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

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2 **cohesive framework across animals and plants**

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4 Running Title: PFL and the timing of defensive investment

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26   **Abstract**

27   The risk of consumption is a pervasive aspect of ecology and recent work has focused on

28   synthesis of consumer-resource interactions (e.g., enemy-victim ecology). Despite this, theories

29   pertaining to the timing and magnitude of defenses in animals and plants have largely developed

30   independently. However, both animals and plants share the common dilemma of uncertainty of

31   attack, can gather information from the environment to predict future attacks and alter their

32   defensive investment accordingly. Here, we present a novel, unifying framework based on the

33   way an organism's ability to defend itself during an attack can shape their pre-attack investment

34   in defense. This framework provides a useful perspective on the nature of information use and

35   variation in defensive investment across the sequence of attack-related events, both within and

36   among species. It predicts that organisms with greater *proportional* fitness loss if attacked will

37   gather and respond to risk information earlier in the attack sequence, while those that have lower

38   *proportional* fitness loss may wait until attack is underway. This framework offers a common

39   platform to compare and discuss consumer effects and provides novel insights into the way risk

40   information can propagate through populations, communities, and ecosystems.

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49 **Animals and plants: both must cope with consumers**

50 Consumption is a pervasive feature of ecological systems, yet our understanding of predator-prey

51 and plant-herbivore interactions has largely developed independently. This separation may have

52 its origins in influential historical work arguing that while prey were limited by predators and

53 parasites, plants were limited by resources rather than their consumers (e.g., Hairston et al.

54 1960). More recently, ecologists have begun to appreciate the similarities among consumers'

55 effects, particularly parasite and predator effects on prey; e.g., enemy-victim ecology (Lafferty

56 and Kuris 2002; Raffel et al. 2008; Lafferty et al. 2015). Far fewer studies have examined the

57 commonality of prey and plant responses to their respective consumers (e.g., Hunter 2016;

58 Karban et al. 2016; Niu et al. 2018). The separate developmental trajectories of these disciplines

59 reflect their obvious differences. Many prey, for example, can employ an array of cognitive and

60 behavioral adaptations to detect predators, track risk in the environment, and avoid predation,

61 because any successful attack is likely to prove lethal. In contrast, plants are rooted in place,

62 have historically been thought to lack sophisticated sensory abilities and complex neural

63 architecture, and can often survive partial consumption. Despite the differences in predator-prey

64 and plant-herbivore interactions, both systems share a common dilemma: when to invest in

65 defense against attack. While considerable attention has been given to understanding the

66 substantial intra- and interspecific variation in defensive investment (e.g., Coley et al. 1985;

67 Lima and Bednekoff 1999; Sih 1992; Stamp 2003; Orrock et al. 2015), differences across taxa

68 are often difficult to reconcile. We suggest that a simple framework based on characteristics that

69 prey and plants share, i.e., differences in proportional fitness loss across the sequence of attack-

70 related events and the ability to gather and use information about the probability of attack, can

71 add to our understanding of predator-prey and herbivore-plant interactions and provide insight

72   into the variation in defense of both prey and plants.

73   Prey and plants must balance the costs of being consumed (or damaged) with the costs of

74   unnecessary defense. They share a common solution to this problem: when information is not too

75   costly to gather (Sih 1992; Chittka et al. 2009), both prey and plants use environmental cues to

76   fine-tune their defensive strategies (Karban et al. 1999; Stankowich and Blumstein 2005). This is

77   one of the foundations of the 'ecology of fear', whose implications have been well studied in

78   predator-prey systems (Brown et al. 1999; Clinchy et al. 2013; Sheriff et al. 2020). Plants can

79   also adjust their responses to both the timing and nature of cues about herbivory (Karban and

80   Baldwin 1997; Karban et al. 1999; Heil 2014), with consequences extending beyond the focal

81   plant (Ohgushi 2005). Given the ubiquity of defensive plasticity and widespread use of

82   information to tailor defensive investment in both prey and plants (Caro 2005; Karban et al.

83   2016), we suggest that an organism's proportional fitness loss if attacked (PFL; Box 1), rather

84   than the prey/plant classification *per se*, most strongly influences the nature of information

85   gathering and use.

86   We propose a framework for predicting the dynamics of defensive investment based upon

87   the rate at which expected fitness is lost across the sequence of attack-related events of predator-

88   prey or herbivore-plant interactions (Fig. 1). Importantly, defensive investment across the

89   sequence depends upon both the costs of not responding and the costs of responding too early,

90   both of which can depend not only on an individual's PFL and their willingness to pay such

91   costs, but also on individual state (e.g., risk of starvation; Box 1). The idea that an individual's

92   PFL is a key factor determining the timing and magnitude of the response to risk of consumption

93   has several implications. *First*, it provides a unifying, common platform among taxa to discuss

94   and compare variable and often context-specific responses to the risk of predation or herbivory.

95   In doing so, it provides a predictive framework for understanding which individuals within a

96   population and which species within a community will be most responsive to changes in the risk

97   of consumption. For example, it provides a clear explanation of why predation risk appears to

98   evoke stronger reactions in small mammals like mice than large ungulates like elk. Our

99   framework reveals that mice have a far higher potential PFL and thus respond earlier – but not

100   necessarily 'more' - than elk (Fig. 1), which may simply be delaying their response given their

101   low PFL if attacked (thus the timing of when prey responses are recorded may significantly

102   biased our perspective of risk responses). *Second*, it provides novel insights into how

103   information about risk can propagate through populations, communities, and ecosystems

104   depending upon the comparative PFL of species within a given system.

105

106   **Defensive investment across a common interaction sequence**

107   The concept of PFL requires an appreciation for the common sequence of attack-related

108   events shared during both predator-prey and herbivore-plant interactions (pre-encounter

109   spatiotemporal overlap, encounter, detection, attack, capture, consumption, post-interaction

110   escape/recovery; Lima and Dill 1990; Karban and Baldwin 1997; Caro 2005; Guiden et al. 2019;

111   Fig. 2). Both prey and plants can alter the outcome of interactions with their attackers by altering

112   the timing of defensive investment as the sequence proceeds.

113   *Pre-encounter Spatiotemporal Overlap.* In consumer-resource interactions, the first step in the

114   interaction sequence is spatiotemporal overlap – when consumers and resources occupy the same

115   area at the same time (Schmitz et al. 2017). Consumers should generally seek to increase this

116   overlap, while their resources should attempt to reduce it (i.e., the space-race concept; Sih 2005);

117   mobile prey have a great advantage in this compared to plants. Defensive initiation at this stage

118   will reduce encounter probability but may come at the costs of unnecessary defense (e.g., not

119   occupying an area of high food availability). Importantly, defensive investment at this stage

120   depends upon information gained by the prey or plant during a prior predation/herbivory event

121   and the potential PFL of the individual based upon this prior event.

122   *Encounter*. An encounter occurs when the distance between a predator and prey is less than the

123   detection range of one or both participants (Lima and Dill 1990). This definition of encounter

124   also applies to herbivore-plant systems; although herbivores typically detect plants from greater

125   distances, plants can detect cues, including volatile signals from other plants and herbivores

126   (Helms et al. 2017, 2019; Markovic et a. 2019). While spatial overlap has traditionally been

127   used to evaluate encounter probability, recent studies also emphasize the importance of temporal

128   overlap (Guiden et al. 2019). Prey can thus avoid encounters by reducing their use of risky areas

129   in both space (e.g., landscape of fear, Laundré et al. 2001) and time (e.g., Smith et al. 2019).

130   Although plants are less able to avoid spatial overlap with herbivores, they may alter their

131   defensive investment in time to avoid encounters and reduce the probability of herbivore attack.

132   For example, foliar nyctinasty (daily movement of plant leaves) may reduce encounters with

133   herbivores by reducing leaf availability at night (Minorsky 2019). There is also evidence that

134   plants may preempt attack in time by adjusting their defensive investment to be greater during

135   times of day when encounter with an attacker is more likely (Falk et al. 2014).

136   *Detection.* Detection can occur sequentially (e.g., the consumer first detects the prey or plant, or

137   vice versa) or simultaneously (the consumer and victim detect each other at the same time).

138   Defensive initiation at this stage requires prey and plants to gather, identify (e.g., recognize the

139   consumer as a threat), and respond to risk information. The type and magnitude of defensive

140   initiation will depend upon costs and benefits of a particular response given the information

141   provided by the cue (Orrock et al. 2015). For example, cues indicative of imminent attack (e.g.,

142   auditory cues or consumption of conspecifics) are likely to evoke greater responses than cues

143   (e.g., feces or urine) that only suggest consumers are within the vicinity (Kim et al. 2011;

144   Hermann and Thaler 2014; Parsons et al. 2017). It is important to note, however, that even

145   informed resources (be they prey or plants) may not respond as expected due to other constraints

146   (McNamara and Houston 1986; Brown and Kotler 2004; Sheriff et al. 2020). For example,

147   *Nucella lapillus* snails (prey) adjusted their foraging response to predatory crabs relative to their

148   body condition (Matassa et al. 2016). Some plants will modify their touch-induced leaf-closing

149   time as a function of available resources (Jensen et al. 2011).

150   These responses can be considered within our framework and will depend upon the PFL

151   of the prey or plant if attack occurs. For example, state-dependent foraging theory (McNamara

152   and Houston 1992) predicts organisms in good condition should initiate defenses early because

153   they can pay the cost of reduced foraging. This dovetails with predictions from our framework:

154   good-condition individuals also have the highest initial fitness potential and thus a relatively high

155   PFL if attacked. In contrast, poor-condition individuals have relatively low initial fitness

156   potential (i.e., they may die regardless of risk) and thus a lower PFL if attacked (Box 1).

157   *Attack, Capture, and Consumption*. If consumers detect prey or plants an attack may occur (e.g.,

158   an approach or chase), which may result in the initiation of consumption if the prey or plant is

159   incapable of avoiding capture. It is at these stages that a clear distinction arises between prey and

160   plants. First, capture is less likely for mobile prey than for immobile plants. Further, once an

161   attack is initiated, prey must initiate defense to avoid their likely-lethal capture and consumption.

162   Plants, particularly mature individuals, may take advantage of the potentially low PFL to wait

163   until attack or even consumption begins to initiate defense (Karban and Baldwin 1997; Kim et al.

164 2011). Interestingly, this does not necessarily hold true for seed predation, which is often lethal

165 to immature plants; consistent with our PFL framework, seeds are often highly defended prior to

166 any attack. Within the idea of PFL, the initiation of defense prior to attack and consumption will

167 depend upon the ability of organisms to defend during an attack (Box 1).

168 *Post-interaction Escape/Recovery*. At any point in the sequence prey and plants may end the

169 interaction depending upon the timing of their defensive investment and ability to evade their

170 consumer. Because consumption is generally lethal for prey, this would benefit prey most prior

171 to their capture; for plants, this is likely to occur post-consumption. Importantly, this stage is not

172 the end of the defensive investment for individuals. For example, we expect individuals with

173 higher PFL to prolong their post-interaction defensive investment relative to individuals with

174 lower PFL (Sih 1992; Gil et al. 2018). This past experience will also prime individuals for their

175 next encounter; their PFL will likely alter the timing and magnitude of their defensive investment

176 during the pre-encounter spatiotemporal overlap stage.

177

178 **A unifying framework to understand defensive investment among taxa**

179 *Proportional fitness loss as an underlying principle*

180   The concept of PFL, as we define it here (Box 1), can be characterized broadly across

181 taxa as the proportional loss of relative fitness if an individual does not initiate defense until

182 attacked. This proportional loss of relative fitness accounts for both the ability of an individual to

183 defend early in the interaction sequence and its ability to defend during an attack. It can be

184 measured as the fitness potential if defense is initiated prior to attack (e.g., during an encounter

185 or detection) compared to that if defense is initiated after attack has begun (Box 1). As such,

186 these ideas can extend beyond the general prey and plant classification and be used to compare

187   individuals within and among populations and can also be broadly applied to compare

188   individuals among species.

189   In natural systems, there are several stages along the interaction sequence prior to attack

190   and the beginning of consumption where individuals can initiate defense. For example, ungulates

191   can initiate defense during both the encounter (e.g., alter temporal habitat use) and the detection

192   stage (e.g., fleeing), yet, there are also many cases where predators are able to initiate an attack

193   (e.g., a chase) prior to prey detection and prey are only able to initiate defense (e.g., flee) after

194   the attack has begun. Plants can also detect the presence of herbivores prior to attack (Helms et

195   al. 2017, 2019; Heil and Karban 2010; Orrock et al. 2018), however, there are also times when

196   plants do not detect herbivore presence until capture (e.g., occupation of a leaf, Pfeiffer et al.

197   2009; ovipositing of herbivore eggs onto leaves, Hilker and Meiner 2006) or even consumption

198   has begun, and thus only initiate defense (e.g., increase alkaloids) thereafter (Kim et al. 2011). It

199   is the comparison of the proportional loss of relative fitness if prey or plants initiate defense at a

200   stage prior to attack vs. if they initiate defense during attack that is the practical measure of PFL

201   (Box 1).

202   It is important to appreciate that the efficacy and timing of any increase in defensive

203   investment may depend upon the unique characteristics of the individual prey or plant and the

204   landscape in which they are encountered. Age, health, the presence of chemically or physically

205   defended parts, sensory ability and cue recognition, relative mobility, size as well as landscape

206   features like refuges can all influence the ability to evade and defend against attack and escape

207   consumption (Stankowich and Blumstein 2005; Preisser and Orrock 2012; Karban et al. 2016;

208   Sheriff et al. 2020). For example, size may reduce an individual's PFL by increasing its ability to

209   evade and thwart an attack (e.g., Luttbeg and Sih 2010; Wishingrad et al. 2014); i.e., if attacked,

210   larger individuals may have stronger escape potential and reduced fitness-loss, shifting

211   individuals from high PFL (dashed line) to low PFL (solid line) in Fig. 1, as they grow.

212   Alternatively, if protecting offspring increases potential fitness costs during an attack,

213   individuals with offspring may have a higher PFL and respond earlier along the interaction

214   sequence, shifting individuals from low PFL (solid line in Fig. 1) to high PFL (dashed line in

215   Fig. 1).

216   It is also important to remember that prey and plants express defenses at some baseline

217   level (i.e., constitutive defenses) independent of risk cues. Use of constitutive defenses are

218   expected when levels of attack are consistently high, when cues from the environment are not

219   useful in predicting attack, or when defenses cannot be induced quickly enough. Work on

220   Trinidadian guppies has shown that their life-history traits (i.e., antipredator behavior) depend

221   upon whether they live in systems with high vs low predation (Reznick and Endler 1982;

222   Reznick et al. 1990). Importantly, appreciating potential prior exposure to the risk of

223   consumption, whether over evolutionary or ecological time, may alter predictions pertaining to

224   individual PFL and the timing of defensive investment; i.e., prior experience may prime

225   individuals in their defensive response. Within our framework, constitutive defenses can be

226   considered to occur prior to the start of the interaction sequence and thus lower PFL compared to

227   not having constitutive defenses. For example, in many plant species, individuals (or their

228   modular parts) that have a high level of constitutive defense (e.g., high levels of xanthotoxin)

229   display weak defensive investment (e.g., induced increases in xanthotoxin) when attacked

230   compared to those individuals (or parts) that do not display constitutive defenses (Zangerl and

231   Rutledge 1996). Additionally, constitutive defenses could be considered to occur very early

232   given the future potential for an attack-related interaction to occur. For example, many studies in

233   both prey and plants have shown that parental exposure to predation risk or herbivory results in

234   offspring with greater antipredator/herbivore defenses even though the offspring have yet to

235   experience risk of consumption (Rossiter 1996; Agrawal et al. 1999; Sheriff et al. 2010; Holeski

236   et al. 2012; Sheriff et al. 2017; Tigreros et al. 2017; Donelan et al. 2020). Within our framework

237   we predict that the magnitude of transgenerational or constitutive defensive investment would be

238   greatest in species or populations where naïve individuals (those without prior information,

239   whether transgenerational or evolutionary) have the highest PFL. Thus, we propose that the

240   concept of relative PFL, both within and across taxa, provides a unifying, common framework

241   for determining how and when individuals should gather and utilize information, and underlies

242   an individual's ability to develop and implement defensive strategies for minimizing the fitness

243   costs of an attack.

244

245   *Defense amidst uncertainty*

246   Although differences in sensory abilities among taxa must be considered (Karban et al.

247   2016; Weissburg et al. 2014), the timing of when to gather and use risk-related information in the

248   interaction sequence can depend greatly on an individual's PFL (Fig. 1). Since the reliability of

249   risk-related information increases as the sequence progresses, later-responding organisms should

250   be more capable of fine-tuning defensive investment and reduce the costs of unnecessary defense

251   – an advantage that must be balanced against the costs of not responding early enough (Bateman

252   et al. 2014; Orrock et al. 2015). For example, small mammals gather and use information very

253   early in the interaction sequences (e.g., moonlight-induced reductions in activity; Prugh and

254   Golden 2014) and continue throughout the sequence, since captured individuals are unlikely to

255   survive. In fact, many prey will continue to collect and process information even after the

256 encounter ends (likely in preparation for another potential attack), since the ability to track and

257 respond to risk cues even in the absence of an attack is highly beneficial (Sih 1992). At the other

258 end of the spectrum, low- to moderate-levels of herbivory often have such low fitness costs for

259 trees or other large plants (Karban and Baldwin 1997) that they can afford to wait until attack or

260 even consumption to gather and use risk-related information. This concept can be extended

261 beyond the generalized classification of prey or plants; by comparing the relative PFL among

262 individuals or among species within a community predictions can be made within populations

263 and across taxa on the timing and magnitude of defensive investment throughout the interaction

264 sequence (Box 1, Fig. 1). It also has implications for how risk information can propagate among

265 individuals and communities.

266

267 **The transmission and use of risk information**

268 *The propagation of risk information among individuals*

269 For many prey, group size and composition are important factors altering the relative risk

270 experienced by a given individual (Hamilton 1971; Bednekoff and Lima 1998a). This may result

271 from improved predator detection (the 'many eyes' hypothesis) or increased dilution of individual

272 risk, assuming that predators can kill only a small number of group members at a time

273 (Bednekoff 1997). Although early models assumed that detection by any group member would

274 provide equal benefits to all members, individuals differ in their vulnerability and information

275 about risk. Within a group, an individual must detect and respond to a predator prior to a certain

276 time point (t) in order to reach safety, or must detect and respond to the primary detector.

277 However, given that a secondary responder has a lag (l) in their response, the primary detector

278 must respond to a predator at $t+l$ in order for the second individual to react in time to reach

279 safety (Bednekoff and Lima 1998b). We can extend this model of primary vs. secondary

280 responders to incorporate the concept of PFL. Take, for example, a group in which all

281 individuals have an equivalent fitness potential if they initiate defense very early (e.g., 100%

282 survival probability). Some group members will have a lower fitness potential if they initiate

283 defense during an attack, and thus, they will have a higher rate of fitness loss across the

284 interaction sequence and a higher PFL (dashed line in Fig 1). Thus, to maintain an equivalent

285 fitness potential, individuals with a higher PFL need to respond earlier in the interaction

286 sequence, and, thus, have a larger value of t (time required to reach safety) compared to

287 individuals with a lower PFL.

288   From this, we can make predictions based on the PFL of the primary, secondary (and

289 tertiary, etc.) responders, which will yield very different outcomes for individual and group

290 responses. Most often, we expect individuals with the highest PFL within a group to be the

291 primary detectors and responders, leaving ample time for other individuals to respond, but this

292 may not always be the case. In semi-fossorial groups (e.g., ground squirrel colonies), individuals

293 living in the periphery of the habitat may have a lower likelihood of surviving an attack, and thus

294 have a higher PFL. However, living in sub-optimal habitats may also lead to reduced visibility

295 (Werner et al. 2015). In such scenarios, individuals with lower PFL may be the primary detectors

296 and, thus, may not respond until later in the interaction sequence, possibly later than the required

297 time ($t+l$) for a secondary responder, particularly if that secondary responder is less likely to

298 survive an attack and needs to respond early (i.e., has a greater value for t). Of course, time

299 required to reach safety may also depend upon how many other individuals are simultaneously

300 fleeing from consumers, and thus, complex games may emerge (Gil et al. 2018). Future work

301 could test hypotheses pertaining to the relationship between PFL, primary vs. secondary

302   detectors/responders, and population level mortality to explore the transmission of risk

303   information among group members and across species (Valone and Templeton 2002; Gil et al.

304   2018).

305   Plants, although single individuals, have multiple redundant parts and may respond more

306   like a group of closely related animals than a single genetically-unique individual (Karban et al.

307   2016). When attack and consumption are initiated, plants respond by inducing defenses and

308   reallocating resources to unattacked and less accessible parts (Schultz et al. 2013). Considering

309   the plant as a group and each component as an individual allows us to ask similar questions as

310   we do with animal groups. For example, do tissues with a higher PFL have a faster and stronger

311   response to herbivory (McKey 1974; Zangerl and Rutledge 1996)? Does the propagation of risk

312   signals occur more quickly through young plants with higher PFL than through mature

313   individuals?

314   Individuals within clonal groups likely have very different responses than individuals

315   within unrelated/partially related groups, given that consumption of a single individual is

316   unlikely to result in death of the entire colony or clonal group (Harvell 1990). They can thus

317   gather highly reliable information late in the interaction sequence to optimize their defense

318   (assuming risk information transfer among clonal individuals occurs). For example, the

319   consumption of some soldiers in clonal aphid colonies alters colony-level allocation to defense

320   without high fitness costs (Aoki and Kurosu 2004). As such, use of risk information and

321   defensive investment should occur at the colony level, not at the individual level. This line of

322   reasoning can be further extended to provide novel insights into defensive investment as a

323   function of colony size or age: young, small colonies of clonal or eusocial organisms should

324   respond strongly and early in the interaction sequence because of the greater cost of losing some

325   individuals, whereas large, mature colonies should respond less strongly at the same point in the

326   interaction sequence. An additional, unappreciated suggestion that follows from our perspective

327   is that the potential to reduce the costs of activating unnecessary defenses may provide a

328   selective advantage to clonality and eusociality. Alternatively, sessile prey may provide an

329   interesting contrast as a single individual that is immobile. Future studies comparing anti-

330   consumptive responses between clonal groups (animals or plants), sessile prey, and plant

331   individuals may provide further insights into the commonalities of defensive investment.

332   Importantly, although we emphasize the role of PFL in information transfer pertaining to

333   the arrival of consumers/predators, PFL also affects the ability of organisms to gain information

334   required to re-emerge from a defended state (a key determinant of the cost of defensive

335   responses; Gil et al. 2018). For example, the fact that organisms with a high PFL often remain in

336   refuges long after predators have left (e.g., Sih 1992) likely influences their willingness to enter

337   such areas. Once defense is initiated plants remain in the defended state for long periods of time;

338   relaxation of this state appears less responsive to cues than the initial induction (Huntzinger et al.

339   2004). Further, organisms with low PFL may re-emerge more quickly from a defensive state and

340   actually facilitate other organisms leaving (Gil et al. 2018). Thus, information about the loss of

341   risk may transfer from individuals with a low PFL to individuals with a higher PFL.

342   Across both prey and plants, our perspective emphasizes how the PFL of one individual

343   (as well as the components of a more modular individual, e.g., plants) can alter the efficacy of

344   signaling to another, and how the PFL of the second can in turn alter the efficacy of its response.

345   A general prediction is that information about increased risk should move from higher- to lower-

346   PFL individuals, while the opposite may occur for information regarding decreased risk. Future

347   work should focus on how risk information moves throughout groups comprised of individuals

348   of similar age/state relative to more heterogeneous groups. In general, our 'susceptibility

349   perspective' illustrates how the value of information depends critically upon the state of the

350   sender relative to the receiver, something the receiver may or may not be able to estimate

351   (Danchin et al. 2004).

352

353   ***The propagation of risk information through communities***

354   We also expect that the rate at which risk information propagates through food webs and

355   across trophic levels (e.g., trait-mediated indirect interactions) may be determined by the relative

356   PFL of species within the system. A simple expectation is that responses to predators should be

357   stronger in systems characterized by prey with relatively higher PFL. For example, Chase (2003)

358   showed that in systems dominated by vulnerable snails (high PFL), predator effects were strong

359   and cascaded to plant resources; however, in systems dominated by relatively invulnerable

360   snails, predator effects were weak and did not cascade to plant resources. Our framework would

361   predict that the reduction in defensive investment by plant resources is likely to be higher in the

362   former system compared to the later. Further, if the timing of response determines the ultimate

363   rate of propagation through a food web, then behaviorally-mediated cascades would be most

364   rapid in systems of prey with relatively high PFL. In addition, information about the loss of risk

365   (i.e., when predators or herbivores leave an area) may be most rapidly transmitted in

366   communities with organisms that have relatively low PFL. Conversely, primary responding

367   species may be those with the greatest competitive ability for resources, while those that transmit

368   information about the loss of risk may be the poorest competitors (Gil et al. 2018). Considering

369   both the PFL and competitive ability of species within a community may provide unique insights

370   into how risk information is transmitted among species.

371   Our perspective may also provide novel insights and predictions pertaining to the

372   magnitude of trophic interactions and the relative strength of top-down and bottom-up factors

373   influencing ecosystem dynamics. For example, because of their extreme vulnerability if attacked

374   (i.e., if attacked they are likely to die and thus a high PFL), rodents and other small mammals

375   respond very early in the interaction sequence (e.g., to moonlight), thereby significantly

376   decreasing their consumption of seeds and plants when there is little risk information (Orrock

377   and Fletcher 2014). Alternatively, large ungulates (with low PFL) may not alter their foraging

378   behavior until an attack is imminent (Middleton et al. 2013), and their foraging activities may be

379   more driven by spatial and temporal variation in food quantity and quality (but see Valeix et al.

380   2009; Tambling et al. 2015). Trophic interactions in systems dominated by organisms with

381   relatively high PFL may be more driven by top-down processes because of the risk-induced

382   shifts in herbivore behavior, while those dominated by organisms with relatively low PFL may

383   be more driven by bottom-up processes.

384

385   **Concluding remarks**

386   The obvious differences between prey and plants can lead us to overlook their

387   similarities: both live in variable environments with uncertain risk, and both utilize information

388   to maximize their fitness. Considering an organism's relative PFL if attacked and the influence

389   of PFL on the timing of information gathering and use across the interaction sequence provides a

390   common framework under which future studies can understand consumer-resource relationship.

391   Further, focusing on productive similarities between the disciplines will provide additional

392   insights and allow cross-talk of theories about the general consequences of consumptive

393   interactions.

394   Although a variety of approaches may be used, comparative studies that use a range of

395 taxa and combinations of risk information cues will be particularly promising in helping

396 disentangle the role of PFL and information in affecting allocation to defense. As such, this

397 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

399   example, in systems where PFL is high (e.g., snowshoe hare – lynx) risk of consumption

400   may be a greater factor than in systems where PFL is low (e.g., wolf-elk).

401 2) How ecological and environmental context influences consumer-resource interactions;

402   for example: (a) Increases in resource (prey or plant) abundance may reduce PFL and

403   thus alter responses to the risk of consumption; (b) The average toxicity of individuals in

404   a population may alter consumer efficacy and thus alter PFL and resource responses to

405   consumption; (c) In areas with more refuges individuals may have reduced PFL, because

406   they can likely better escape when attacked, and thus, will delay their response to

407   predation risk compared to areas without refuges; (d) Ambush predators may create a

408   significant increase in PFL compared to cursorial predators, and this drives the earlier and

409   greater response in prey (Schmitz 2007).

410 3) The role of consumer risk in mediating trophic interactions and how risk information

411   transfers within and among systems; for example: (a) Understanding individual PFL may

412   help distinguish between information transfer about impending/arriving risk vs.

413   information transfer about safety (allowing organisms to resume activity); (b) Cross-

414   species information transfer may be mediated by the relative PFL of different species

415   within the community.

416 4) How the ontogeny of prey and plants alters their investment in defense; for example, PFL

417   likely differs across ontogeny and this may help predict changes in defensive investment,

418   with stages where individuals have greater PFL having increased defensive investment.

419

427

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618

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

619

620 We suggest the proportional fitness loss (PFL) if an individual does not initiate defense until

621 attacked is a critical component of understanding its defensive investment. PFL relies on an

622 individual's fitness potential if it initiates defense prior to an attack compared to its fitness

623 potential if it initiates defense during an attack. For example, if individual A is 50% likely to

624 survive if it defends during the detection stage and only 20% likely to survive if it defends during

625 an attack, its PFL is 60% ((50-20)/50). If individual B has a 95% chance of surviving if it

626 defends during the detection stage and a 30% chance of survival if it defends during an attack, its

627 PFL is 68%. From this scenario, it becomes clear that the PFL of an individual depends on both

628 its ability to survive an attack and, also, the effectiveness of its early defense. In such a scenario

629 individual B has a higher PFL and should initiate defense earlier than individual A, even though

630 it has a higher probability of surviving an attack. Our concept helps to clarify why individuals

631 with low expected fitness, regardless of whether they initiate defense early or late (thus a low

632 PFL), would be expected to wait and initiate defense late (if at all) given the ineffectiveness of

633 their (early) defense.

634 The fact that consumer-resource encounters progress through time along a common

635 interaction sequence of events (Lima and Dill 1990; Karban and Baldwin 1997, Caro 2005; Fig.

636 1) allows us to build relative PFL curves across the interaction sequence to better understand the

637 timing of defensive investment. As individuals delay their defensive investment their fitness

638 potential will approach that which they would have if they did not invest in defense until

639 attacked. This also allows us to visualize inflection points where fitness potential will greatly

640 decrease if defense is not initiated. In the first two examples above, the fitness potential

641 difference between early and late defensive investment is relatively large and, if their PFL curve

642   was relatively linear, both individuals may greatly increase their survival for incremental

643   advances in the timing of their defense. Alternatively, if, for example, we extend the above

644   scenario such that individual A had a 95% chance of survival if it defended during the encounter

645   stage (thus a PFL of 79% between encounter and attack, but a 47% PFL between encounter and

646   detection), while individual B had a 99.9% chance of survival if it defended during the encounter

647   stage (thus a PFL of 70%, but only 4% PFL between encounter and detection), our curve would

648   predict that individual A would most benefit from defending during the encounter stage, while

649   individual B may benefit from delaying defensive investment until the detection stage.

650   Additionally, if individuals invest too early or respond to unreliable information they will

651   pay a cost of unnecessary defense (e.g., cost of defense itself, missed opportunity costs,

652   reductions in growth and reproduction). The willingness of individuals to pay a cost of

653   unnecessary defense will also depend on their PFL. Individuals with a high PFL can pay a

654   relatively high cost of unnecessary defense and still benefit significantly from early defensive

655   investment. Alternatively, individuals with a low PFL if attacked may not be willing to pay as

656   high a cost of unnecessary defense and should defend relatively later.

657   While we discuss the fitness aspect of PFL as a loss of survival, individual fitness could

658   also be measured as a loss of reproduction (number of babies born or weaned, loss of litters, loss

659   of seed set or flowers, etc.) or a loss of growth or tissue (in many species growth is directly

660   related to reproductive potential and in the case of plants or other organisms that can be partially

661   consumed a loss of tissue may be a better metric) if attacked. It is important to appreciate that in

662   these latter two fitness measures, with respect to PFL, the loss of fitness is due to attack not the

663   initiation of defense (as is often the case). Because of this, however, these latter two fitness

664   measures may be particularly insightful given i) they can be used to estimate PFL if attacked but

665   also the cost of unnecessary defense (defending too early) and ii) that they can be used to

666   estimate the loss of relative fitness at any point along the interaction sequence when defense is

667   initiated. Understanding an individual's PFL across the interaction sequence will provide

668   valuable insights into when it should initiate defense and has significant implications for

669   understanding how prey and plants will respond to the risk of consumption.

670

671   **Figure 1.** An individual's proportional fitness loss if defense is initiated during attack (PFL; Box

672   1) should reflect the timing and magnitude of defensive investment across the interaction

673   sequence. We highlight two qualitative scenarios that represent the range of possibilities we

674   envision. (Dashed Line) Individuals that experience rapid, significant losses of fitness once an

675   attack begins (i.e., individuals with higher PFL; dashed line panel A) should implement defenses

676   relatively early in the interaction sequence (dashed line panel B), as implementation of early

677   defenses maximizes that likelihood that the predator or herbivore attack will be unsuccessful or

678   attack will not occur. (Solid Line) Individuals that experience lower PFL if an attack begins, and

679   may even be able to survive partial consumption (solid line panel A), should respond late in the

680   encounter sequence (solid line panel B) in order to minimize the costs of unnecessary defense.

681   The magnitude of defense exhibited by individuals during the pre-encounter stage may depend

682   upon their prior experience, as such individuals with higher PFL (dashed line) will likely have

683   higher defensive investment during this stage. While individuals can alter the sequence by

684   escaping during this stage (and thus entering the escape recovery stage directly), the return of

685   individuals to a baseline defense level (panel B) and maximum fitness potential (panel A) will

686   likely be slower in individuals with higher PFL; which in turn will alter the initial magnitude of

687   defense during the pre-encounter stage. Because this is a relative scale, the magnitude and timing

688   of defensive investment may differ among individuals within and among populations or among

689   individuals of different species within a community. Note that as the interaction sequence

690   progresses the reliability of risk information also increases.
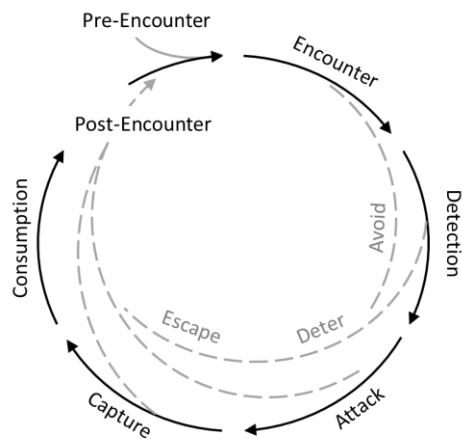
691

692   **Fig. 1**
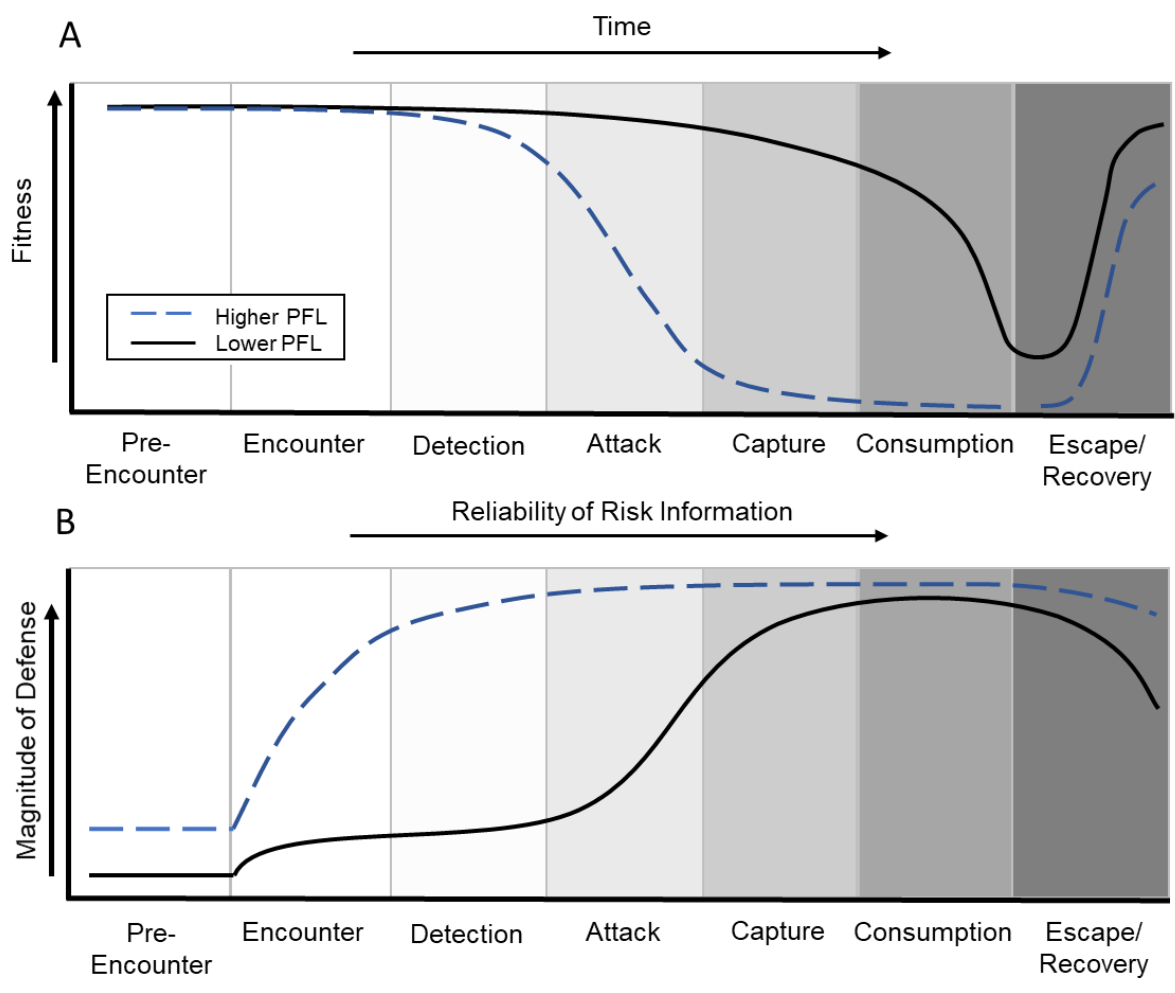
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696　**Fig. 2.** The common sequence of attacked-related events shared during both predator-prey and

697　herbivore-plant interactions. Interactions begin during a pre-encounter spatiotemporal overlap

698　stage and end in a post-encounter escape/recovery stage (or death if consumption is lethal).

699　Depending upon the timing and magnitude of prey/plant defense (which is reliant on their PFL),

700　prey/plants can avoid, deter, and escape from their consumers altering the outcome of this

701　sequence at any stage and enter the post-encounter stage (dashed lines). Importantly, this

702　sequence does not proceed in a simple linear fashion and any previous encounter with a

703　consumer will influence future encounters (i.e., the post-encounter experience will influence pre-

704　encounter defensive investment).

705

706　**Fig. 2.**

707