

Ecophysiological effects of predation risk; an integration across disciplines

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Introduction

Predation is a central organizing process in ecology (Krebs et al. 2001; Schmitz 2008). Since the inception of the discipline, ecologists have strived to understand the importance of the direct effects of predation—mainly the killing of prey. Further, almost a century ago, Walter B. Cannon, a pioneer in the study of stress, recognized that the risk of predation could induce changes in prey physiology (Canon 1915) and established the “fight or flight” paradigm (Wingfield et al. 1998). However, ecologists and resource managers were slow to recognize the importance of these non-consumptive effects as they were believed to be too transitory to affect prey demography. Only recently have we begun to appreciate that predation risk itself can influence prey demography, community structure, and ecosystem processes (Fig. 1). Predation risk, the non-consumptive effects a predator can have on prey (also called “non-lethal effects,” “risk effects,” “fear,” etc.), can drive changes in prey behavior, morphology, physiology, and can alter developmental pathways, changes which can persist into adulthood (Skelly and Werner 1990; Sheriff et al. 2010; Clinchy et al. 2013). Further, studies have demonstrated that these non-lethal effects can be as large if not larger than actual lethal, killing of prey (Preisser et al. 2005). While we know prey deploy multiple responses to predation risk, the

integration of physiological responses has received less attention. This is the subject of this special issue.

Prey physiological responses are important at all stages of the predator–prey interaction. They are a major part of the prey’s primary, fight or flight, response, are mechanistic drivers of behavioral and morphological changes, help prepare prey for future attack, and secondarily respond to changes caused by primary responses. We are beginning to understand how, in the initial steps of predator detection, sensory systems, such as visual and olfactory ones, may act synergistically to gather information regarding risk (Kats and Dill 1998; Hartman and Abrahams 2000). Following detection, the physiological status of the prey (Koivula et al. 1995; Martin and Lopez 1999), prey genotype (Dennis et al. 2010), and personality (Sih et al. 2004) influence whether and how they respond. Physiological responses also aid in defense once the predator initiates attack. For example, tadpoles previously exposed to predator cues have adaptive morphological changes linked to elevated stress hormone levels giving them an advantage in escaping predation (Hossie et al. 2010), dragonfly predators select for higher arginine kinase enzyme that powers faster swimming speed and escape performance in damselfly prey (Strobbe et al. 2010), and caterpillars can increase digestive efficiency to compensate for reductions in feeding (Thaler et al. 2012). Finally, parental exposure to predation risk can influence offspring behavior, morphology, and physiology (Agrawal et al. 1999; Sheriff et al. 2009, 2010; Storm and Lima 2010; Zanette et al. 2011) and these effects may lead to adaptive phenotypes dependent upon the match between the maternal and offspring environment (Sheriff and Love 2013). Given that the primary response of prey to the immediate threat of predation is the “stress response” (Sapolsky et al. 2000) and central to this is the activation of the hypothalamic–pituitary–adrenal axis, much work has

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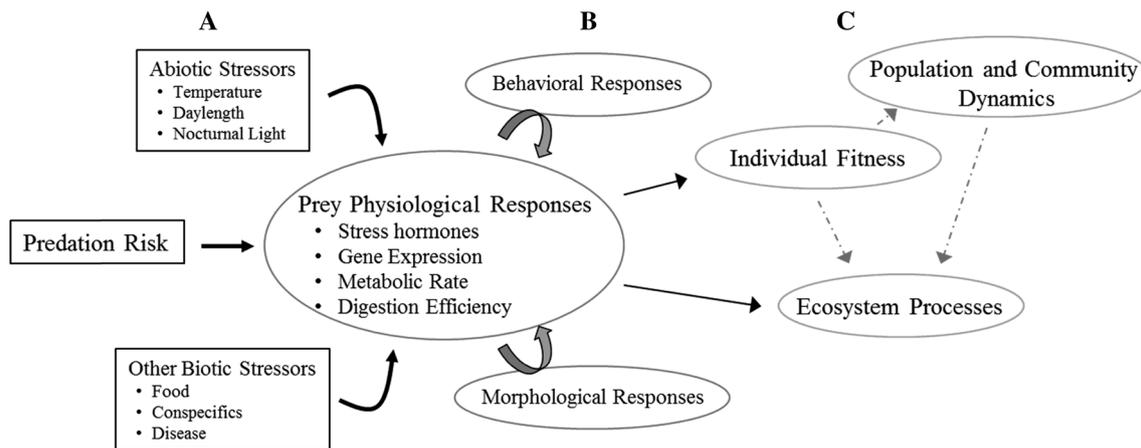


Fig. 1 Via changes in prey physiology, predation risk can scale up to alter population and community dynamics, and ecosystem processes. **A** The interactive effects of both abiotic and biotic stressors with predation risk will shape the physiological response of prey; **B** prey physiological responses are mechanistic drivers of behavioral and morphological responses to predation risk, which in turn feedback to

alter prey physiology; **C** these responses directly (*solid lines*) impact individual prey fitness, which can scale up to alter population and community dynamics. Further, these responses can both directly, via changes in nutrient cycling, and indirectly (*dashed lines*), via changes in population and community dynamics, alter ecosystem processes

focused on changes in stress hormone levels in response to predation risk (Boonstra 2013). Here we build on this understanding and delve into other functional physiological traits that are deployed in the face of predation risk. For example, snowshoe hares are well studied for the impact of predation risk on stress hormone levels (e.g., Boonstra et al. 1998; Sheriff et al. 2011); here, Lavergne et al. (2014) build upon this understanding and show that gene expression involved in metabolic processes, hormone responses, immune function, and blood cell formation also change in response to increased risk. Importantly, whether a prey escapes or otherwise survives attack, the presence of predators can have widespread long-term consequences on prey physiology.

The eight papers in this special feature explore the ecophysiological responses of prey to predation risk from the level of the individual to the ecosystem. The objective of this special feature is to explore the ecophysiological effects of predation risk across the disciplines of ecology, physiology, and neurobiology, and to highlight in a single issue the great diversity of ways that predation risk can alter prey. We hope this issue may act to inspire new questions, integrating across disciplines.

Features of the special issue

1. One of the tenets of ecology is that animals must eat and not be eaten. As such, one of the primary challenges in studying the ecophysiological effects of predation risk is that prey respond to multiple stressors; principal among these are predation and food, but importantly, scared prey

also typically eat less. Thus, can we distinguish prey responses to predation risk from those caused by food limitation and can we separate responses caused by predator-induced reductions in food intake from absolute food shortage (Capellan and Nicieza 2007). These challenges are discussed by Zanette et al. (2014) who explore how physiological measures may be used to unambiguously diagnose predation risk effects. The authors begin by reviewing recent papers investigating physiological effects of risk and present a conceptual framework describing the pathways by which predators and food can affect prey. To construct an effective diagnostic toolkit to distinguish predation risk effects (including reduced food intake) from reductions in absolute food availability it is critical to collect multiple physiological measures.

In addition to distinguishing predation risk effects from other stressors, it is also important to understand the interactions between predation risk and other potentially stressful ecological factors such as disease, conspecifics, and food availability (Clinchy et al. 2004; Monclús et al. 2009; Sheriff et al. 2012; Thaler et al. 2013; Janssens and Stoks 2014). For most prey, food quality and predation risk vary greatly across a landscape. Prey often face a foraging dilemma of choosing between high-quality food in a risky environment or low-quality food in a safe environment. McArthur et al. (2014) explores how and why the interaction between toxic food and predation risk affects foraging decisions. Central to their argument is that detoxification physiology induced by toxic food and stress physiology induced by exposure to predators are not independent because toxic food may also induce stress physiology via the hypothalamic–pituitary–adrenal axis. Thus,

prey foraging decisions will integrate both stresses (Kaplan and Thaler 2010). Further, they predict that the degree of diet specialization (specialist to generalist) and personality (bold to shy) will alter the relative costs of foraging and risk, and that this can scale down to the individual level, thus creating an individualistic landscape of food and fear.

Abiotic stressors can also influence responses to predation risk. For example, physiological processes are generally sensitive to temperature and accordingly, most organisms adjust their growth and behavior in response to shifts in temperature. Culler et al. (2014) explores this idea, investigating the interactive effects of fish predation risk and temperature on damselfly nymphs. Their experiments and models show that predation risk dampens the typical positive effect of temperature on growth rates. Growth rates were low even at high temperatures in the presence of predator cues, likely due to the higher metabolic rate under risk that was only partially compensated for by changes in consumption and assimilation efficiencies. Not only can predators shape prey growth responses to temperature, but predation risk may have complex impacts on behavioral thermoregulation within and across generations. A recent paper by Bestion et al. (2014) shows that gravid female lizards exposed to snake predator cues give birth to offspring that thermoregulate differently, choosing cooler environments and reducing basking behavior. Collectively, these findings have strong implications for our general understanding of how climate warming will impact species interactions.

2. Information quality plays a key role in prey appropriately responding to predators. Information can be collected from a number of sources and from different modalities. Prey organisms rely on visual, chemical, and mechanical cues from predators and, as a general rule from behavioral studies, the stronger and riskier the cue detected, the stronger the resulting antipredator response (Relyea 2003). In this issue, Hermann and Thaler (2014) show that a terrestrial beetle uses olfactory cues and other information to detect predators and that the olfactory cues differ for male and female predators. Interestingly, beetles find male predators “smellier” than females even though females are more lethal, potentially creating a disjunct between information and actual risk. Differences in prey personality may also affect their ability to assess information and learn. DePasquale et al. (2014) show how an individual’s personality can alter their associative learning ability, which could have upstream effects on foraging ability and predator detection, particularly if predators are sit-and-wait hunters and risky areas are associated with habitat cues.

3. Predation risk acts at the level of the individual and the consequences of individual responses can scale up to alter ecosystem processes. Risk effects can begin not only at first encounter, but prenatally through epigenetic programming and maternal stress effects (Weaver et al. 2004;

Sheriff and Love 2013). Thus, predators can cause not only activational responses (those changes which alter behavioral pathways) but also organizational responses (alterations in developmental pathways) in prey; predators can induce phenotypic plasticity among prey. Elucidating the developmental and genetic control of predator-induced phenotypic plasticity is critical to understanding the full impact predators have on prey, particularly because these traits will feedback to direct the entire life history of the prey and their future perception of risk (sensu McArthur et al. 2014). In this issue, Dennis et al. (2014) uses molecular tools to test alternative mechanisms of developmental control in daphnia. They show how a small network of genes can differentiate phenotypic expression, linking predator-induced plasticity to juvenile hormone regulation. Lavergne et al. (2014) also found differential gene expression in the hippocampus of wild snowshoe hares exposed to different intensities of risk. Compared to hares that lived during the population peak (relatively safe), hares that lived during the decline (extreme predation risk) showed increased expression of genes involved in metabolic processes and hormonal responses, and decreased expression of genes involved in immune responses and blood cell formation. This is the first study to link changes in neuronal RNA transcript abundance to changes in population demography.

Ecosystem processes can also be altered by predation risk, indirectly via changes in population demography (e.g., Peckarsky et al. 2008) or by directly altering ecosystem processes through consumer-driven nutrient recycling, changing the availability of limiting nutrients at the base of food webs (Schmitz 2003). A physiological mechanism for the changes in ecosystem processes was first proposed by Hawlena and Schmitz (2010) who showed that predation risk altered metabolism, food selectivity, digestive efficiency and tissue nutrient content of grasshoppers. In this issue, Dalton and Flecker (2014) test the effects of predation risk on the nutrient recycling and nutrient budgets of Trinidadian guppies. They show that although guppies strongly reduce food intake, they increased nitrogen retention efficiency when exposed to predation risk, excreting 39 % less nitrogen than control guppies. Thus, by changing prey excretion rates of a limiting nutrient, predators may reduce the primary productivity and alter ecosystem processes via bottom-up control.

As we explore further we are finding more and more physiological systems play a role in the prey’s responses to predators and are important mechanisms of predator–prey interactions. These mechanisms underlie many of the costs, benefits and trade-off decisions prey make in defensive investment and antipredator responses (Relyea and Auld 2004). Clearly, predators alter prey directly through killing and indirectly through alterations in their physiology. Yet, we are a long way from fully understanding the impact of

risk on prey physiology. For example, de Vos et al. (2010) found that aphids exposed to their alarm pheromone up- or down-regulated almost 15 % of the 10,000 genes measured, yet we know little related to the control these genes exert. The field of ecophysiological effects of predation risk is in its infancy and we must move beyond simple stress hormone analysis and delve into other physiological responses and understand their interactive effects to fully appreciate how predation risk shapes system-wide changes in prey.

References

- Agrawal AA, Laforsch C, Tollrian R (1999) Transgenerational induction of defences in animals and plants. *Nature* 401:60–63. doi:[10.1038/43425](https://doi.org/10.1038/43425)
- Bestion E, Teyssier A, Aubret F, Clobert J, Cote J (2014) Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal. *Proc R Soc B* 281 doi:[10.1098/rspb.2014.0701](https://doi.org/10.1098/rspb.2014.0701) (pii: 20140701)
- Boonstra R (2013) Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. *Funct Ecol* 27:11–23
- Boonstra R, Hik D, Singleton GR, Tinnikov A (1998) The impact of predator-induced stress on the snowshoe hare cycle. *Ecol Monogr* 79:317–394
- Canon WB (1915) Bodily changes in pain, hunger, fear and rage. Appleton, New York
- Capellan E, Nicieza AG (2007) Non-equivalence of growth arrest induced by predation risk or food limitation: context-dependent compensatory growth in anuran tadpoles. *J Anim Ecol* 76:1026–1035
- Christianson D, Creel S (2010) A nutritionally mediated risk effect of wolves on elk. *Ecology* 91:1184–1191
- Clinchy M, Zanette L, Boonstra R, Wingfield JC, Smith JNM (2004) Balancing food and predator pressure induces chronic stress in songbirds. *Proc R Soc B* 271:2473–2479
- Clinchy M, Sheriff MJ, Zanette L (2013) Predator-induced stress and the ecology of fear. *Funct Ecol* 27:56–65
- Culler LE, McPeck MA, Ayres MP (2014) Predation risk shapes thermal physiology of a predaceous damselfly. *Oecologia*. doi:[10.1007/s00442-014-3058-8](https://doi.org/10.1007/s00442-014-3058-8) (this issue)
- Dalton CM, Flecker AS (2014) Metabolic stoichiometry and the ecology of fear in Trinidadian guppies: consequences for life histories and stream ecosystems. *Oecologia*. doi:[10.1007/s00442-014-3084-6](https://doi.org/10.1007/s00442-014-3084-6) (this issue)
- De Vos M, Cheng WY, Summers HE, Raguso RA, Jander G (2010) Alarm pheromone habituation in *Myzus persicae* has fitness consequences and causes extensive gene expression changes. *Proc Natl Acad Sci* 107:14673–14678
- Dennis SR, Carter MJ, Hentley WT, Beckerman AP (2010) Phenotypic convergence along a gradient of predation risk. *Proc R Soc B* 278(1712):1687–1696. doi:[10.1098/rspb.2010.1989](https://doi.org/10.1098/rspb.2010.1989)
- Dennis SR, LeBlanc GA, Beckerman AP (2014) The endocrine regulation of predator-induced phenotypic plasticity. *Oecologia*. doi:[10.1007/s00442-014-3102-8](https://doi.org/10.1007/s00442-014-3102-8) (this issue)
- DePasquale C, Wagner T, Archard GA, Ferguson B, Braithwaite VA (2014) Learning rate and temperament in a high predation risk environment. *Oecologia*. doi:[10.1007/s00442-014-3099-z](https://doi.org/10.1007/s00442-014-3099-z) (this issue)
- Hartman EJ, Abrahams MV (2000) Sensory compensation and the detection of predators: the interaction between chemical and visual information. *Proc R Soc B* 267:571–575. doi:[10.1098/rspb.2000.1039](https://doi.org/10.1098/rspb.2000.1039)
- Hawlena D, Schmitz OJ (2010) Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proc Natl Acad Sci* 107:15503–15507
- Hermann SL, Thaler JS (2014) Prey perception of predation risk: volatile chemical cues mediate non-consumptive effects of a predator on a herbivorous insect. *Oecologia*. doi:[10.1007/s00442-014-3069-5](https://doi.org/10.1007/s00442-014-3069-5) (this issue)
- Hossie TJ, Ferland-Raymond B, Burness G, Murray DL (2010) Morphological and behavioural responses of frog tadpoles to perceived predation risk: a possible role for corticosterone mediation? *Ecoscience* 17:100–108
- Janssens L, Stoks R (2014) Reinforcing effects of non-pathogenic bacteria and predation-risk: from physiology to life history. *Oecologia* 176:323–332. doi:[10.1007/s00442-014-3030-7](https://doi.org/10.1007/s00442-014-3030-7)
- Kaplan I, Thaler JS (2010) Plant resistance attenuates the consumptive and non-consumptive impacts of predators on prey. *Oikos* 119:1105–1113
- Kats LB, Dill LM (1998) The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience* 5:361–394
- Koivula K, Rytkonen S, Orell M (1995) Hunger-dependency of hiding behaviour after a predator attack in dominant and subordinate willow tits. *Ardea* 83:397–404
- Krebs CJ, Boutin S, Boonstra R (2001) Ecosystem dynamics of the boreal forest. The Kluane Project. Oxford University Press, New York
- Lavergne SG, McGowan PO, Krebs CJ, Boonstra R (2014) Impact of high predation risk on genome-wide hippocampal gene expression in snowshoe hares. *Oecologia*. doi:[10.1007/s00442-014-3053-0](https://doi.org/10.1007/s00442-014-3053-0) (this issue)
- Martin J, Lopez P (1999) When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. *Behav Ecol* 10:487–492. doi:[10.1093/beheco/10.5.487](https://doi.org/10.1093/beheco/10.5.487)
- McArthur C, Banks PB, Boonstra R, Forbey JS (2014) The dilemma of foraging herbivores: dealing with food and fear. *Oecologia*. doi:[10.1007/s00442-014-3076-6](https://doi.org/10.1007/s00442-014-3076-6) (this issue)
- Monclús R, Palomares F, Tablado Z, Martínez-Fontúrbel A, Palme R (2009) Testing the threat-sensitive predator avoidance hypothesis: physiological responses and predator pressure in wild rabbits. *Oecologia* 158:615–623
- Peckarsky BL, Abrams PA, Bolnick DI, Dill L, Grabowski JH, Lutt-beg B, Orrock JL, Peacor SD, Preisser EL, Schmitz OJ, Trussell GC (2008) Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology* 89:2416–2425
- Preisser EL, Bolnick DI, Bernard MF (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86:501–509
- Relyea RA (2003) How prey respond to combined predators: a review and an empirical test. *Ecology* 84:1827–1839
- Relyea RA, Auld JR (2004) Having the guts to compete: how intestinal plasticity explains costs of inducible defenses. *Ecol Lett* 7:869–875
- Rigby MC, Jokela J (2000) Predator avoidance and immune defence: costs and trade-offs in snails. *Proc R Soc B* 267:171–176
- Sapolsky RM, Romero LM, Munck AU (2000) How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr Rev* 21:55–89
- Schmitz OJ (2003) Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol Lett* 6:156–163
- Schmitz OJ (2008) Effects of predator hunting mode on grassland ecosystem function. *Science* 320:1388–1399
- Sheriff MJ, Love OP (2013) Determining the adaptive potential of maternal stress. *Ecol Lett* 16:271–280
- Sheriff MJ, Krebs CJ, Boonstra R (2009) The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. *J Anim Ecol* 78:1249–1258

- Sheriff MJ, Krebs CJ, Boonstra R (2010) The ghosts of predators past: population cycles and the role of maternal programming under fluctuating predation risk. *Ecology* 91:2983–2994
- Sheriff MJ, Krebs CJ, Boonstra R (2011) From process to pattern: how fluctuating predation risk impacts the stress axis of snowshoe hares during the 10-year cycle. *Oecologia* 166:593–605
- Sheriff MJ, Wheeler H, Donker SA, Krebs CJ, Palme R, Hik DS, Boonstra R (2012) Mountain-top and valley-bottom experiences: the stress axis as an integrator of environmental variability in arctic ground squirrel populations. *J Zool* 287:65–75
- Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* 19:372–378
- Skelly DK, Werner EE (1990) Behavioral and life-history responses of larval American toads to an odonate predator. *Ecology* 71:2313–2322
- Storm JJ, Lima SL (2010) Mothers forewarn offspring about predators: a transgenerational maternal effect on behavior. *Am Nat* 175:382–390
- Strobbe F, McPeck MA, De Block M, Stoks R (2010) Survival selection imposed by predation on a physiological trait underlying escape speed. *Funct Ecol* 24:1306–1313. doi:[10.1111/j.1365-2435.2010.01752.x](https://doi.org/10.1111/j.1365-2435.2010.01752.x)
- Thaler JS, McArt SH, Kaplan I (2012) Compensatory mechanisms for ameliorating the fundamental tradeoff between predator avoidance and foraging. *Proc Natl Acad Sci* 109:12075–12080
- Thaler JS, Contreras H, Davidowitz G (2013) Effects of predation risk and plant resistance on *Manduca sexta* caterpillar feeding behavior and physiology. *Ecol Entomol* 39:210–216
- Weaver ICG, Cervoni N, Champagne FA, D’Alessio AC, Sharma S, Seckl JR, Dymov S, Szyf M, Meaney MJ (2004) Epigenetic programming by maternal behavior. *Nat Neurosci* 7:847–854
- Wingfield JC, Maney DL, Breuner CW, Jacobs JD, Lynn S, Ramenofsky M, Richardson RD (1998) Ecological bases of hormone-behavior interactions: the “emergency life history stage”. *Am Zool* 38:191–206
- Yin M, Laforsch C, Lohr JN, Wolinska J (2011) Predator-induced defense makes *Daphnia* more vulnerable to parasites. *Evolution* 65:1482–1488
- Zanette LY, White AF, Allen MC, Clinchy M (2011) Perceived predation risk reduced the number of offspring songbirds produce per year. *Science* 334:1398–1401
- Zanette LY, Clinchy M, Suraci JP (2014) Diagnosing predation risk effects on demography: can measuring physiology provide the means? *Oecologia*. doi:[10.1007/s00442-014-3057-9](https://doi.org/10.1007/s00442-014-3057-9) (this issue)