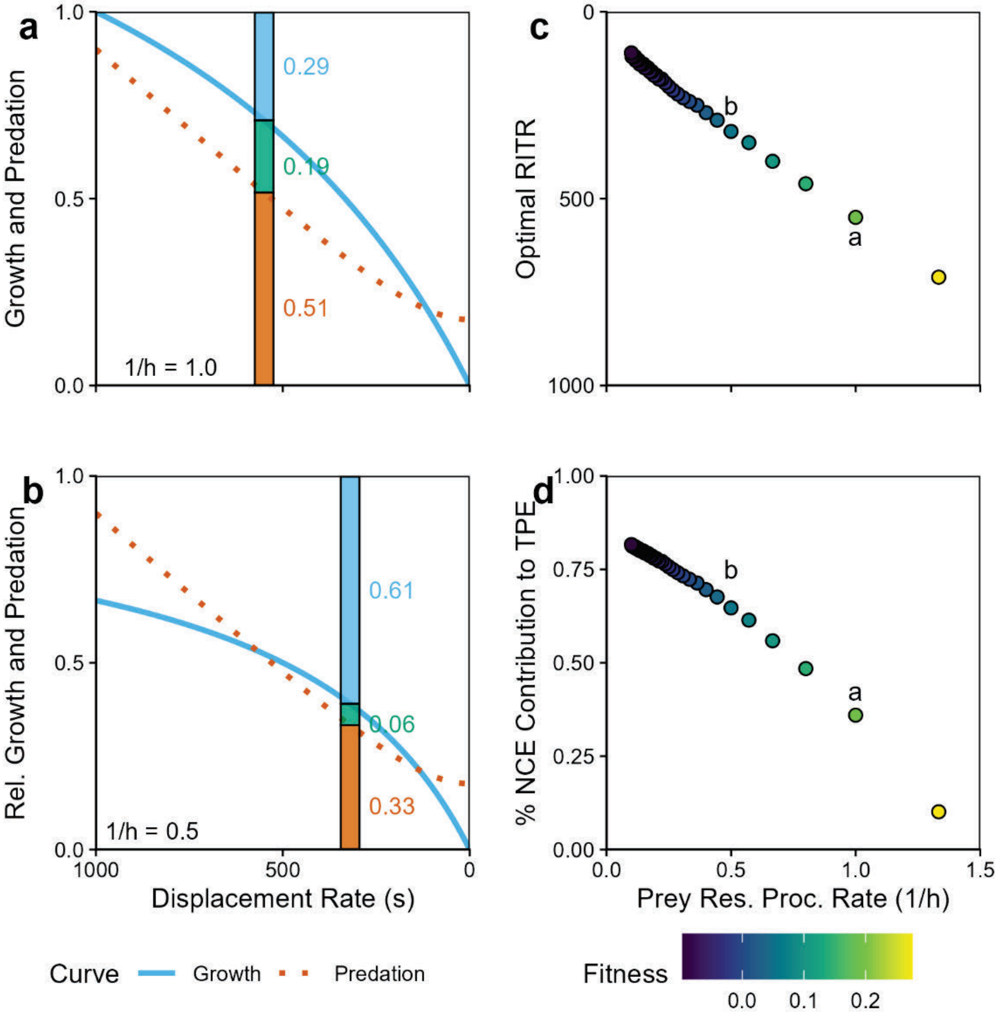
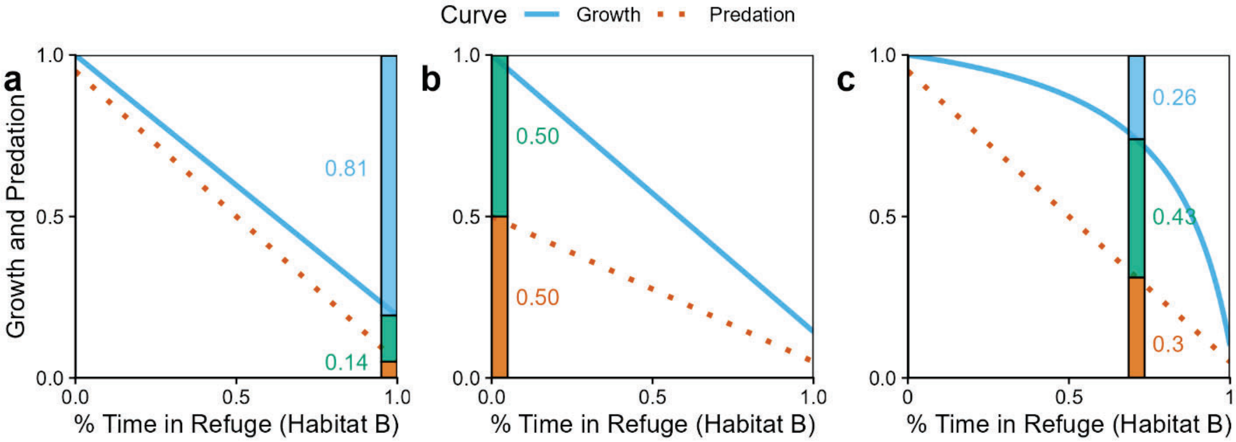

a
1.0
0.5
0.0
Growth and Predation
0.29
0.19
0.51
1/h = 1.0
c
0
500
1000
Optimal RITR
b
a
b
1.0
0.5
0.0
Rel. Growth and Predation
0.61
0.06
0.33
1/h = 0.5
1000
500
0
Displacement Rate (s)
d
1.00
0.75
0.50
0.25
0.00
% NCE Contribution to TPE
b
a
0.0
0.5
1.0
1.5
Prey Res. Proc. Rate (1/h)
Curve
Growth
Predation
Fitness
0.0
0.1
0.2

Figure 5.



Curve
Growth
Predation
a
b
c
Growth and Predation
1.0
0.5
0.0
0.81
0.14
0.50
0.50
0.26
0.43
0.3
0.0
0.5
1.0
0
1
% Time in Refuge (Habitat B)

Appendix

Other Approaches to Optimizing Prey Fitness

In this study, we demonstrate one approach to determining the optimal RITR by prey by assuming that prey fitness will be optimized at the level of trait expression that maximizes the difference between the growth-trait curve (i.e., the costs associated with the response) and mortality-trait curve (i.e., the reduction in mortality associated with the response; hereafter "b – d"). However, there are other approaches that can be used to measure prey fitness and determine the optimal trait response by prey. For example, Werner and Gilliam's (1984) "μ/g rule" can also be used to determine the optimal response by solving for the level of trait expression where the ratio of mortality due to predation (μ) to growth (g) is minimized. In other words, under this approach, prey should express RITRs in a way that minimizes their exposure to risk relative to their growth rate. Here, we explore how – depending on how we assume prey maximize their fitness – we can generate both similar and contrasting predictions about how prey should respond under different contexts.

Optimizing trait expression using μ/g instead of b – d leads to both qualitatively and quantitatively different predictions about how prey should respond to differing levels of predator density (Fig. S1a-b, S2a). Because increasing predator density increases risk proportionally across all levels of trait expression (compare Fig. S1a to S1b), the minimum remains at the same level of trait expression (i.e., the relative risk faced by prey is the same). Thus, when predators are present at any density, prey should employ the same strategy if they optimize fitness by minimizing μ/g (Fig. S2a).

Optimizing trait expression using μ/g instead of b – d leads to quantitatively different but qualitatively similar predictions regarding how prey should respond to predators that employ different foraging modes (Fig. S1a, c; S2b). The relationship between the relative amount of risk prey face and their displacement rate changes, such that the optimal strategy is to increase their displacement rate. This is because, as in the main text, when predators are more active, prey displacement rate is relatively less important in determining how frequently they encounter predators. Optimizing fitness by minimizing μ/g does not qualitatively change this finding, but it does lead to slightly different predictions about how much more active prey should be (Fig. S2b).

The reason for differences lies in the underlying assumptions that the two approaches make about how fitness-optimizing prey should behave. Werner and Gilliam's (1984) "μ/g rule" was initially theorized as a way to describe how prey in size- or stage-structured populations should make use of habitats with different levels of resources and risk as they grow to adulthood. Biologically, this places heavier emphasis on minimizing exposure to risk so that prey can survive to reproductive age, and changes in "growth" incurred by responding to risk primarily affect somatic or developmental growth rates to the next size or stage. Quantitatively, μ/g rule also involves taking the ratio of risk to reward, and that ratio can remain the same despite underlying changes in the amount of absolute risk or growth so long as those changes are proportional to one another (as in Fig. S1a-b, Fig. S2a).

By contrast, determining optimal fitness using our approach takes a more population dynamical approach by making use of changes in instantaneous rates to parameterize the growth and mortality curves. Thus, under our assumptions, prey should make decisions based on immediate gains and losses to growth (including reproduction) and mortality. The strength of the

IREF lies in being able to make these types of assumptions explicit, and to contrast how they influence our predictions.

Figures and Tables

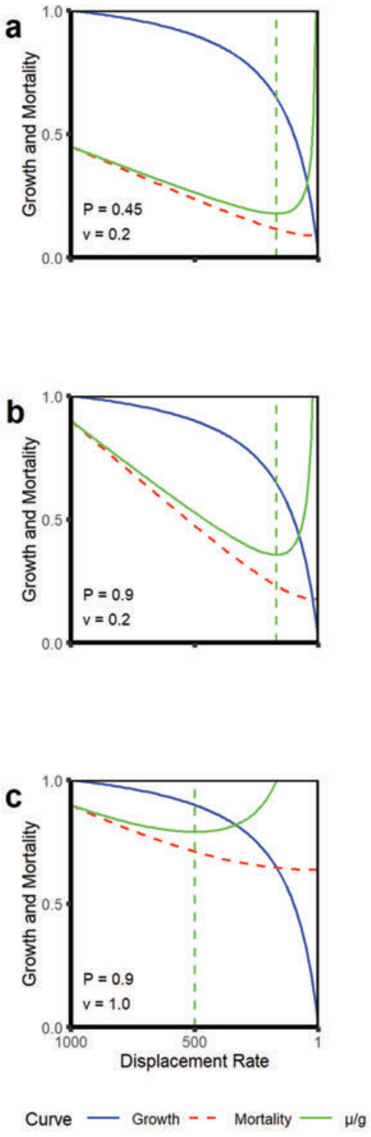


Fig. S1. Differences in the predicted optimal prey RITR for a prey that reduces foraging activity (measured as displacement rate) in response to risk, when prey optimize fitness by minimizing μ/g (green line). The growth-trait curve (blue line) and mortality-trait curve (dashed red line) show the relationship between RITR expression and costs, in terms of reduction in growth rate, and benefits, in terms of reduction in mortality rate due to predation, respectively. The vertical dashed green line indicates the level of trait expression where μ/g is minimized. Doubling predator density (*P*) from a) to b) yields the same predicted optimal RITR. Meanwhile, exposure to a more actively foraging predator (i.e., increasing *v*) c) shifts the optimal displacement rate to the left (i.e., prey should be more active, as compared to a sit-and-wait predator). The x-intercept was scaled to the same value between panels b) and c) to hold overall predator lethality constant between the two examples.

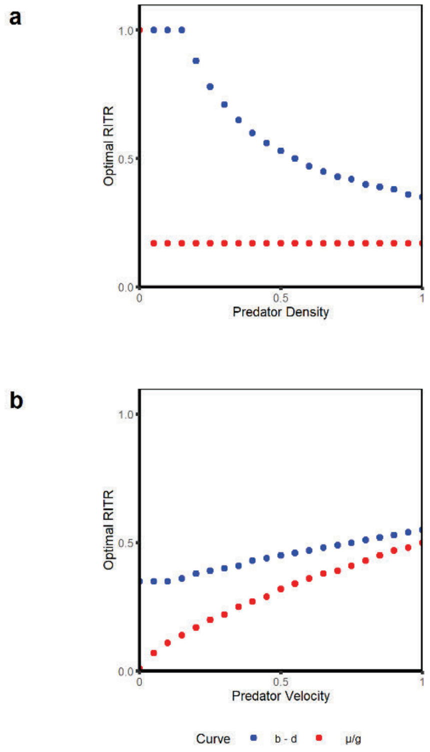


Fig. S2. The relationship between the predicted optimal RITR and a) predator density and b) predator velocity, where a predator with a low velocity is akin to a "sit-and-wait" predator, while a predator with a high velocity is more akin to an actively foraging predator. Blue dots represent the optimal RITR when fitness is optimized by maximizing the difference between growth and mortality due to predation (b – d, as in the main text), while red dots show the optimal RITR when fitness is optimized by minimizing μ/g. When using μ/g rule, the optimal RITR a) does not change with increasing predator density, but b) increases when prey are faced with a more actively foraging predator.