The Landscape of Fear: Ecological Implications of Being Afraid

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Abstract: "Predation risk" and "fear" are concepts well established in animal behavior literature. We expand these concepts to develop the model of the "landscape of fear". The landscape of fear represents relative levels of predation risk as peaks and valleys that reflect the level of fear of predation a prey experiences in different parts of its area of use. We provide observations in support of this model regarding changes in predation risk with respect to habitat types, and terrain characteristics. We postulate that animals have the ability to learn and can respond to differing levels of predation risk. We propose that the landscape of fear can be quantified with the use of well documented existing methods such as giving-up densities, vigilance observations, and foraging surveys of plants. We conclude that the landscape of fear is a useful visual model and has the potential to become a unifying ecological concept.

Keywords: Predators, prey, landscape of fear, predation risk, fear.

INTRODUCTION TO THIS SPECIAL ISSUE

This special issue attempts to investigate how the fear a prey has of being killed by its predator may affect the basic predator-prey interactions as we understand them and how the resulting interplay in this two player game can cascade to other ecological effects. The incorporation of fear into ecology is a relatively new concept and is just now being explored more fully. Because fear in ecology or the ecology of fear (Brown *et al.* 1999) is new, it is appropriate that the first article in this special issue begins with an overview of fear and why we can apply it to animals in an ecological setting. We investigate one of the major implications of fear prey have of their predators: how they use the landscape in which they live. We propose that the spatial and temporal use of the landscape is fear driven: a landscape of fear (Laundré *et al.* 2001). We introduce the basic assumptions of the landscape of fear and analyze its utility as an ecological concept. We investigate its possible advantages over how we have viewed landscape use in the past and why it would be advantageous to physically measure the landscape of fear for a species. We then propose that the landscape of fear is a useful, concise visual model that relates to how prey and their predators move about the landscape in a real life game of cat and mouse. We conclude that the landscape of fear has the potential to become a unifying concept in animal ecology.

What follows are articles on various aspects of the ecology of fear by some of the leading researchers in this area. The breadth of the articles indicates how rapidly the concept of fear in ecology has grown since its introduction (Brown *et al.* 1999, Laundré *et al.* 2001). Because of the efforts of these and a growing number of other innovative

and creative researchers, the ecology of fear is poised to make a significant contribution in all areas of ecology. What lies ahead should be some exciting and interesting developments in our understanding of how fear permeates all aspects of ecological processes. This special issue should provide a stimulating introduction to what lies ahead.

1. INTRODUCING THE CONCEPT

"Fear" is defined by Merriam-Webster (www.merriam-webster.com, accessed 11/29/09) as "an unpleasant often strong emotion caused by anticipation or awareness of danger". For emerging primitive humans, fear of known dangers from mega predators drove them to seek refuge in caves and trees (Hart and Sussman 2005). As human populations grew, fear of another predator, other humans, developed. From Alexander the Great, the Caesars, Attila the Hun, the Aztecs, to common thieves, the list of human predators is endless. In response to the actual danger or anticipated risk of danger from human predation, fear has and continues to be a major individual and social, psychological and emotional force in human history. We lock our house doors, our car doors, our luggage, and our bicycles, even when the danger of "predation" is not immediate, "just in case". Thus fear not only drives our reactions to the danger of eminent predation but, as defined, the anticipation or risk of predation. The multi-million dollar security industry is driven by our fear from this risk of predation.

Fear, however, is not an emotion limited to the human species. When cockroaches scurry away from the sudden light or elk (*Cervus elaphus*) flee from approaching wolves (*Canis lupus*), the underlying emotion driving these responses to eminent danger can only be expressed as fear of being killed by a predator. However, like humans, prey should not only express fear from the imminent attacks of their predators but also from the anticipation or risk of possible attacks. As a prey individual rarely operates with

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perfect information on the whereabouts of predators, it hardly ever knows if or when a predator is near (Brown *et al.* 1999). In this case, the evolutionary stable strategy is to maintain a certain level of background fear of predation (Brown *et al.* 1999). If an animal does not have this underlying fear of the risk of predation, it puts itself and its genes in mortal danger (Boissy 1995). Aldo Leopold (1966) eloquently identified fear as an element of the predator-prey relationship: "… as a deer herd lives in mortal *fear* (our emphasis) of its wolves, so does a mountain live in mortal fear of its deer." Fear then, should be an important behavioral element in the predator-prey relationship. However, how do we measure it?

Internally, fear can be measured *via* changes in cortico-steroid levels stimulated by nervous impulses (Boissy 1995, Korte 2001, Creel *et al.* 2002, Faure *et al.* 2003, Bonier *et al.* 2004), which increase with risk levels (Harlow *et al.* 1992, Boonstra 1998, Roy and Woolf 2001, Millspaugh *et al.* 2001, Cockrem and Silverin 2002, Creel *et al.* 2002). Outwardly, fear can be measured by levels of vigilance (Welp *et al.* 2004). Studies have demonstrated that the more fearful an animal is the more vigilant it should be (Quenette 1990, Hunter and Skinner 1998, Rushen 2000, Laundré *et al.* 2001, Childress and Lung 2003, Treves *et al.* 2003, Wolff and Van Horn 2003, Halofsky and Ripple 2008, just to list a few). Brown (1988) proposed that fear could be measured as a foraging cost where the benefits of foraging in a food patch (H) is the sum of the metabolic (C), predation (P), and missed opportunity (MOC) costs (H = C + P + MOC). Brown (1988) further demonstrated that P within a given area could be titrated by measuring the giving up densities (GUDs) or amount of food left behind in depletable food sources. Others have shown that these changes in time allocation are a common response to predation risk (Brown *et al.* 1994, Altendorf *et al.* 2001, Brown and Kotler 2004).

Fear in animals is real, measurable and, most impor-tantly, drives the actions of prey in response to predation risk from their predators, which, in turn, generally drives the actions of the predator in a two-player game of stealth and fear (Brown *et al.* 1999, Holmes and Laundré 2006). Recently, Brown *et al.* (1999) proposed the concept of the "ecology of fear" and applied it to traditional ecological predator-prey models. They demonstrated that incorporating fear helped avoid the logistical conflicts ("Catch-22") inherent in these models (Rosenzweig and MacArthur 1963). About the same time, the concept of fear was also proposed by Laundré *et al.* (2001) and Altendorf *et al.* (2001) as being useful in explaining foraging patterns of animals. They introduced the term "landscape of fear" as a visual model to help explain how fear could alter an animal's use of an area as it tries to reduce its vulnerability to predation. More recently, Ripple and Beschta (2006) proposed a "terrain fear factor" which was used to explain variability in ungulate browsing levels and corresponding heights of preferred woody browse plant species. Here, we expand on the concept of the landscape of fear, provide evidence for its validity as an ecological/ behavioral model, and explore its potential as a unifying concept in animal ecology.

The ideas behind the landscape of fear are not new. Many researchers have laid the ground work with studies of predation risk, prey refugia, predator efficiency and related phenomenon (Edwards 1983, Stephens and Peterson 1984, Lima and Dill 1990, Chapman *et al.* 1996, Novotny *et al.* 1999, Norrdahl and Korpimäki *et al.* 2000, Lewis and Eby 2002, Gude 2006, Creel and Christianson 2008, Halofsky and Ripple 2008). These studies demonstrated that predation risk can be variable, as implied by the presences of refugia, areas of low predation risk. Meanwhile, others, as noted earlier, have sufficiently demonstrated that prey respond to these changes in predation risk by altering their behavior (changes in vigilance and/or foraging) or time allocation patterns (avoiding high risk areas). The landscape of fear combines these variations in predation risk and the behavioral responses, incorporating the element of fear to explain the resulting spatial use patterns of individuals over the physical landscape. Under this model, predation risk varies in an identifiable manner over time and space. Animals then respond to this predation risk by altering their behavior/time allocation patterns based on the level of fear they have of being killed in the different areas of their home range.

A 16 year study of mule deer (*Odocoileus hemionus*) and pumas (*Puma concolor*) demonstrated that habitat structure is important in defining these levels of predation risk (Laundré and Hernández 2003). Pumas were more successful in killing deer along forest edges (73% of kill sites) than in open areas (6%). This difference is because pumas are stalking hunters that need cover to approach their prey (Hornocker 1970). Other studies have also demonstrated habitat-mediated differences in predator success, or lethality, primarily because of limits on the hunting capabilities of the predator (Van Orsdol 1984, Lewis and Eby 2002, see Brown and Kotler 2004 for a review). Further, studies of prey responses to these differences in predation risk per habitat demonstrate that prey, from insects to elk, realize these risks and adjust their behavior accordingly, even at the loss of feeding opportunities (Sih 1980, Edwards 1983, Stephens and Peterson 1984, Sweitzer 1996, Gilliam and Fraser 1987, Altendorf *et al.* 2001, Hernández and Laundré 2005, Fortin *et al.* 2004, 2005, Ripple and Beschta 2004a, Bergman *et al.* 2006).

Given that habitat and terrain heterogeneity is common over the landscape (Longland and Price 1991) and that a particular predator is not adapted to be skillful in all landscape types, it is easy to conceive of a system where predator lethality and thus predation risk, varies with spatial changes in habitat type or structure. This, then, is the landscape of fear, a three dimensional landscape whose peaks and valleys are defined by the level of predation risk related to changes in habitat as they affect the lethality of the predator (Fig. **1**). The scale of the vertical z axis is variable and can be expressed in any measure of fear, e.g. percent vigilance, GUDs, or foraging levels on plants. The landscape of fear on the horizontal x-y axis can also be on a variety of spatial macrohabitat and microhabitat scales. For example, when the wolves were reintroduced into Yellowstone National Park, the scale was the entire Park (kilometers), with the peaks being the areas where the wolves originally established and the valleys being the "wolf-free" zones (Laundré *et al.* 2001) and at a finer scales, in buffer zones between wolf pack territories (Ripple *et al.* 2001), habitat types (Hernández and Laundré 2005, Creel and Winnie 2005), terrain characteristics (Table **1**, Ripple and Beschta

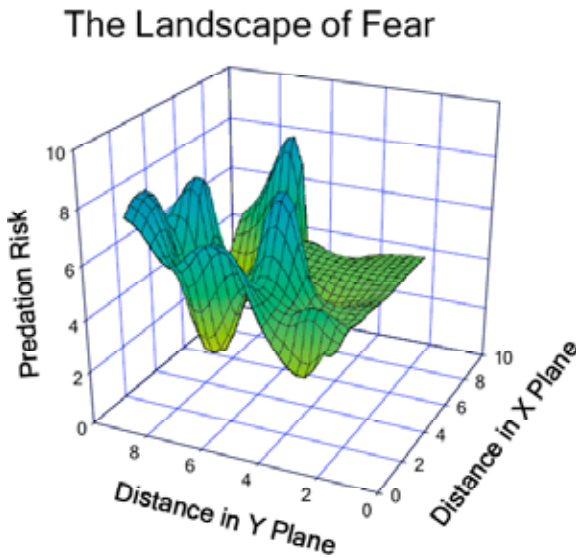2004b), and escape impediments (Ripple and Beschta 2006, 2007).

Fig. (1). Visual depiction of the landscape of fear where the x and y axis represent the physical coordinates of an area and can be in meters or kilometers, depending on the scale. The z axis is the level of predation risk as measured by indices of fear, e.g. vigilance, giving up densities (GUDs), etc.

2. BASIC ASSUMPTION OF THE CONCEPT

Implicit in the concept of the landscape of fear is that animals already have the ability or can learn to differentiate the dangerous versus safe habitats before they are killed! Do they have the ability to learn? Animals such as elk and moose (*Alces alces*) responding to newly introduced wolves (Laundré *et al.* 2001, Berger *et al.* 2001, Hernández and Laundré 2005) indicate an ability to learn. Do they have a chance to learn safe and risky areas before they are killed? Studies have demonstrated that predator efficiency (% success per kill attempts) for a variety of predators is commonly around 8-26 % (Nellis and Keith 1968, Mech 1966, Temple 1987, Longland and Price 1991, Mech *et al.* 2001). This means that generally around 80 % or more of the time, the prey escapes! We argue that escaping near death is an effective learning tool for prey, especially if their narrow escapes are even narrower in certain areas. If we add the advantages of social learning about predation risk (Kavaliers and Choleris 2001), prey not only have the ability but ample opportunity to learn the peaks and valleys of their landscape of fear and adjust their behavior accordingly.

3. UTILITY AND ADVANTAGES OF THE CONCEPT

Besides providing a visual picture of how fear should change over the landscape, of what value is the landscape of fear model? We propose that this model can help explain many of the ecological concepts concerning animals and their use of their landscape. The first example is the home range, originally defined by Burt (1943) as the area an animal uses in its pursuit of food, mates, and a place to rear young. Why would an animal confine its activity to a single area? The answer normally given is it provides familiarity, an animal knows (= learns) where to find food and shel-

ter. Combine these two needs, specifically shelter from predation, and they define the landscape of fear and the value

Table 1. General Types of Factors that Individually or in Combination may Contribute to Changes in Predation Risk for Ungulates Under the Risk of Predation by Wolves (Ripple and Beschta 2004b)

Terrain Factors
Point bars
Wide channels
Multiple channels
Tributary junctions
Islands
Gravelly/rocky surfaces
Gullies
High, steep channel banks
High terraces, steep terrace sideslopes
Undulating terrain
Narrowing valley
Cliffs, steep slopes
Canyons
Rushing water (noise)
Biotic Factors
Vegetation thickets
Woody debris
Jack-strawed trees
Beaver dams, ponds, and channels
Cultural Factors
Roads/traffic
Fences
Snowpack Factors
Aerial cover and drifts
Depth and density
Ice lenses and crusts
Frozen ground/ice

of a home range. Each day prey need to forage and survive not only within their home ranges but that of their predators, which is an area where the predators know the best places to hunt or where they are most lethal (Holmes and Laundré 2006). It is important to note that the flipside of the landscape of fear is the landscape of opportunity for the predator! Knowing safe and dangerous areas has survival advantages to prey (Clarke *et al.* 1993), and a home range provides that advantage. An animal then integrates this information with knowledge of food resources to make its

Fig. (2). August 2006 photographs of (**A**) recent aspen recruitment (aspen 3-4m tall) in a riparian area along Lamar River and (**B**) a lack of recent aspen recruitment (aspen <1m tall) in an adjacent upland. These differences shown in aspen heights were likely due to differences in perceived predation risk due to differences in escape terrain. (Ripple and Beschta 2007).

daily foraging decisions (Brown *et al.* 1994, Brown and Kotler 2004).

Having defined the landscape of fear, we need to ask what are the advantages of this model over what has existed in the past? First, while past research has previously identified predation risk and responses of prey to this risk, these two concepts were not joined in a clear, concise physical concept. As mentioned, the landscape of fear coalesces earlier works into a concise visual model and suggests that the different levels of predation risk can be quantified. If the levels of predation risk vary physically over space and time, we should be able to actually measure that risk relative to the specific prey and predator system we are considering. If we can measure levels of risk, we can then quantify total amounts of safe *versus* risky habitat, and map the size and juxtaposition of safe and risky patches. This then takes predation risk and behavioral responses and puts them on a quantifiable spatial scale.

How do we measure or map the landscape of fear? We argue that as the prey's perception of predation risk will be the most sensitive, this should be the best measure of that risk relative to habitat and terrain types (Table **1**). This has the added advantage of integrating the total risk in a multiple predator system. Earlier work has shown that the use of giving up densities (GUDs), levels of vigilance, and frequency of trapping as three possible techniques (Hernández and Laundré *et al.* 2001, Laundré *et al.* 2002). We could then represent the different levels of GUDs, vigilance, trapping
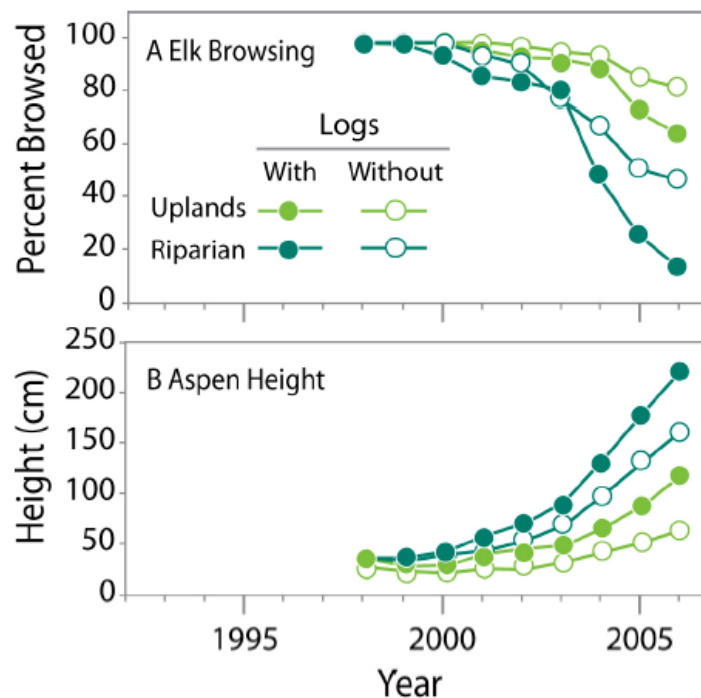
Fig. (3). Percentage of aspen leaders browsed (**A**), and mean aspen heights in Yellowstone's northern range (**B**). The percentage of aspen leaders browsed decreased the most and aspen grew tallest at high predation risk sites in riparian areas with downed logs affecting escape terrain. (Ripple and Beschta 2007).

success as contour lines, producing a topographic map-like depiction of the landscape of fear (Shrader 2008, Van der Merwe and Brown 2008). Another method is to let the plants tell the story (Schmitz *et al.* 2004). Ripple and Beschta (2003, 2004a, 2004b) documented vegetation changes in Yellowstone National Park after wolf reintroductions and indicated that these changes resulted from browsing changes by elk due to their fear of wolves in risky terrain (Figs. **2** and **3**, Ripple and Beschta 2006, 2007). White *et al.* (2003) also noted that distribution patterns of aspen (*Populus tremuloides*) could be explained by predation-driven foraging patterns of elk. The amount of browsing on preferred plants of a prey then, could also be a method of mapping the landscape of fear. These and likely other ingenious methods can give us estimates of the level of risk perceived by the prey, help us map the landscape of fear, and evaluate the overall risk level of an area.

4. WHY QUANTIFY THE LANDSCAPE OF FEAR: A CASE STUDY

Relative to community and ecosystem structure, Ripple and Beschta (2004a) poised the question, "Wolves and the ecology of fear: can predation risk structure ecosystems?" Based on the findings they presented, their answer was "yes". We concur with their assessment but add that this restructuring is accomplished and actually was predicted via the landscape of fear model. In an early study of elk vigilance, Laundré *et al.* (2001) found female elk had increased their level of vigilance from 20% to 47% in response to the reintroduction of wolves into Yellowstone National Park. In that article, based on the landscape of fear model, they made three predictions. The first was that we should see a shift in habitat use by elk in response to the

predation risk from wolves. They should abandon the newly established high risk open areas, the peaks of the landscape of fear, and seek the safer forest edges (the "valleys"). The second prediction was that this shift should result in a poorer quality diet because any shift, by default, would be to lower quality habitat or it soon would be because of increased use (Brown and Kotler 2004). Lastly, they predicted that the shift in use should result in changes in vegetation as plants were released from grazing pressure in high risk areas (Laundré *et al.* 2001, p. 1409).

A concurrent study of habitat use by elk during the 1998-2000 time period by Hernández and Laundré (2005) supported the first and second predictions. Within the first five years of the reintroduction of wolves into the Lamar Valley of Yellowstone, they found elk made a significant shift toward the forest edges. In a later study within the Park region, Creel and Winnie (2005) also documented higher use of edge areas by elk in response to predation by wolves. As predicted, this shift in habitat use was at the expense of foraging opportunities because Hernández and Laundré (2005) also found a significant decline in the diet quality of elk. The work of Ripple and Beschta (2003, 2004a, 2004b, 2006, 2007), demonstrated spatially patchy changes in vegetation in Yellowstone Park, thus supporting the third prediction.

In addition to the original three predictions, Laundré (2001) also suggested that the new landscape of fear that had been established should result in even further changes in community and ecosystem structure. In support of this idea, Ripple and Beschta (2004a) not only reported increases in willows (*Salix* sp.) and aspen in Yellowstone National Park but a resurgence of beavers (*Castor canadensis*) because of the return of their woody food supply. In addition, Frank

(2008) identified behavioral responses of elk to wolf predation likely altered net nitrogen mineralization in grasslands. Furthermore, Halofsky *et al.* (2008) found that the combined effects of fire disturbance, changes in elk density and predation risk, and decreased herbivory following wolf reintroduction likely facilitated the growth of young aspen. Additionally, the presence of the wolves in Yellowstone Park has also reduced the coyote population, which could favor other mesopredators (Smith *et al.* 2003) and alter the whole predator community. Thus, as a general conceptual model, the landscape of fear has had relatively good predictive power in this well documented example.

Changes in the landscape of fear can thus alter the predator-prey relationship and produces a cascading effect on a variety of ecological levels. If we quantify the landscape of fear for a particular predator-prey system, we propose that we can make more precise predictions as to outcomes of the predator-prey relationship. Additionally, we could also predict the impact of this relationship on competitive interactions, plant successional changes, and many other aspects of ecosystem structure.

Lastly, on a more practical level, quantifying the landscape of fear can be useful in the management and conservation of wildlife populations. If, as we predict, the impact of predators is mediated by the amount and configuration of risky habitat, quantifying and possibly changing the landscape of fear could benefit a desired species or help in assessing the adequacy of an area before reintroducing species, e.g. bighorn sheep (*Ovis canadensis*) (Laundré *et al.* 2002). Obviously, further research needs to be conducted on this issue. If such research supports our predictions, the landscape of fear model could become a valuable management and conservation tool.

5. CONCLUSION

In summary, we propose the landscape of fear is a useful, concise, visual model with measurable physical characteristics that relate the landscape to the interactions of the prey and predator found there. We have demonstrated that it has utility in describing ecological phenomena (e.g. home range, trophic cascades). This concept can be quantified to improve existing ecological models and has practical applications for animal conservation and management. We propose, then, that the concept of the landscape of fear is valid and has the potential to become a unifying concept in animal ecology.

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