CONCEPTS, REVIEWS AND SYNTHESES

Proportional fitness loss and the timing of defensive investment: a cohesive framework across animals and plants

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Abstract

The risk of consumption is a pervasive aspect of ecology and recent work has focused on synthesis of consumer–resource interactions (e.g., enemy–victim ecology). Despite this, theories pertaining to the timing and magnitude of defenses in animals and plants have largely developed independently. However, both animals and plants share the common dilemma of uncertainty of attack, can gather information from the environment to predict future attacks and alter their defensive investment accordingly. Here, we present a novel, unifying framework based on the way an organism's ability to defend itself during an attack can shape their pre-attack investment in defense. This framework provides a useful perspective on the nature of information use and variation in defensive investment across the sequence of attack-related events, both within and among species. It predicts that organisms with greater proportional fitness loss if attacked will gather and respond to risk information earlier in the attack sequence, while those that have lower proportional fitness loss may wait until attack is underway. This framework offers a common platform to compare and discuss consumer effects and provides novel insights into the way risk information can propagate through populations, communities, and ecosystems.

Keywords Predation risk · Herbivory · Induced defense · Anti-predator response · Information · Non-consumptive effects · Trait-mediated effects · Vulnerability

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Animals and plants: both must cope with consumers

Consumption is a pervasive feature of ecological systems, yet our understanding of predator–prey and plant–herbivore interactions has largely developed independently. This separation may have its origins in influential historical work arguing that while prey were limited by predators and parasites, plants were limited by resources rather than their consumers (e.g., Hairston et al. 1960). More recently, ecologists have begun to appreciate the similarities among consumers' effects, particularly parasite and predator effects on prey; e.g., enemy–victim ecology (Lafferty and Kuris 2002; Raffel et al. 2008; Lafferty et al. 2015). Far fewer studies have examined the commonality of prey and plant responses to their respective consumers (e.g., Hunter 2016; Karban et al. 2016; Niu et al. 2018). The separate developmental trajectories of these disciplines reflect their obvious differences. Many prey, for example, can employ an array of cognitive and behavioral adaptations to detect predators, track risk in the environment, and avoid predation, because

any successful attack is likely to prove lethal. In contrast, plants are rooted in place, have historically been thought to lack sophisticated sensory abilities and complex neural architecture, and can often survive partial consumption. Despite the differences in predator–prey and plant–herbivore interactions, both systems share a common dilemma: when to invest in defense against attack. While considerable attention has been given to understanding the substantial intra- and interspecific variation in defensive investment (e.g., Coley et al. 1985; Lima and Bednekoff 1999; Sih 1992; Stamp 2003; Orrock et al. 2015), differences across taxa are often difficult to reconcile. We suggest that a simple framework based on characteristics that prey and plants share, i.e., differences in proportional fitness loss across the sequence of attack-related events and the ability to gather and use information about the probability of attack, can add to our understanding of predator–prey and herbivore–plant interactions and provide insight into the variation in defense of both prey and plants.

Prey and plants must balance the costs of being consumed (or damaged) with the costs of unnecessary defense. They share a common solution to this problem: when information is not too costly to gather (Sih 1992; Chittka et al. 2009), both prey and plants use environmental cues to fine-tune their defensive strategies (Karban et al. 1999; Stankowich and Blumstein 2005). This is one of the foundations of the 'ecology of fear', whose implications have been well studied in predator–prey systems (Brown et al. 1999; Clinchy et al. 2013; Sheriff et al. 2020). Plants can also adjust their responses to both the timing and nature of cues about herbivory (Karban and Baldwin 1997; Karban et al. 1999; Heil 2014), with consequences extending beyond the focal plant (Ohgushi 2005). Given the ubiquity of defensive plasticity and widespread use of information to tailor defensive investment in both prey and plants (Caro 2005; Karban et al. 2016), we suggest that an organism's proportional fitness loss if attacked (PFL; Box 1), rather than the prey/plant classification per se, most strongly influences the nature of information gathering and use.

We propose a framework for predicting the dynamics of defensive investment based upon the rate at which expected fitness is lost across the sequence of attack-related events of predator–prey or herbivore–plant interactions (Fig. 1). Importantly, defensive investment across the sequence depends upon both the costs of not responding and the costs of responding too early, both of which can depend not only on an individual's PFL and their willingness to pay such costs, but also on individual state (e.g., risk of starvation; Box 1). The idea that an individual's PFL is a key factor determining the timing and magnitude of the response to risk of consumption has several implications. First, it provides a unifying, common platform among taxa to discuss and compare variable and often context-specific responses

to the risk of predation or herbivory. In doing so, it provides a predictive framework for understanding which individuals within a population and which species within a community will be most responsive to changes in the risk of consumption. For example, it provides a clear explanation of why predation risk appears to evoke stronger reactions in small mammals like mice than large ungulates like elk. Our framework reveals that mice have a far higher potential PFL and thus respond earlier—but not necessarily 'more'—than elk (Fig. 1), which may simply be delaying their response given their low PFL if attacked (thus the timing of when prey responses are recorded may significantly bias our perspective of risk responses). Second, it provides novel insights into how information about risk can propagate through populations, communities, and ecosystems depending upon the comparative PFL of species within a given system.

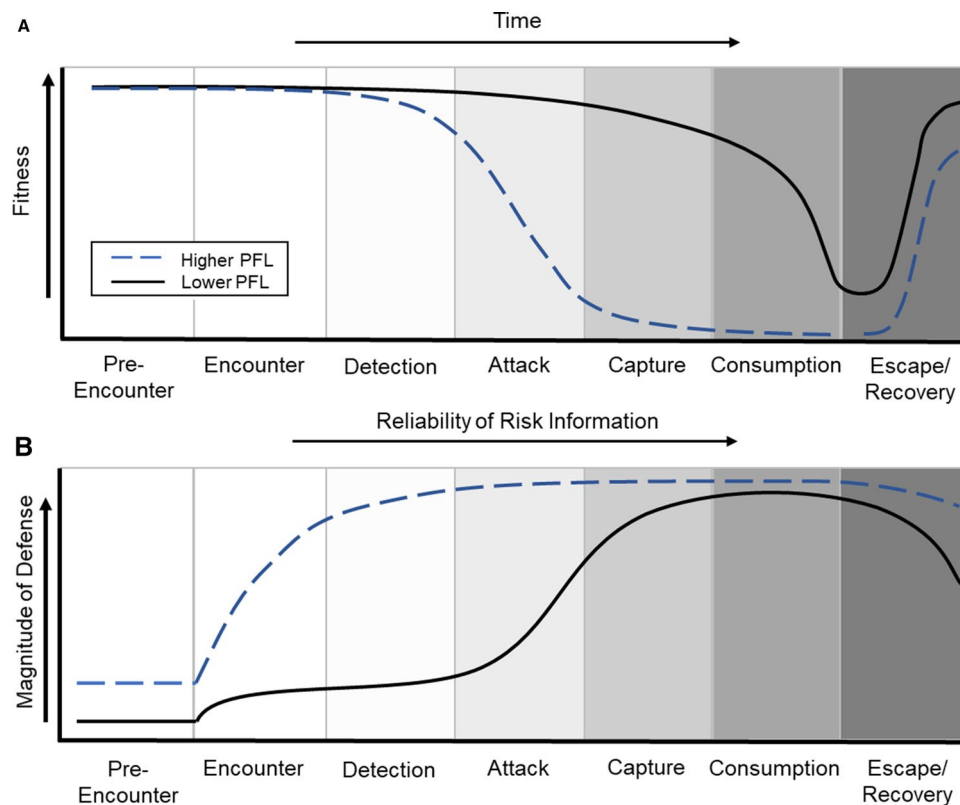# Defensive investment across a common interaction sequence

The concept of PFL requires an appreciation for the common sequence of attack-related events shared during both predator–prey and herbivore–plant interactions (pre-encounter spatiotemporal overlap, encounter, detection, attack, capture, consumption, post-interaction escape/recovery; Lima and Dill 1990; Karban and Baldwin 1997; Caro 2005; Guiden et al. 2019; Fig. 2). Both prey and plants can alter the outcome of interactions with their attackers by altering the timing of defensive investment as the sequence proceeds.

Pre-encounter spatiotemporal overlap

In consumer–resource interactions, the first step in the interaction sequence is spatiotemporal overlap—when consumers and resources occupy the same area at the same time (Schmitz et al. 2017). Consumers should generally seek to increase this overlap, while their resources should attempt to reduce it (i.e., the space-race concept; Sih 2005); mobile prey have a great advantage in this compared to plants. Defensive initiation at this stage will reduce encounter probability but may come at the costs of unnecessary defense (e.g., not occupying an area of high food availability). Importantly, defensive investment at this stage depends upon information gained by the prey or plant during a prior predation/herbivory event and the potential PFL of the individual based upon this prior event.

Encounter

An encounter occurs when the distance between a predator and prey is less than the detection range of one or both participants (Lima and Dill 1990). This definition of encounter

Fig. 1 An individual's proportional fitness loss if defense is initiated during attack (PFL; Box 1) should reflect the timing and magnitude of defensive investment across the interaction sequence. We highlight two qualitative scenarios that represent the range of possibilities we envision. (Dashed Line) Individuals that experience rapid, significant losses of fitness once an attack begins (i.e., individuals with higher PFL; dashed line panel A) should implement defenses relatively early in the interaction sequence (dashed line panel B), as implementation of early defenses maximizes that likelihood that the predator or herbivore attack will be unsuccessful or attack will not occur. (solid line) Individuals that experience lower PFL if an attack begins, and may even be able to survive partial consumption (solid line panel A), should respond late in the encounter sequence (solid line panel B) to minimize the costs of unnecessary defense. The magnitude of

defense exhibited by individuals during the pre-encounter stage may depend upon their prior experience, as such individuals with higher PFL (dashed line) will likely have higher defensive investment during this stage. While individuals can alter the sequence by escaping during this stage (and thus entering the escape recovery stage directly), the return of individuals to a baseline defense level (panel B) and maximum fitness potential (panel A) will likely be slower in individuals with higher PFL; which in turn will alter the initial magnitude of defense during the pre-encounter stage. Because this is a relative scale, the magnitude and timing of defensive investment may differ among individuals within and among populations or among individuals of different species within a community. Note that as the interaction sequence progresses the reliability of risk information also increases

also applies to herbivore–plant systems; although herbivores typically detect plants from greater distances, plants can detect cues, including volatile signals from other plants and herbivores (Helms et al. 2017, 2019; Markovic et al. 2019). While spatial overlap has traditionally been used to evaluate encounter probability, recent studies also emphasize the importance of temporal overlap (Guiden et al. 2019). Prey can thus avoid encounters by reducing their use of risky areas in both space (e.g., landscape of fear, Laundré et al. 2001) and time (e.g., Smith et al. 2019). Although plants are less able to avoid spatial overlap with herbivores, they may alter their defensive investment in time to avoid encounters and reduce the probability of herbivore attack. For example, foliar nyctinasty (daily movement of plant leaves) may reduce encounters with herbivores by reducing leaf

availability at night (Minorsky 2019). There is also evidence that plants may preempt attack in time by adjusting their defensive investment to be greater during times of day when encounter with an attacker is more likely (Falk et al. 2014).

Detection

Detection can occur sequentially (e.g., the consumer first detects the prey or plant, or vice versa) or simultaneously (the consumer and victim detect each other at the same time). Defensive initiation at this stage requires prey and plants to gather, identify (e.g., recognize the consumer as a threat), and respond to risk information. The type and magnitude of defensive initiation will depend upon costs and benefits of a particular response given the information
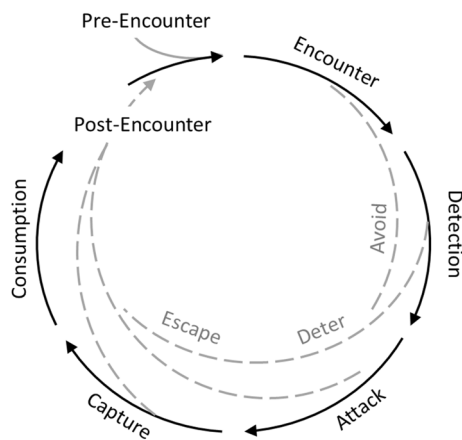
Fig. 2 The common sequence of attack-related events shared during both predator–prey and herbivore–plant interactions. Interactions begin during a pre-encounter spatiotemporal overlap stage and end in a post-encounter escape/recovery stage (or death if consumption is lethal). Depending upon the timing and magnitude of prey/plant defense (which is reliant on their PFL), prey/plants can avoid, deter, and escape from their consumers altering the outcome of this sequence at any stage and enter the post-encounter stage (dashed lines). Importantly, this sequence does not proceed in a simple linear fashion and any previous encounter with a consumer will influence future encounters (i.e., the post-encounter experience will influence pre-encounter defensive investment)

provided by the cue (Orrock et al. 2015). For example, cues indicative of imminent attack (e.g., auditory cues or consumption of conspecifics) are likely to evoke greater responses than cues (e.g., feces or urine) that only suggest consumers are within the vicinity (Kim et al. 2011; Hermann and Thaler 2014; Parsons et al. 2018). It is important to note, however, that even informed resources (be they prey or plants) may not respond as expected due to other constraints (McNamara and Houston 1986; Brown and Kotler 2004; Sheriff et al. 2020). For example, *Nucella lapillus* snails (prey) adjusted their foraging response to predatory crabs relative to their body condition (Matassa et al. 2016). Some plants will modify their touch-induced leaf-closing time as a function of available resources (Jensen et al. 2011).

These responses can be considered within our framework and will depend upon the PFL of the prey or plant if attack occurs. For example, state-dependent foraging theory (McNamara and Houston 1992) predicts organisms in good condition should initiate defenses early because they can pay the cost of reduced foraging. This dovetails with predictions from our framework: good-condition individuals also have the highest initial fitness potential and thus a relatively high PFL if attacked. In contrast, poor-condition individuals have relatively low initial fitness potential (i.e., they may die regardless of risk) and thus a lower PFL if attacked (Box 1).

Attack, capture, and consumption

If consumers detect prey or plant an attack may occur (e.g., an approach or chase), which may result in the initiation of consumption if the prey or plant is incapable of avoiding capture. It is at these stages that a clear distinction arises between prey and plants. First, capture is less likely for mobile prey than for immobile plants. Further, once an attack is initiated, prey must initiate defense to avoid their likely-lethal capture and consumption. Plants, particularly mature individuals, may take advantage of the potentially low PFL to wait until attack or even consumption begins to initiate defense (Karban and Baldwin 1997; Kim et al. 2011). Interestingly, this does not necessarily hold true for seed predation, which is often lethal to immature plants; consistent with our PFL framework, seeds are often highly defended prior to any attack. Within the idea of PFL, the initiation of defense prior to attack and consumption will depend upon the ability of organisms to defend during an attack (Box 1).

Post-interaction escape/recovery

At any point in the sequence prey and plants may end the interaction depending upon the timing of their defensive investment and ability to evade their consumer. Because consumption is generally lethal for prey, this would benefit prey most prior to their capture; for plants, this is likely to occur post-consumption. Importantly, this stage is not the end of the defensive investment for individuals. For example, we expect individuals with higher PFL to prolong their post-interaction defensive investment relative to individuals with lower PFL (Sih 1992; Gil et al. 2018). This past experience will also prime individuals for their next encounter; their PFL will likely alter the timing and magnitude of their defensive investment during the pre-encounter spatiotemporal overlap stage.

A unifying framework to understand defensive investment among taxa

Proportional fitness loss as an underlying principle

The concept of PFL, as we define it here (Box 1), can be characterized broadly across taxa as the proportional loss of relative fitness if an individual does not initiate defense until attacked. This proportional loss of relative fitness accounts for both the ability of an individual to defend early in the interaction sequence and its ability to defend during an attack. It can be measured as the fitness potential if defense is initiated prior to attack (e.g., during an encounter or detection) compared to that if defense is initiated after attack has

begun (Box 1). As such, these ideas can extend beyond the general prey and plant classification and be used to compare individuals within and among populations and can also be broadly applied to compare individuals among species.

In natural systems, there are several stages along the interaction sequence prior to attack and the beginning of consumption where individuals can initiate defense. For example, ungulates can initiate defense during both the encounter (e.g., alter temporal habitat use) and the detection stage (e.g., fleeing), yet, there are also many cases where predators are able to initiate an attack (e.g., a chase) prior to prey detection and prey are only able to initiate defense (e.g., flee) after the attack has begun. Plants can also detect the presence of herbivores prior to attack (Helms et al. 2017, 2019; Heil and Karban 2010; Orrock et al. 2018), however, there are also times when plants do not detect herbivore presence until capture (e.g., occupation of a leaf, Peiffer et al. 2009; ovipositing of herbivore eggs onto leaves, Hilker and Meiner 2006) or even consumption has begun, and thus only initiate defense (e.g., increase alkaloids) thereafter (Kim et al. 2011). It is the comparison of the proportional loss of relative fitness if prey or plants initiate defense at a stage prior to attack vs. if they initiate defense during attack that is the practical measure of PFL (Box 1).

It is important to appreciate that the efficacy and timing of any increase in defensive investment may depend upon the unique characteristics of the individual prey or plant and the landscape in which they are encountered. Age, health, the presence of chemically or physically defended parts, sensory ability and cue recognition, relative mobility, size as well as landscape features like refuges can all influence the ability to evade and defend against attack and escape consumption (Stankowich and Blumstein 2005; Preisser and Orrock 2012; Karban et al. 2016; Sheriff et al. 2020). For example, size may reduce an individual's PFL by increasing its ability to evade and thwart an attack (e.g., Luttbeg and Sih 2010; Wishingrad et al. 2014); i.e., if attacked, larger individuals may have stronger escape potential and reduced fitness-loss, shifting individuals from high PFL (dashed line) to low PFL (solid line) in Fig. 1, as they grow. Alternatively, if protecting offspring increases potential fitness costs during an attack, individuals with offspring may have a higher PFL and respond earlier along the interaction sequence, shifting individuals from low PFL (solid line in Fig. 1) to high PFL (dashed line in Fig. 1).

It is also important to remember that prey and plants express defenses at some baseline level (i.e., constitutive defenses) independent of risk cues. Use of constitutive defenses is expected when levels of attack are consistently high, when cues from the environment are not useful in predicting attack, or when defenses cannot be induced quickly enough. Work on Trinidadian guppies has shown that their

life-history traits (i.e., antipredator behavior) depend upon whether they live in systems with high vs low predation (Reznick and Endler 1982; Reznick et al. 1990). Importantly, appreciating potential prior exposure to the risk of consumption, whether over evolutionary or ecological time, may alter predictions pertaining to individual PFL and the timing of defensive investment; i.e., prior experience may prime individuals in their defensive response. Within our framework, constitutive defenses can be considered to occur prior to the start of the interaction sequence and thus lower PFL compared to not having constitutive defenses. For example, in many plant species, individuals (or their modular parts) that have a high level of constitutive defense (e.g., high levels of xanthotoxin) display weak defensive investment (e.g., induced increases in xanthotoxin) when attacked compared to those individuals (or parts) that do not display constitutive defenses (Zangerl and Rutledge 1996). Additionally, constitutive defenses could be considered to occur very early given the future potential for an attack-related interaction to occur. For example, many studies in both prey and plants have shown that parental exposure to predation risk or herbivory results in offspring with greater antipredator/herbivore defenses even though the offspring have yet to experience risk of consumption (Rossiter 1996; Agrawal et al. 1999; Sheriff et al. 2010, 2017; Holeski et al. 2012; Tigreros et al. 2017; Donelan et al. 2020). Within our framework, we predict that the magnitude of transgenerational or constitutive defensive investment would be greatest in species or populations where naïve individuals (those without prior information, whether transgenerational or evolutionary) have the highest PFL. Thus, we propose that the concept of relative PFL, both within and across taxa, provides a unifying, common framework for determining how and when individuals should gather and utilize information, and underlies an individual's ability to develop and implement defensive strategies for minimizing the fitness costs of an attack.

Defense amidst uncertainty

Although differences in sensory abilities among taxa must be considered (Karban et al. 2016; Weissburg et al. 2014), the timing of when to gather and use risk-related information in the interaction sequence can depend greatly on an individual's PFL (Fig. 1). Since the reliability of risk-related information increases as the sequence progresses, later-responding organisms should be more capable of fine-tuning defensive investment and reduce the costs of unnecessary defense—an advantage that must be balanced against the costs of not responding early enough (Bateman et al. 2014; Orrock et al. 2015). For example, small mammals gather and use information very early in the interaction sequences (e.g., moonlight-induced reductions in activity; Prugh and

Golden 2014) and continue throughout the sequence, since captured individuals are unlikely to survive. Many prey will continue to collect and process information even after the encounter ends (likely in preparation for another potential attack), since the ability to track and respond to risk cues even in the absence of an attack is highly beneficial (Sih 1992). At the other end of the spectrum, low to moderate levels of herbivory often have such low fitness costs for trees or other large plants (Karban and Baldwin 1997) that they can afford to wait until attack or even consumption to gather and use risk-related information. This concept can be extended beyond the generalized classification of prey or plants; by comparing the relative PFL among individuals or among species within a community predictions can be made within populations and across taxa on the timing and magnitude of defensive investment throughout the interaction sequence (Box 1, Fig. 1). It also has implications for how risk information can propagate among individuals and communities.

The transmission and use of risk information

The propagation of risk information among individuals

For many prey, group size and composition are important factors altering the relative risk experienced by a given individual (Hamilton 1971; Bednekoff and Lima 1998a). This may result from improved predator detection (the 'many eyes' hypothesis) or increased dilution of individual risk, assuming that predators can kill only a small number of group members at a time (Bednekoff 1997). Although early models assumed that detection by any group member would provide equal benefits to all members, individuals differ in their vulnerability and information about risk. Within a group, an individual must detect and respond to a predator prior to a certain time point (t) to reach safety, or must detect and respond to the primary detector. However, given that a secondary responder has a lag (l) in their response, the primary detector must respond to a predator at $t + l$ in order for the second individual to react in time to reach safety (Bednekoff and Lima 1998b). We can extend this model of primary vs. secondary responders to incorporate the concept of PFL. Take, for example, a group in which all individuals have an equivalent fitness potential if they initiate defense very early (e.g., 100% survival probability). Some group members will have a lower fitness potential if they initiate defense during an attack, and thus, they will have a higher rate of fitness loss across the interaction sequence and a higher PFL (dashed line in Fig. 1). Thus, to maintain an equivalent fitness potential, individuals with a higher PFL need to respond earlier in the interaction sequence, and, thus, have a larger value of t (time required to reach safety) compared to individuals with a lower PFL.

From this, we can make predictions based on the PFL of the primary, secondary (and tertiary, etc.) responders, which will yield very different outcomes for individual and group responses. Most often, we expect individuals with the highest PFL within a group to be the primary detectors and responders, leaving ample time for other individuals to respond, but this may not always be the case. In semi-fossorial groups (e.g., ground squirrel colonies), individuals living in the periphery of the habitat may have a lower likelihood of surviving an attack, and thus have a higher PFL. However, living in sub-optimal habitats may also lead to reduced visibility (Werner et al. 2015). In such scenarios, individuals with lower PFL may be the primary detectors and, thus, may not respond until later in the interaction sequence, possibly later than the required time ($t + l$) for a secondary responder, particularly if that secondary responder is less likely to survive an attack and needs to respond early (i.e., has a greater value for t). Of course, time required to reach safety may also depend upon how many other individuals are simultaneously fleeing from consumers, and thus, complex games may emerge (Gil et al. 2018). Future work could test hypotheses pertaining to the relationship between PFL, primary vs. secondary detectors/responders, and population level mortality to explore the transmission of risk information among group members and across species (Valone and Templeton 2002; Gil et al. 2018).

Plants, although single individuals, have multiple redundant parts and may respond more like a group of closely related animals than a single genetically-unique individual (Karban et al. 2016). When attack and consumption are initiated, plants respond by inducing defenses and reallocating resources to unattacked and less accessible parts (Schultz et al. 2013). Considering the plant as a group and each component as an individual allows us to ask similar questions as we do with animal groups. For example, do tissues with a higher PFL have a faster and stronger response to herbivory (McKey 1974; Zangerl and Rutledge 1996)? Does the propagation of risk signals occur more quickly through young plants with higher PFL than through mature individuals?

Individuals within clonal groups likely have very different responses than individuals within unrelated/partially related groups, given that consumption of a single individual is unlikely to result in death of the entire colony or clonal group (Harvell 1990). They can thus gather highly reliable information late in the interaction sequence to optimize their defense (assuming risk information transfer among clonal individuals occurs). For example, the consumption of some soldiers in clonal aphid colonies alters colony-level allocation to defense without high fitness costs (Aoki and Kurosu 2004). As such, use of risk information and defensive investment should occur at the colony level, not at the individual

level. This line of reasoning can be further extended to provide novel insights into defensive investment as a function of colony size or age: young, small colonies of clonal or eusocial organisms should respond strongly and early in the interaction sequence because of the greater cost of losing some individuals, whereas large, mature colonies should respond less strongly at the same point in the interaction sequence. An additional, unappreciated suggestion that follows from our perspective is that the potential to reduce the costs of activating unnecessary defenses may provide a selective advantage to clonality and eusociality. Alternatively, sessile prey may provide an interesting contrast as a single individual that is immobile. Future studies comparing anti-consumptive responses between clonal groups (animals or plants), sessile prey, and plant individuals may provide further insights into the commonalities of defensive investment.

Importantly, although we emphasize the role of PFL in information transfer pertaining to the arrival of consumers/predators, PFL also affects the ability of organisms to gain information required to re-emerge from a defended state (a key determinant of the cost of defensive responses; Gil et al. 2018). For example, the fact that organisms with a high PFL often remain in refuges long after predators have left (e.g., Sih 1992) likely influences their willingness to enter such areas. Once defense is initiated, plants remain in the defended state for long periods of time; relaxation of this state appears less responsive to cues than the initial induction (Huntzinger et al. 2004). Further, organisms with low PFL may re-emerge more quickly from a defensive state and actually facilitate other organisms leaving (Gil et al. 2018). Thus, information about the loss of risk may transfer from individuals with a low PFL to individuals with a higher PFL.

Across both prey and plants, our perspective emphasizes how the PFL of one individual (as well as the components of a more modular individual, e.g., plants) can alter the efficacy of signaling to another, and how the PFL of the second can in turn alter the efficacy of its response. A general prediction is that information about increased risk should move from higher- to lower-PFL individuals, while the opposite may occur for information regarding decreased risk. Future work should focus on how risk information moves throughout groups comprised of individuals of similar age/state relative to more heterogeneous groups. In general, our 'susceptibility perspective' illustrates how the value of information depends critically upon the state of the sender relative to the receiver, something the receiver may or may not be able to estimate (Danchin et al. 2004).

The propagation of risk information through communities

We also expect that the rate at which risk information propagates through food webs and across trophic levels (e.g., trait-mediated indirect interactions) may be determined by the relative PFL of species within the system. A simple expectation is that responses to predators should be stronger in systems characterized by prey with relatively higher PFL. For example, Chase (2003) showed that in systems dominated by vulnerable snails (high PFL), predator effects were strong and cascaded to plant resources; however, in systems dominated by relatively invulnerable snails, predator effects were weak and did not cascade to plant resources. Our framework would predict that the reduction in defensive investment by plant resources is likely to be higher in the former system compared to the later. Further, if the timing of response determines the ultimate rate of propagation through a food web, then behaviorally mediated cascades would be most rapid in systems of prey with relatively high PFL. In addition, information about the loss of risk (i.e., when predators or herbivores leave an area) may be most rapidly transmitted in communities with organisms that have relatively low PFL. Conversely, primary responding species may be those with the greatest competitive ability for resources, while those that transmit information about the loss of risk may be the poorest competitors (Gil et al. 2018). Considering both the PFL and competitive ability of species within a community may provide unique insights into how risk information is transmitted among species.

Our perspective may also provide novel insights and predictions pertaining to the magnitude of trophic interactions and the relative strength of top-down and bottom-up factors influencing ecosystem dynamics. For example, because of their extreme vulnerability, if attacked (i.e., if attacked they are likely to die and thus a high PFL), rodents and other small mammals respond very early in the interaction sequence (e.g., to moonlight), thereby significantly decreasing their consumption of seeds and plants when there is little risk information (Orrock and Fletcher 2014). Alternatively, large ungulates (with low PFL) may not alter their foraging behavior until an attack is imminent (Middleton et al. 2013), and their foraging activities may be more driven by spatial and temporal variation in food quantity and quality (but see Valeix et al. 2009; Tambling et al. 2015). Trophic interactions in systems dominated by organisms with relatively high PFL may be more driven by top-down processes because of the risk-induced shifts in herbivore behavior, while those dominated by organisms with relatively low PFL may be more driven by bottom-up processes.

Concluding remarks

The obvious differences between prey and plants can lead us to overlook their similarities: both live in variable environments with uncertain risk, and both utilize information to maximize their fitness. Considering an organism's relative PFL if attacked and the influence of PFL on the timing of information gathering and use across the interaction sequence provides a common framework under which future studies can understand consumer–resource relationship. Further, focusing on productive similarities between the disciplines will provide additional insights and allow cross-talk of theories about the general consequences of consumptive interactions.

Although a variety of approaches may be used, comparative studies that use a range of taxa and combinations of risk information cues will be particularly promising in helping disentangle the role of PFL and information in affecting allocation to defense. As such, this framework could be used to gain a better understanding of:

1. Why predation risk or herbivory seems more of a factor in some systems than others; for example, in systems where PFL is high (e.g., snowshoe hare—lynx) risk of consumption may be a greater factor than in systems where PFL is low (e.g., wolf-elk).
2. How ecological and environmental context influences consumer–resource interactions; for example: (a) increases in resource (prey or plant) abundance may reduce PFL and thus alter responses to the risk of consumption; (b) the average toxicity of individuals in a population may alter consumer efficacy and thus alter PFL and resource responses to consumption; (c) in areas with more refuges, individuals may have reduced PFL, because they can likely better escape when attacked, and thus, will delay their response to predation risk compared to areas without refuges; (d) ambush predators may create a significant increase in PFL compared to cursorial predators, and this drives the earlier and greater response in prey (Schmitz 2007).
3. The role of consumer risk in mediating trophic interactions and how risk information transfers within and among systems; for example: (a) understanding individual PFL may help distinguish between information transfer about impending/arriving risk vs. information transfer about safety (allowing organisms to resume activity); (b) cross-species information transfer may be mediated by the relative PFL of different species within the community.
4. How the ontogeny of prey and plants alters their investment in defense; for example, PFL likely differs across ontogeny and this may help predict changes in defensive investment, with stages where individuals have greater PFL having increased defensive investment.

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Box. 1: Proportional fitness loss of an individual and its timing of defense

We suggest the proportional fitness loss (PFL) if an individual does not initiate defense until attacked is a critical component of understanding its defensive investment. PFL relies on an individual's fitness potential if it initiates defense prior to an attack compared to its fitness potential if it initiates defense during an attack. For example, individual A is 50% likely to survive if it defends during the detection stage and only 20% likely to survive if it defends during an attack, its PFL is 60% ((50−20)/50). Individual B has a 95% chance of surviving if it defends during the detection stage and a 30% chance of survival, if it defends during an attack, its PFL is 68%. From this scenario, it becomes clear that the PFL of an individual depends on both its ability to survive an attack and, also, the effectiveness of its early defense. In such a scenario, individual B has a higher PFL and should initiate defense earlier than individual A, even though it has a higher probability of surviving an attack. Our concept helps to clarify why individuals with low expected fitness, regardless of whether they initiate defense early or late (thus a low PFL), would be expected to wait and initiate defense late (if at all) given the ineffectiveness of their (early) defense.

The fact that consumer-resource encounters progress through time along a common interaction sequence of events (Lima and Dill 1990; Karban and Baldwin 1997, Caro 2005; Fig. 1) allows us to build relative PFL curves across the interaction sequence to better understand the timing of defensive investment. As individuals delay their defensive investment, their fitness potential will approach that which they would have if they did not invest in defense until attacked. This also allows us to

visualize inflection points where fitness potential will greatly decrease if defense is not initiated. In the first two examples above, the fitness potential difference between early and late defensive investment is relatively large and, if their PFL curve was relatively linear, both individuals may greatly increase their survival for incremental advances in the timing of their defense. Alternatively, if, for example, we extend the above scenario such that individual A had a 95% chance of survival if it defended during the encounter stage (thus a PFL of 79% between encounter and attack, but a 47% PFL between encounter and detection), while individual B had a 99.9% chance of survival if it defended during the encounter stage (thus a PFL of 70%, but only 4% PFL between encounter and detection), our curve would predict that individual A would most benefit from defending during the encounter stage, while individual B may benefit from delaying defensive investment until the detection stage.

Additionally, if individuals invest too early or respond to unreliable information they will pay a cost of unnecessary defense (e.g., cost of defense itself, missed opportunity costs, reductions in growth and reproduction). The willingness of individuals to pay a cost of unnecessary defense will also depend on their PFL. Individuals with a high PFL can pay a relatively high cost of unnecessary defense and still benefit significantly from early defensive investment. Alternatively, individuals with a low PFL if attacked may not be willing to pay as high a cost of unnecessary defense and should defend relatively later.

While we discuss the fitness aspect of PFL as a loss of survival, individual fitness could also be measured as a loss of reproduction (number of babies born or weaned, loss of litters, loss of seed set or flowers, etc.) or a loss of growth or tissue (in many species growth is directly related to reproductive potential and in the case of plants or other organisms that can be partially consumed a loss of tissue may be a better metric) if attacked. It is important to appreciate that in these latter two fitness measures, with respect to PFL, the loss of fitness is due to attack not the initiation of defense (as is often the case). Because of this, however, these latter two fitness measures may be particularly insightful given (i) they can be used to estimate PFL if attacked, but also the cost of unnecessary defense (defending too early) and (ii) that they can be used to estimate the loss of relative fitness at any point along the interaction sequence when defense is initiated. Understanding an individual's PFL across the interaction sequence will provide valuable insights into when it should initiate defense and has significant implications for understanding how prey and plants will respond to the risk of consumption.

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