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The Dilemma of Foraging Herbivores: Dealing with Food and Fear

Clare McArthur
University of Sydney

Peter B. Banks
University of Sydney

Rudy Boonstra
University of Toronto Scarborough

Jennifer Sorensen Forbey
Boise State University

THE DILEMMA OF FORAGING HERBIVORES: DEALING WITH FOOD AND FEAR

Clare McArthur*

School of Biological Sciences
The University of Sydney
Camperdown, Australia
clare.mcarthur@sydney.edu.au

Peter B Banks

School of Biological Sciences
The University of Sydney
Camperdown, Australia

Rudy Boonstra

Centre for the Neurobiology of Stress
University of Toronto Scarborough
Toronto, Ontario, Canada

Jennifer Sorensen Forbey

Department of Biological Sciences
Boise State University
Boise ID, USA

Abstract

For foraging herbivores, both food quality and predation risk vary across the landscape. Animals should avoid low quality food patches in favour of high quality ones, and seek safe patches while avoiding risky ones. Herbivores often face the foraging dilemma, however, of choosing between high quality food in risky places or low quality food in safe places.

Here, we explore how and why the interaction between food quality and predation risk affects foraging decisions of mammalian herbivores, focusing on browsers confronting plant toxins in a landscape of fear. We draw together themes of plant-herbivore and predator-prey interactions, and the roles of animal ecophysiology, behaviour and personality.

The response of herbivores to the dual costs of food and fear depends on the interplay of physiology and behaviour. We discuss detoxification physiology in dealing with plant toxins, and stress physiology associated with perceived predation risk. We argue that behaviour is the interface enabling herbivores to stay or quit food patches in response to their physiological tolerance to these risks.

We hypothesise that generalist and specialist herbivores perceive the relative costs of plant defence and predation risk differently and intra-specifically, individuals with different personalities and physiologies should do so too, creating individualised landscapes of food and fear. We explore the ecological significance and emergent impacts of these individual-based foraging outcomes on populations and communities, and offer predictions that can be clearly tested. In doing so, we provide an integrated platform advancing herbivore foraging theory with food quality and predation risk at its core.

Keywords: detoxification, personality, plant toxin, predation risk, stress physiology

Risks Faced by Herbivores in the Ecological Landscape

Herbivores forage in a patchy landscape of food and fear, as the quality and quantity of food and the risk of predation all vary in space and time. Plant defences, for example, vary in concentration among closely related species (Moore and Foley 2005; Frye et al. 2013), populations within species (O'Reilly-Wapstra et al. 2004), individual plants (Andrew et al. 2007; Frye et al. 2013) and leaves on a plant (Loney et al. 2006), across time as a plant grows (McArthur et al. 2010) or in response to being eaten (Karban and Baldwin 1997). Such variation provides herbivores with scope to forage selectively for high quality food (Moore and Foley 2005; Marsh et al. 2014; Ulappa et al. in press), but as they move through the landscape they pass through peaks and troughs of predation risk (Laundre et al. 2001; Brown and Kotler 2004). Patches of vegetation can provide safety through concealment and by affecting sightlines (Banks et al. 1999; Embar et al. 2011). Vegetation can offer refuge from some predators while increasing risk from others (Embar et al. 2014). Some herbivores find safety by foraging above, rather than on, the ground (Mella et al. 2014). Unless the troughs in foraging costs associated with food and fear co-occur, the dilemma emerges of how to balance the two.

From the herbivore perspective, food quality is determined by plant primary metabolites, nutrients and energy, and by plant secondary metabolites which act as plant defences such as toxins and digestibility reducers. We differentiate these two food “axes” because herbivores strive for an appropriate mix of the former while confronting the costs of the latter (Freeland and Janzen 1974; Foley et al. 1999; Simpson et al. 2004), and because physiological tolerance along these axes varies among herbivore species (Sorensen et al. 2005b; Shipley et al. 2012) and populations (Dearing 1996). Predation risk can also vary within prey species as a function of population size or an individual's reproductive condition, sex, age, body size; between prey species as a function of body size (Sinclair et al. 2003) and prey evolutionary history (acute or chronic response to predation risk (Boonstra 2013)); and among communities depending on the diversity of prey and predators.

Our first aim was to explore how herbivores respond to multiple axes of food and fear while foraging by understanding how their physiology and behaviour together influence these foraging decisions. Our second aim was to consider the consequences of these responses and decisions both for herbivores themselves and for the broader ecological community. Herbivores play a key role in ecosystems as both consumers and the consumed. How they interact with the world around them therefore affects not only their own success, but also the fitness of plants they eat and predators that eat them with potentially far-reaching ecological and evolutionary ramifications.

Herbivores: Foraging Theory, Plant-Herbivore and Predator-Prey Interactions

Decisions at a food patch, such as how long to stay, what to eat and when to quit, are fundamental to the cost-benefit outcomes of foraging, and understanding the basis for such decisions is central to foraging theory. The two disciplines of plant-herbivore and predator-prey interactions both inform foraging theory but with a different focus. Plant-herbivore research concentrates on how herbivores respond to plants and vice versa. It recognises a continuum of mammalian herbivores based on feeding niche from browsers, which consume foliage from shrubs and trees with high levels of chemical defence, to grazers, which consume structurally defended grasses (McArthur et al. 1991). Importantly, the discipline also differentiates generalists, which consume broad diets, and specialists, which consume narrow diets, because these herbivores seek rewards in different ways (Freeland and Janzen 1974; Shipley et al. 2009). In contrast, predator-prey research generally lumps herbivores in the trophic level called “prey”, considering prey feeding niche to be unimportant. The focus is on generic functional or numerical responses of predators, such as prey switching or population dynamics (e.g. Pech et al. 1992), and the associated lethal and sublethal effects on prey (Banks et al. 1999; Salo et al. 2010; Sheriff et al. 2011).

Yet prey, including herbivores, make complex foraging decisions often involving a trade-off between food quality and predation risk (Lima and Dill 1990). To understand the foraging choices of herbivores, we therefore need to synthesise plant-herbivore and predator-prey disciplines in the context that herbivores consume parts of immobile, defended “prey” (i.e., plants) while being individual mobile prey items themselves. We build this synthesis here by discussing the physiology and behaviour of herbivores associated first with consuming plants, second with avoiding being consumed, and third as combined effects. We focus on mammalian browsers, the predation risk they confront, and toxins as an important type of plant defence and component of food quality faced by browsers. This system represents the key interactions of herbivores with higher and lower trophic levels concerning safety and food, and so while details may differ, it should provide insight into foraging decisions of herbivores more generally.

Dealing with Plant Chemistry

Plant defence compounds such as toxins and digestibility reducers impose significant costs on foraging herbivores, including a range of negative pharmacological consequences (reviewed in Forbey et al. 2013) and energetic costs of detoxification (Sorensen et al. 2005b). Many compounds can cause physiological damage, force a reduction in food intake or may cause starvation (Bryant and Kuropat 1980; Sorensen et al. 2005a; Shipley et al. 2012). Ultimately, plant defences can lower herbivore reproductive success (DeGabriel et al. 2009).

Herbivores can mitigate costs of these plant defences via their physiology and behaviour (McArthur et al. 1991). Physiologically, for example, enzymes metabolise toxins into products for rapid excretion (McLean and Duncan 2006; Sorensen et al. 2006), but the capacity to do so differs among herbivores. Specialists can cope with higher toxin concentrations than generalists by reducing toxin absorption (Sorensen et al. 2004) or by using more efficient or less expensive metabolic pathways (Boyle et al. 1999; Shipley et al. 2012). These processes delay the physiological feedback affecting intake, which is instigated by the plasma concentration of the toxin or its metabolites (McLean et al. 2007), the emetic system (Provenza et al. 1994; Lawler et al. 1998), dose-dependent inhibition of cellular function (Forbey et al. 2011) or possibly acidosis (Foley 1992).

Behaviourally, herbivores respond to feedback from plant defences by altering their temporal feeding patterns and their spatial foraging patterns. As toxin concentration in food increases, captive herbivores eat more slowly in smaller feeding bouts (Wiggins et al. 2003; Sorensen et al. 2005a; Wiggins et al. 2006a; Torregrossa and Dearing 2009), and eat less in total (Marsh et al. 2006). Free-ranging herbivores quit food patches earlier and alter their choice of food patches. Brushtail possums (*Trichosurus vulpecula*), swamp wallabies (*Wallabia bicolor*) (Bedoya-Perez et al. 2014) and African bushbabies (*Otolemur crassicaudatus*) (McArthur et al. 2012) all demonstrate earlier patch quitting, quantified as higher Giving-Up-Density (GUD) at food patches with increasing toxin concentration. Similarly, free-ranging koalas (*Phascolarctos cinereus*), pygmy rabbits (*Brachylagus idahoensis*) and the avian herbivore, the greater sage-grouse (*Centrocercus urophasianus*) select plants or plant patches with low toxin concentration (Moore and Foley 2005; Frye et al. 2013; Ulappa et al. in press).

From the foraging perspective, herbivores have a behavioural choice once physiological feedback from plant toxins starts to reduce food intake. They can either wait until they have detoxified sufficiently to continue eating or change their food source by quitting the patch. The “sit and wait” strategy appears better suited to specialist herbivores, which tend to have efficient physiological mechanisms for dealing with toxins and a lower resting metabolism, such as koalas (Degabriele and Dawson 1979) and woodrats (*Neotoma stephensi*) (Sorensen et al. 2005b). We suggest generalists are more likely benefit from moving to another food source. By doing so, they can switch to plants that lack plant toxins, have complementary toxins, i.e., have little overlap in their detoxification pathways (Marsh et al. 2006), or have nutrients that off-set costs (Nersesian et al. 2012b). Consistent with this, captive brushtail possums ate more and maintained weight when provided with two complementary diets than when offered either alone (Dearing and Cork 1999; Marsh et al. 2006). Switching diets within the timeframe of feeding bouts can enhance the benefit derived from mixing complementary diets, increasing total food intake (Wiggins et al. 2006b). However, if switching foods entails moving some distance to find a suitable new food patch, the costs of this strategy include substantially reduced foraging efficiency (Wiggins et al. 2006c; Nersesian et al. 2012a), time and metabolic costs of moving, and costs of encountering enemies in the process. These captive animal results suggest that, ecologically, a herbivore’s foraging strategy will be strongly influenced not only by whether it is a generalist or a specialist, but by the spatial scale of food patch heterogeneity.

Herbivores can select higher quality, less defended plants if plant heterogeneity occurs within the spatial scale of the home range (Lawler et al. 2000; Moore and Foley 2005; Marsh et al. 2014; Ulappa et al. in press). Foraging is further enhanced by small scale patch heterogeneity, i.e., within a feeding station, because it leads to high foraging efficiency (Wiggins et al. 2006c; Nersesian et al. 2012a). We therefore predict that herbivores will be more likely to adopt the strategy of switching food sources when the spatial scale of plant heterogeneity is small, and home ranges with high small scale heterogeneity should be high quality. Field studies have yet to quantify the fine-scale temporal patterns of switching among food sources to test these predictions, or to test whether free-ranging generalists and specialists use different strategies. This area is ripe for investigation now GPS- and video-collars can provide highly detailed location and foraging information (Wirsing and Heithaus 2014).

It is clear from the above that plant secondary metabolites such as plant toxins play an important role in foraging decisions of herbivores. But plant primary metabolites, such as nutrients, comprise the other axis of food quality and add to the complexity of foraging decisions. Nutrients are of course the fundamental reason why herbivores consume plants, and so foraging must reflect this drive to find them. Nutrients also interact with and alter the effectiveness of plant defences. For example, the effect of high concentration of the plant toxin, cineole, on reducing food intake was completely negated in captive brushtail possums *provided* animals were simultaneously allowed to alter their relative consumption of carbohydrate to protein (Nersesian et al. 2012b). The physiology underpinning this outcome is unclear. On one level, nutrients may allow herbivores to buffer or over-ride the toxic consequences in the short-term if there is a nutritional net gain from the meal (Au et al. 2013). On another level, greater intake of compounds used for conjugation with toxins, such as glycine, immediately reduces food intake suppression (Marsh et al. 2005). Whatever the physiological explanation, there is evidence that plant nutrients also modify the influence of plant defences on free-ranging foraging herbivores. Swamp wallabies ate more and quit food patches later when diets were high-toxin, high-nitrogen rather than high-toxin, low nitrogen (Bedoya-Perez et al. 2014). Thus the cost and hence effectiveness of the plant toxin was reduced in a high nutrient food source.

In summary, plant defences such as toxins drive herbivores away from food patches whereas plant nutrients delay this process. If food quality as defined by these two axes was the only factor affecting foraging herbivores, the foraging outcome across the landscape could be relatively easily predicted in terms of net nutritional and energetic gains. It is usually not as simple, however, because most herbivores must simultaneously contend with predation risk.

Dealing with Predation Risk

The enormous impact that herbivores have on plant communities, once predators are lost from ecosystems (Estes et al. 2011), is testament to the ecologically significant role those predators play. Predators affect prey directly through mortality and indirectly via predation risk (Lima and Dill 1990). The physiological response of prey, including herbivores, to predation risk varies. Some prey become chronically stressed and some do not, yet evidence suggests the responses are adaptive rather than pathological (Boonstra 2013).

Predation exerts the ultimate cost on the fitness of prey. The fear of being eaten is therefore a powerful modifier of prey behaviour that carries significant physiological, foraging and fitness costs. To avoid predation, potential prey may forego foraging opportunities but to avoid starvation, they may need to forgo safety to access resources. These sub-lethal costs of predation can have as much influence on overall prey dynamics as mortality (Preisser et al. 2005; Creel and Christianson 2008). Predation risk is often associated with indirect cues from the environment, including open habitat (Powell and Banks 2004) or moonlight (Kotler et al. 2010), or for arboreal animals, being on the ground (Mella et al. 2014); and with direct cues such as the scats and urine of predators (Apfelbach et al. 2005). As these cues vary spatially and temporally (Carthey et al. 2011; Hughes et al. 2012; Price and Banks 2012), so does the landscape of fear (Laundre et al. 2001; van der Merwe and Brown 2008). Animals will forage in safe areas if they can (Banks 2001; Verdolin 2006) but when they must forage in risky areas, they adopt many behaviours to manage their risk, including reduced time allocation, increased vigilance, central place foraging and group foraging (Lima and Dill 1990). Thus predation risk has clearly demonstrated sublethal behavioural impacts on prey, including herbivores, modifying where they go and how long they stay at a feeding patch (Brown et al. 1999; Laundre et al. 2010).

A crucial question in terms of herbivore physiology is whether this behavioural response to predation risk translates into a chronic stress response. Chronic stress will occur when prey cannot predict exactly where predators are (Brown et al. 1999) and when predation risk is high and either virtually constant or frequently recurrent. The stress response will then be of long duration, from days to weeks. When herbivores experience acute stress responses over shorter timeframes, chronic stress will not result and we will not deal with that here.

The landscape of fear for foraging herbivores is really the landscape of fear avoidance—at least initially or in the absence of other constraints—because the best response of herbivores is to avoid areas of high predation risk, and hence of high fear. If they can avoid such areas, they can avoid a chronic stress response while reducing the chance of being eaten. Chronic stress occurs when the hypothalamic-pituitary-adrenal axis is activated long-term by unpredictable or uncontrollable stressors (Boonstra 2013). Thus the nub of the problem with respect to predation risk is one of stress control. Physiologically, the critical point is not that there is a greater chance of being killed in riskier habitats (there is), but rather whether there is a net benefit in choosing to forage there and if so, how stress and risk can be managed.

A herbivore will choose to forage in risky places from necessity when enough food of the right quality is unavailable in safe places, or when the food benefits outweigh the risk of predation (Kotler 1997). Once this happens, it must face this risk to avoid the certainty of starvation (McNamara and Houston 1987). The fear of predation has now become a stressor.

A stressor is any environmental stimulus that either directly threatens an organism's survival and homeostasis, a reactive stressor, or is perceived to do so, an anticipatory stressor (Herman et al. (2003) and see Boonstra (2013) Fig. 1). Both classes of stressors activate the hypothalamus but through different pathways. From the hypothalamus downstream, however, the precipitated hormonal cascade is similar and culminates in the release of glucocorticoids from the adrenal cortex. These hormones influence the expression of approximately 10% of the genome. Their targets include genes controlling metabolism, growth, repair, reproduction, and the management of resource allocation (Le et al. 2005), signalling the body to mobilize energy and suppress physiological processes not required immediately to deal with the stressor (e.g., growth, reproduction, digestion). Following chronic stress, this feedback is attenuated and the suppression of the physiological processes grades into inhibition (Sapolsky et al. 2000; Wingfield and Romero 2001). Such feedback attenuation may physiologically explain the predation risk allocation hypothesis (Lima and Bednekoff 1999) that animals living in chronically risky environments do not perpetually increase time spent on risk avoidance behaviours and simply focus on foraging (e.g., Bytheway et al. 2013).

Dealing with the Dilemma of Food and Fear

Given the heterogeneous landscape of food and fear, it is not surprising that foraging decisions concerning the two are intertwined and that herbivores often trade off the two behaviourally. For example elk feed on lower quality food closer to the safety of the forest when wolves are nearby (Hernandez and Laundre 2005; Creel et al. 2009). Why animals often make this trade-off, and in particular, why herbivores do not forage to minimise costs of predation and plant defence while maximising nutrient/energy intake is likely that they cannot do so. Ecologically, good food in safe places is hard to find. Physiologically, we suggest the stress responses to risks from food and fear may compete for resources.

Ecologically, the "best" solution of foraging in safe places for high quality food is unlikely to be sustainable. If it were, poorly defended plants would be quickly consumed by herbivores and predators would starve through lack of access to herbivores. Evolutionarily, the strong selective imperative for plants is therefore to defend, for predators to attack, and for both to find ways of doing so. Thus in natural ecosystems the world is often green and trophic levels extend above the herbivore. The closest we see to mammalian herbivores at least intermittently escaping these constraints is the cycling of some herbivore populations, such as snowshoe hares, along with cycling predators (Krebs et al. 1995) and theoretically also plant defences (Feng et al. 2008). At the community level, most mammalian herbivores are clearly pinned by both bottom-up and top-down control. At the individual level, they must search for good food in risky places (that is why it is still there) or poor food in safe places (that is all that remains).

Free-ranging mammals do integrate the influences of plant toxins and predation risk when foraging (e.g. Fedriani and Boulay 2006; Hochman and Kotler 2006; Kirmani et al. 2010). Importantly, the relative cost of toxin and fear shifts depending on toxin concentration. In titration experiments where food in safe patches was made more toxic, captive and free-ranging mammalian herbivores and frugivores all shifted their preference so they foraged relatively more in risky, non-toxic patches (Fig. 1a, Nersesian et al. 2011; McArthur et al. 2012). Such experiments allow us to pinpoint the equivalence point, where animals perceive the costs associated with food and fear to be equal (Fig. 1a). More generally, mammals have shown complex integrated foraging responses to predation risk and different types of plant defences (Schmidt 2000) or different plant nutrient levels (Bakker et al. 2005).

Physiologically, the response to plant secondary chemistry such as toxins and predation risk differs. The former runs mainly through enzyme pathways associated with ingested and absorbed foods and the latter via hormone pathways associated with stress (Fig. 2). At this proximate level, therefore, they should not compete. Physiological stress responses, however, arise not only from fear but also from food (Fig. 2). Predation risk is an anticipatory stressor whereas lack of sufficient food is a reactive stressor. Predation risk requires evaluation by cortical-based cognitive and decision-making brain areas before signals are sent to the hypothalamus to initiate the hormonal cascade (Boonstra 2013). Hunger imposes a direct physiological challenge to homeostasis and requires no cognitive input; with lowered energy balance, a blood borne signal is transmitted to the hypothalamus (Dallman and Bhatnagar 2001), causing an increase in glucocorticoid levels (Harris et al. 1994), increasing appetite and food-seeking behaviour (Wingfield and Romero 2001). The key is that both stressors

invoke a response via the hypothalamic-pituitary-adrenal axis (Fig. 2). Thus the impact of fear on the stress axis cannot be decoupled from the simultaneous stressor of the lack of food, because both culminate in the same downstream stress physiology. Hungry animals do not ignore the physiological feedback of fear but must respond to both risks. They may forage in risky places if they must (Berger-Tal et al. 2010) or they may choose to deal with poor quality food in safe places. For browsing herbivores, the latter means dealing with plant defences including toxins.

The pathways for dealing with food and fear are therefore linked directly through stress responses to hunger and predation risk, and indirectly, because detoxification physiology and stress physiology are both maintained by nutrients and energy. We suggest that herbivores are constrained by the need to balance these responses (Figs 2, 3). Animals that cope well with fear may therefore deal poorly with plant toxins. We know of no study that has explored whether there is any relation between the physiology of dealing with food, in particular the capacity to deal with plant toxins, and predation risk via stress hormones.

We suggest that the outcome of the foraging constraints imposed by the ecological landscape, and the proposed physiological trade-offs between responding to the risks of food and fear, is manifest at the inter-specific level along the dietary spectrum of herbivore generalists and specialists (Fig. 3). We also suggest that, at least for generalist herbivores, individuals vary intra-specifically in how each trades off food and fear (Fig. 3). Thus although herbivore dietary specialisation has been considered mainly in terms of food, not surprisingly, in the broader context of foraging it has important ramifications in the context of predation risk.

Inter-Specific Variation in Strategies for Dealing with Food and Fear

Shiple et al. (2009) differentiated (obligate) specialist from generalist herbivores. The former are often relatively immobile with low absolute metabolic rates, and have ritualised foraging behaviour appropriate for obtaining a narrow diet but requiring little behavioural plasticity. An additional yet crucial ecological layer is to consider the characteristics and consequences of herbivore foraging strategies in relation to predation risk. We suggest that generalist and specialist goals lie along different parts of the food-fear axes.

We hypothesise that in searching for a variety of food, dietary generalists confront and better cope with higher predation risk than specialists, and allocate resources differently to the physiologies associated with food or predation risk (Fig. 3). We suggest that specialists forage for poor, often toxic, food in safe places, avoiding predation risk more than generalists and devoting their physiological resources predominantly to dealing with plant defences such as toxins (Fig. 3). This is not to say that specialists are not vulnerable to predation, particularly in modified landscapes. Rather, the lack of behavioural plasticity of obligate specialist herbivores in their search for food may, in fact, also make them more vulnerable to predation than generalists in risky environments. In the context of animal personality, which we discuss below, boldness is the propensity to take risks (Reale et al. 2007). At the inter-specific level we predict generalist herbivores to be bolder than specialists (Fig. 3).

Intra-Specific Variation in Strategies for Dealing with Food and Fear

Individuals of many species differ in their personality, that is, they show individual differences in behaviour that are consistent over time or across contexts (Reale et al. 2007). The bold–shy continuum (Wilson et al. 1994) is one key ecologically relevant personality trait. Others include degrees of exploration, activity and aggressiveness (Reale et al. 2007). The existence of personality traits, such as boldness, has clear ecological and evolutionary consequences (Wolf and Weissing 2012) with demonstrated links between personality and life-history traits or fitness surrogates (Reale et al. 2007). Personality traits can co-vary as behavioural syndromes (Sih et al. 2004) and animal personality has been linked to stress physiology (Koolhaas et al. 2010; Montiglio et al. 2012).

Personality has been shown to affect foraging behaviour. For example, in captivity bolder sheep (*Ovis aries*) were more likely to explore their environment and cause the herd to separate than the shy (Michelena et al. 2009), and bolder fallow deer (*Dama dama*) ate more novel food and ate more in novel situations (Bergvall et al. 2011). Personality has also been shown to affect an individual's perceived landscape of fear. Free-ranging bold grey mouse lemurs (*Microcebus murinus*), for example, take less time than shy individuals to enter the same risky feeding stations (Dammhahn and Almeling 2012). Personality has yet to be considered in the context of mammalian herbivores foraging in a heterogeneous landscape of food and fear. We argue that how herbivores solve the foraging dilemma they often face in these landscapes will depend on their personality.

In captivity, individual brushtail possums differed in how each balanced the costs of food toxin and fear, seen statistically as variation about the mean (Nersesian et al. (2011), Fig. 1a). At the population-level equivalence point, responses ranged from Individual A that strongly preferred to feed in the risky non-toxic patch to Individual H that strongly preferred the safe, toxic food patch (Fig. 1b). We hypothesise that these individual responses arose from differences in physiology and personality, illustrated along the boldness continuum in Fig. 1b.

One consequence of personality is that in a given landscape varying in food quality and predation risk (Fig. 4a), individual animals will each perceive and value patches within that landscape differently (Fig. 4b, c). These different perceptions will affect where each decides to forage. The bold put a lower relative price on predation risk than do the shy and, we suggest, a higher relative price on plant defence (Fig. 4b versus 4c). This provides an explanation for why bold animals may risk death for good food whereas shy ones may take fewer risks but settle for poor food. Along with this, individuals should demonstrate differences in their underlying stress physiology and their physiology for dealing with the costs of food, paralleling the inter-specific patterns we proposed earlier.

We hypothesise that in dietary specialist species, individuals all have a similar equivalence point between food and fear, with a physiology focussed on dealing with plant defences and a low propensity to take risks. We suggest that in many generalists species, perhaps all, the equivalence point will differ among individuals. Where this point lies for an individual will depend on its (1) personality for coping with predation risk, itself linked to its stress physiology; (2) physiological capacity to deal with low quality food, which for browsing herbivores is strongly defined by plant defences such as toxins.

We therefore predict that intra-specifically, individuals express a variety of physiological-behavioural syndromes based on different but equally adaptive foraging strategies dealing with food and fear (Fig. 3). Generalist herbivore species may themselves be differentiated along a gradient. In some species, individuals may all be bold, search for high quality food, “live fast and die young” (left hand end of the spectrum in Fig. 3). In other species, individuals may differ across the spectrum in Fig. 3. We have used boldness to illustrate our arguments because this trait, the propensity to take risks, is most explicitly linked to predation risk. Individuals that have more active and exploratory personalities, of course, may also be more vulnerable to predation as they forage. The adaptive advantage for all these behavioural types, however, would lie in greater opportunity to exploit more and better quality food as they forage in risky places. The adaptive advantage for the shy, on the other hand, would lie in low risk of predation despite lower quality food. We would still predict these physiological-behavioural syndromes even if there is no physiological trade-off between dealing with food and fear, because of the ecological constraint of poor food in safe places and good food in risky places. Clearly these predictions remain to be tested.

Future Research Directions

Herbivores are truly between a rock and a hard place—where they forage is constrained top-down by predation and predation risk, and bottom-up by plants and plant defence. Although predators and plants may not collaborate directly, they do, together, form a trans-trophic mutualism that shapes herbivore foraging. By synthesising how and why this occurs from a physiological and behavioural perspective, we have presented several key questions about herbivore foraging that have yet to be answered. We have also made testable predictions about the inter- and intra-specific diversity of foraging strategies in response to food and fear:

- (1) Herbivores trade off resource allocation to stress physiology versus food physiology. Testing this will fill a mechanistic gap in our understanding of how ecophysiology underpins the behavioural foraging decisions made by herbivores.
- (2) Inter-specifically, dietary generalist herbivores confront and cope with predation risk more than specialists, aligned with a different balance in resource allocation to stress and food physiology. Generalists should quit low quality food patches and experience greater predation risk earlier than specialists.
- (3) Intra-specifically, individuals (particularly generalists) solve the foraging dilemma in different ways as a function of their individual physiological capabilities and personality phenotype. The solutions are equally adaptive or adaptive in different contexts.

A first step in testing our inter-specific predictions is to study sympatric generalist and specialist herbivores under low and high predation risk, quantifying what they eat and where they forage to find it. This needs to be done on a fine temporal scale, using, for example, GPS- and video-collars.

The stress physiology of generalists and specialists could be compared, as done for the physiology of detoxification (Boyle et al. 1999). More specifically, we should compare the stress physiology of obligatory specialists versus facultative generalists, which represent the least and most diverse of the herbivore dietary niches (Shipley et al. 2009), under varying doses of predation risk.

Ecologically, we could also compare rates of predation on generalist versus specialist herbivores. If the patterns play out at the lethal level, we predict greater mortality, hence greater regulation through predation of generalist than specialist herbivores in natural ecosystems. One test of this may be the red squirrel (*Tamiasciurus hudsonicus*) and snowshoe hare herbivore community in the boreal forest in North America. In winter, red squirrels are facultative specialists on conifer seeds whereas hares are generalists on shrubs. Red squirrels are largely unaffected by the 10 year predation-driven cycle of the hares (Boonstra et al. 2001) and we have no evidence that they are ‘stressed’ by the predators that stress hares. Food specialization may remove predators as a regulator of red squirrel populations.

Quantifying rates of mortality may be less revealing, however, if the sublethal influence of predators is more important. In this case, experiments that test the responses of generalist and specialist herbivores to cues of predation risk may instead be useful. Giving-up-density (GUD) experiments reveal the population level landscape of fear (Brown 1988) but making meaningful comparisons between species can be problematic, not least because equivalent GUD can occur for different reasons (Bedoya-Perez et al. 2013). An alternative or complementary approach may be to obtain realistic measures to quantify what animals are feeling physiologically on a moment to moment basis as they forage through their natural world. This could be achieved through activity monitors measuring heart rate, blood pressure, body temperature that, with validation, is then related to stress (e.g., Wascher et al. 2011; Viblanc et al. 2012).

A first step in testing our intra-specific predictions is to quantify how much individuals within a species vary in the diets they select and how they forage, then to test whether this variation is consistent with predictions associated with their individual personalities. Do bold individuals indeed have a higher quality diet than the shy? Do they forage in riskier food patches? Again, GPS collars for spatial mapping of individual movement over fine-scale foraging timeframes will be an important tool. GUD experiments that simultaneously quantify foraging behaviour (following McArthur et al. 2012), but at the level of individuals whose personality profile is defined, will allow us to test how the bold and shy, for example, differ in how they use food patches.

Pharmacologically manipulating an individual’s response to food and fear using standard chemicals that modulate toxicity and stress would allow us to quantify how equivalence points shift as a function of an animal’s physiology. Several enzymes influence systemic plasma concentrations of ingested toxins and determine toxic responses (Sorensen and Dearing 2006; Sorensen et al. 2006). Commercially available drugs can reduce systemic exposure and toxicity of ingested toxins (Seneca et al. 2010). Likewise, the physiological stress response can be suppressed (Gagne et al. 1985) or elevated (Muller et al. 2009).

Conclusions and Ecological Implications

We argue that the fields of plant–herbivore and predator-prey interactions present a compelling opportunity for developing integrative research that further explores the foraging of generalist and specialist herbivores in relation to the interplay of food and fear. Crucially, we need to incorporate how individual variation, and personality in particular, affects this interaction. The scientific literature has over 18000 papers on plant-herbivore interactions (Web of Science search, 7 Feb 2014, for “plant + herbiv*”) and over 700 on personality in ecology (search for “personality + ecolog*”) having doubled over the last year. Currently there are just two papers (Bergvall et al. 2011; Tremmel and Muller 2013) integrating the topics (“plant + herbiv* + personality”). Research has yet to explore the broader implications of personality from both herbivore *and* plant perspectives, or in free-ranging systems.

We offer several fundamental and applied ecological implications, particularly related to variation in the responses of individual herbivores to food and fear:

- (1) *Herbivore populations*: The perceived quality of the landscape will differ as individuals differ in how they respond to food and fear (Fig. 4). As a result, there should be reduced intra-specific foraging competition between individuals of different personality and physiology profiles; with potentially greater packing of individuals and a higher population density in the landscape than predicted by a single adaptive peak.

- (2) *Trophic interactions*: Plant defences should be more effective deterring the bold than the shy, because bold animals could avoid highly defended plants by foraging in high-quality but risky areas, out of bounds for shy ones. In so doing, predators should especially benefit from plant defence if it drives bold herbivores into risky places to feed. Similarly, plants may benefit from predation risk to herbivores, needing fewer defences in risky places where fear acts as an indirect defence. In this way, spatial variation in risk can help promote plant and plant species diversity. However, the effectiveness and outcome of the interaction will depend on the personality-physiological profile of individual herbivores. Shy, dietary specialists should still exert browsing pressure on plants in safe areas.
- (3) *Conservation and management of herbivores*: Heterogeneity of the landscape of food and fear at the appropriate spatial scale(s) may be key to maximising the net value of that landscape, providing differentially valuable patches for a suite of personality-physiological phenotypes within and across species. Modelling the combined food- and fear-scapes would provide a mechanistic understanding of the landscape requirements for the conservation of vulnerable and endangered herbivores. At the other end of the spectrum, more than 10% of the world's 100 worst invasive species (IUCN list) are mammalian plant-eaters, causing environmental and economic problems globally. Novel solutions for these species are critical. The use of fear-based deterrence for crops against pest herbivores is challenging if personality affects behavioural responses: fear will be less effective against the bold than the shy, requiring an alternative approach for these animals.
- (4) *Conservation of plants and predators*: Trophic cascades from the loss of large carnivores (Ripple et al. 2014) is presently interpreted via numerical (lethal) and spatial (sublethal) shifts in herbivores with consequent effects on plants. For herbivores whose populations are currently regulated by these large predators, elimination of the latter will mean that the landscape of fear disappears, and the safe haven for plants ceases to exist. A major restructuring of the communities is predicted and the pressure to evolve plant toxicity will be intense. In addition, the selective advantages and costs for variation in herbivore personality (bold versus shy) relative to foraging will shift, so that intraspecific competitive interactions, alone, become the preeminent selective force.

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Fig. 1 a Food eaten (g dry matter DM per kg body weight BW) by captive common brushtail possums (*Trichosurus vulpecula*) when offered pairs of food patches; one risky patch with non-toxic food *versus* one safe patch with food at one of five concentrations of the plant toxin, 1,8-cineole [figure modified from (Nersesian et al. 2011)]. The equivalence point defines where food intake at the two patches, hence the cost of food and fear, is equal. At the population level, this point occurred when the risky non-toxic patch was paired with 5% toxin in the safe patch. **b** Range in relative intake of food eaten by individuals (A - H) from the risky, non-toxic food patch versus the safe, 5% toxin food patch i.e., at the population-level equivalence point.

Fig. 2 Model of the direct and indirect physiological links between food and fear. The physiological costs of food depend on whether a herbivore chooses to eat or not. For browsing herbivores, food consumption means an intake of plant toxins and the cost is primarily associated with detoxification physiology (left hand side). If food is not consumed and the herbivore is then hungry, the cost of food (or its lack) shifts pathways, becomes a reactive stressor and is now associated with stress physiology, activating the hypothalamic-pituitary-adrenal axis (HPA). Fear is an anticipatory stressor and also activates the HPA axis. Thus food and fear are linked ultimately by costs associated with detoxification or stress physiology, but a component of the cost of food is directly linked to the cost of fear via stress physiology.

Fig. 3 Conceptual model of the ecophysiological variation in the capacity of herbivores to deal plant toxins and predation risk. We hypothesise that there is a behavioural-physiological syndrome, both inter- and intra-specifically, associated with the axes of food and fear. Specialists are predicted to be at the shy end of the spectrum with a physiology adapted to deal with plant defence, here as toxins, while avoiding fear. Individuals should vary little in personality. The strategy of generalists is predicted to vary both inter- and intra-specifically. At one end of the spectrum, bold individuals with a propensity to take risks have a high capacity to deal with predation risk as a stressor while spending little physiologically on dealing with plant defence. At the other extreme, shy individuals shift the physiological and behavioural balance, avoiding predation risk while dealing physiologically with plant defence.

Fig. 4 Conceptual summary of the ecological landscape of food and fear for herbivores moving in space or time (x axis) and the cost (y axis) of plant defence and predation risk, **a** actual amounts, and as valued by, **b** bold and, **c** shy herbivores. The bold are prepared to take risks (are perhaps less fearful) and so the perceived cost of foraging in risky patches is diminished relative to the cost of plant defence. Bold individuals should prefer good food in risky patches. The shy perceive risky patches as more costly relative to patches with high plant defence, hence they should value safe patches though the food is poor. Under this scenario, there is low spatial overlap between foraging bold and shy individuals, although rare safe patches with good food will be highly valued by all.

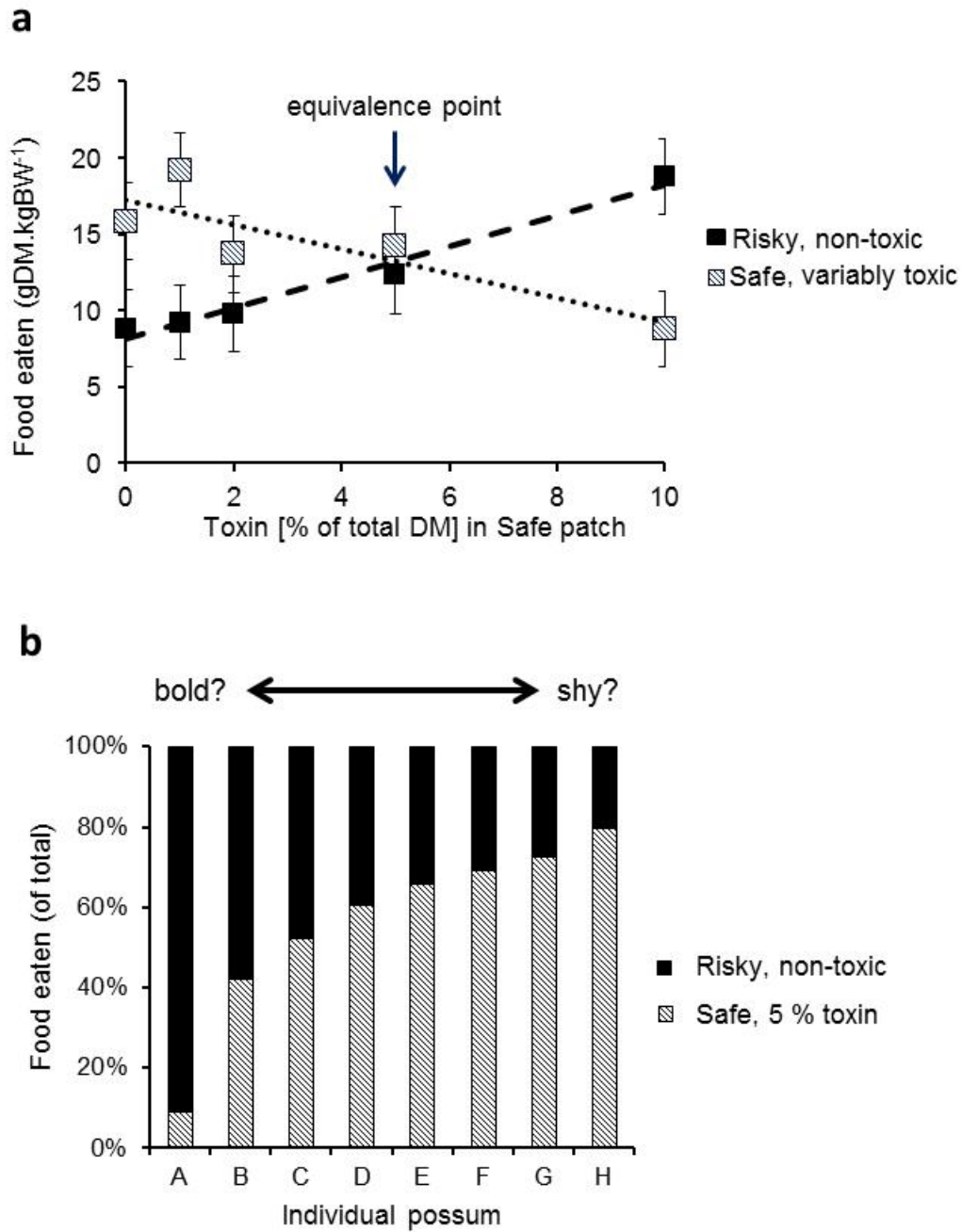


Figure 1

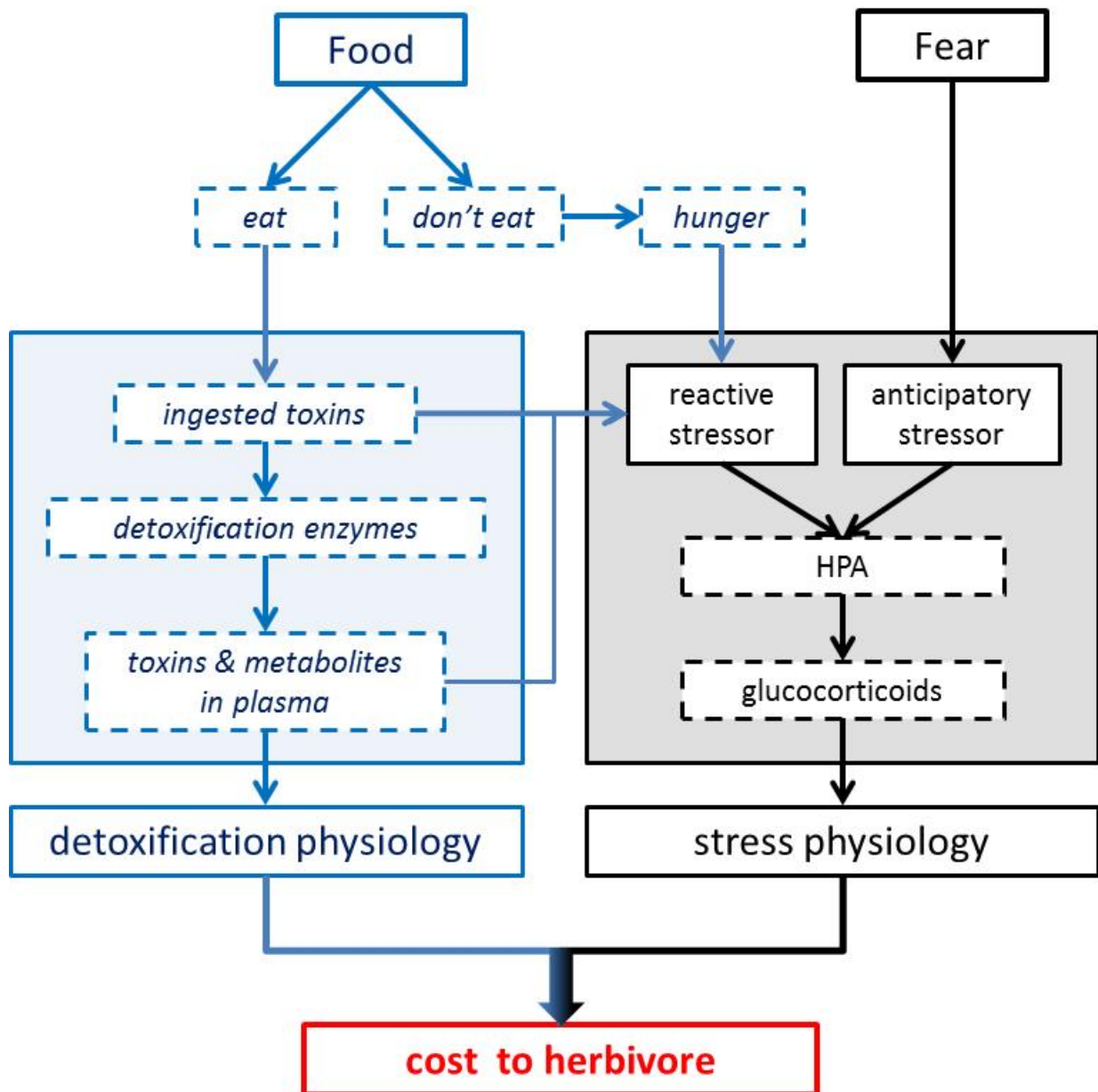


Figure 2

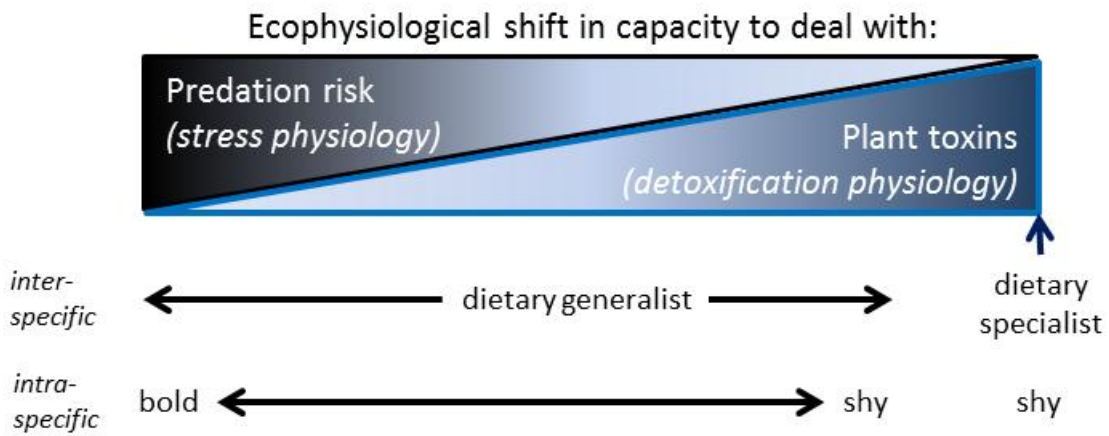


Figure 3

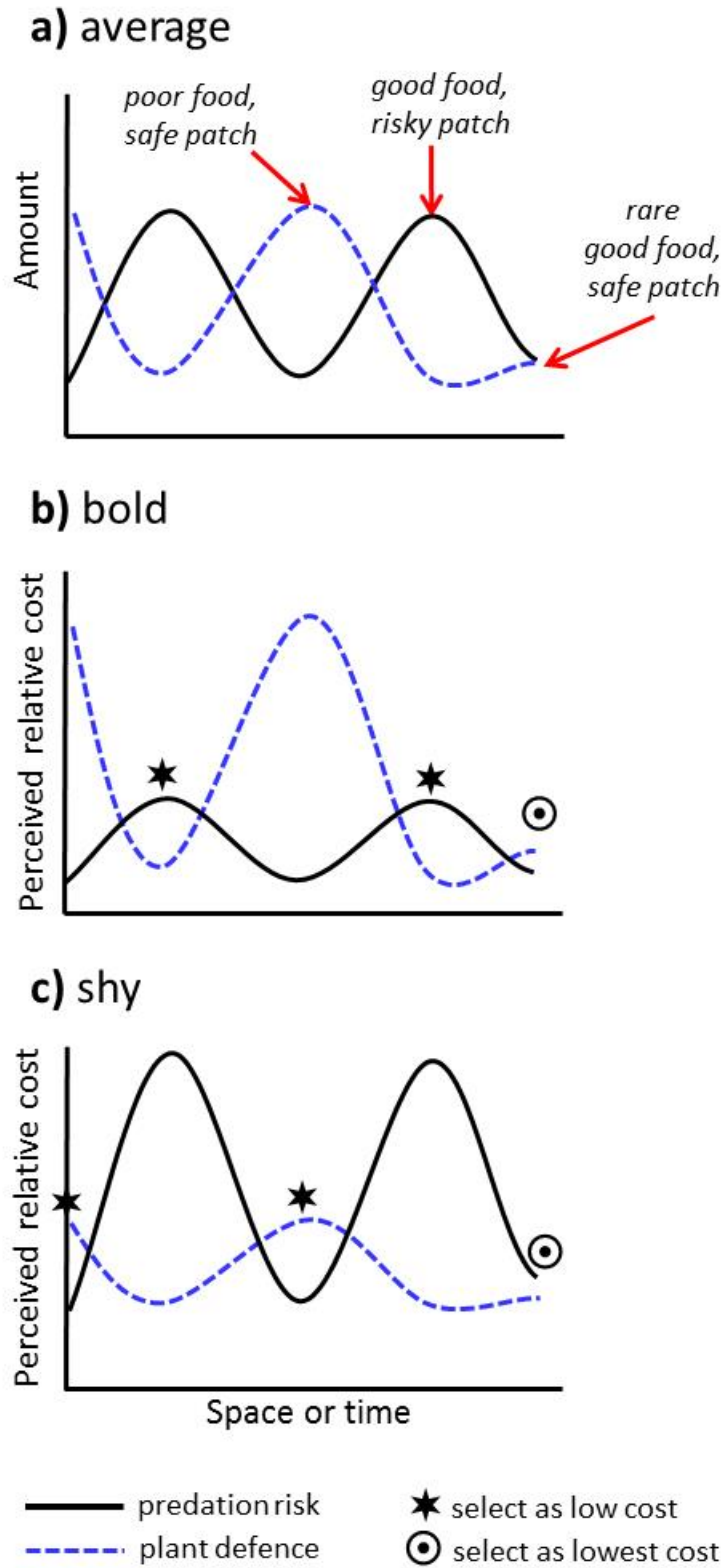


Figure 4