

Landscapes of fear: from trophic cascades to applied management and population ecology

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Predator-Prey dynamics, and their trophic impacts, have functioned as a focal point in both community and population biology for five decades. The work-group focusing on these dynamics has however largely changed the focus of their work from trophic effects to the study of non-consumptive effects of predation-- the “ecology of fear”. An increasing number of studies chose to spatially chart wildlife populations’ risk assessment and of those the majority use optimal patch-use (giving-up densities) as a continuous measure of fear. These charts, “landscapes-of-fear” (LOFs) originated in conservation literature and the reintroduction of wolves to Yellowstone. Today, they are used to study population habitat selection and venture into the evolutionary context with studies examining the mechanisms by which species coexist in the same physical space. This review predicts increase in, and encourages the use of, LOFs: as a conservation tool to assess species land-use; as a bridge between ecology and neurology with stress hormones as indicators fear; and as a tool to compare species’ evolutionary dynamics within a community context.

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Introduction

The study of community ecology has developed from a study of how species affect each other in terms of resource competition to the study of how that competition over evolutionary history; i.e. how the ability of species to extract resources impacted the interactions between species historically, and to the community structure we observe at the present. This historical shift can be traced back to the models that formed the study of trophic cascades, and with that the birth of the predator-prey dynamics research group. Naturally this group continued to focus and narrow the research, eventually leading to the study of non-consumptive effects of predators on entire communities colloquially named “the ecology of fear”.

While the ecology of fear continued to focus on means by which the community structure impacts specific species behaviors, some of the researchers involved chose to broaden the study onto a system level. These researchers began to assess ecosystem health using the trophic cascades as the basis for a new theory of behavioral cascades reverberating down the food chain and affecting habitat selection of species along the chain.

John Laundré (2001) called this effect “Landscapes of fear” (LOF), and it has gained dominance in studies ever since (Figure 1). This review is directed to analyze how the LOF has changed from a theory based in trophic cascades and became a useful tool for conservation and a measurable attribute of population behavior. This review is intended to build on the previous review (Laundré *et al.*, 2010) and will guide the reader through three major sections: (1) the historical background leading to the development of the ecology of fear research group and segue to the early applications of the LOF. (2) It will discuss the methods by which researchers worldwide have measured the LOF and how they applied the theory. And lastly, (3) this review will make predictions for the directions in which the study of the LOF is developing and identify possible applications for future use.

Historical base: Trophic cascades

The world is green because predators manage the populations of grazing species concluded Hairston (Hairston, Smith & Slobodkin, 1960) in what later became known as the “Green World Hypothesis”. Since this ground breaking paper a large focus in community ecology was directed at the study of trophic cascades, i.e. the idea that through direct predation the size of a population impacts multiple trophic levels below it and the size of the population of prey dictates the availability of resources that sustain the predators above them.

The textbook example used to teach these interactions is population fluxes in Lotka-Volterra of lynx-hare (and mastings) predator-prey cycles in Canadian boreal forests (Hewitt, 1921; Fox & Bryant, 1984; Krebs *et al.*, 1995; Lima, 1998). This example highlights the trophic cascades from a bottom-up perspective, i.e. how the availability of resources influences the populations of predators. Resource availability dictates the availability of niches for species to occupy in the community; however, the top-down interactions greatly dictate the traits the

species must have to survive within those niches. Robert Paine pioneered the study of the predation implications on prey when he described how a diverse predator community results in diverse prey community (Paine, 1963). In this example, the predation pressure from multiple intertidal zone predators (sea stars) removed the competitive ability of the dominant barnacles and allowed for higher mollusk diversity. More recently, Schmitz and Price (2011) showed a strong positive correlation between the biomass of arachnid predators on the vegetation biomass in an agricultural system. In this system, spiders feed on grasshoppers that damage vegetation. The biomass of spiders thus positively correlates with the health of the vegetation crop. These examples show that the predators negatively affect the prey populations and thus indirectly have positive effects on the vegetation. However a few questions remained unanswered: (1) Do predators manage the populations of prey solely by consuming them? And (2) would the evolution of prey species to manage the risk of predation not overcome the negative impacts these predators have on their prey populations? Thus a study of non-consumptive predator effects was created, i.e. the “ecology of fear”.

Non- Consumptive Effects of Predators: an “Ecology of Fear”

One does not have to study wildlife behavior to understand the effects predation risk has on animal behavior. All one has to do, is think of our own body’s response to a risky situation. Our bodies instinctively respond to the risk in the environment by producing stress hormones. This production results in increased blood pressure, pulse and sensory sensitivity. In essence, our bodies tell us to get out of harm’s way as fast as we can. In this example of our own day-to-day life we find the evidence for the millions of years evolutionary race between predators and prey to maintain the energetic needs of both groups. Prey evolve mechanisms to avoid the risk, and predators find ways to out-gun these defense mechanisms.

In non-human examples we expect that predators would have to find a balance between over-hunting a naïve food resource into extinction and starvation from aiming to hunt over vigilant prey (Brown & Vincent, 1992; Lima, 1998, 2002; Wolf & Mangel, 2007; Brown, 2010). The predators must manage the fear in the prey into an optimal state of vigilance (Embar, Mukherjee & Kotler, 2014) and the prey counteracts the predator management through a variety of behavioural strategies, or choices. I will examine a few case studies of such strategies.

Many species choose their habitat based on the risk which this habitat poses to them. For example, heteromyid rodents choose habitat based on the density of vegetation. Species (kangaroo rats) that can hop out of harm's way prefer *the* un-encumbered open, and species that are limited in predator evasion strategies (pocket mice) find shelter under thick vegetation (Rosenzweig, 1973; Bleicher, 2014). In kangaroo rats specifically the presence of vipers was shown to be a driver of the choice of the open habitat (Bouskila, 1995). In another example, Gerbilline rodents responded to owls with clear preference for sheltered microhabitats (Kotler, Blaustein & Brown, 1992; Abramsky et al., 1996; Rosenzweig, Abramsky & Subach, 1997; Kotler et al., 2002; St. Juliana et al., 2011; Embar et al., 2014). Habitat fragmentation, or edge effect, has been shown to affect the habitat use (predominantly in the form of avoidance) by song birds (Storch, Witke & Krieger, 2005; Fischer & Lindenmayer, 2007). The final example is of larger animals (ungulates and primates) selecting habitat where the sightlines allow good visibility of approaching predators (Tadesse, 2012; Abu Baker & Brown, 2013; Sandford, 2013; Coleman & Hill, 2014).

Other strategic choices of prey driven by the predator-prey dynamics can include dietary selection and movement patterns. For example (again in the Heteromyid rodents), foragers better equipped for risk management (kangaroo rats) have a more diverse diet than the foragers less

well equipped for predator management (pocket mice) who forage what they can (Davidson, Brown & Inouye, 1980). In another example, in the Simpson Desert, dasyurid marsupials avoid risk by covering large distances to search for refuge. These small mammals (20 grams on average) inhabit burrows in the swale of sand dunes located away from the resource dense habitats at the dune crests (Haythornthwaite, 2005; Haythornthwaite & Dickman, 2006). All of these adaptations clearly suggest that a trade-off between resources and predation risk occurs within a spatial dynamic, and as such these predator-prey games can and should be studied using a spatial analysis, a “landscape of fear”.

Spatial Analysis of Risk and Resources: A “landscape of fear”

A. Theory

Two major research labs (Brown and Laundré), cooperatively pioneered the development of theory of the LOF (Laundré, Hernandez & Ripple, 2010). Initially, the landscapes of fear were proposed as metaphor for the implications of the predators on prey behavior on a landscape level. It was used to predict the implications of reintroduction of predators such as wolves on the populations of elk and bison (Laundré, Hernández & Altendorf, 2001). Only a relatively low proportion of the literature actually develops the theory (Figure 2) and further information on its development may be found in Laundré (2010). The theory was expanded to study the effects of landscape heterogeneity (Brown & Kotler, 2004) culminating in measured maps combining vegetation, refuge, resource availability and risk. In an example with cape ground squirrels (*Xerus inauris*), the LOF was interpreted as a cost benefit analysis of energetic values over change in the landscape (Joules/ meter) (Van Der Merwe & Brown, 2008). This conversion allowed researchers to weigh the study of energetic gain from food patches and compare those gains to the cost of risk avoidance (*cf.* Brown 1988)

It is important to draw attention to a common misinterpretation ~~on the~~ LOF ~~theory~~. The LOF is not the study of how ~~the~~ features in the landscape cause ~~the~~ organisms to assess risk ~~differently~~, but rather how a population of organisms sense the risk in the environment as a continuous variable of the landscape itself. This virtual, spatially dependent, variable is influenced by multiple factors: (1) the intensity of predation the population senses in the environment (predator community structure and activity); (2) the population size (safety in numbers); (3) inter-species competition (competition may embolden populations when resources are scarce) and (4) the energetic state of the population (hungry animals will take more risk). Some features of physical environment influence the LOF (e.g. blocked sightlines). However given the dependency on all the above, one should observe these separately, or combine these features with a spatial analysis.

Descriptive attributes of the LOF began taking increased priority in the literature as the variety of applications increased (see section on applications below). The various attributes of the LOF drew inspiration from other ecological and evolutionary theories to describe the zones of different risk characteristics. In a study of striped mice, the features of risky habitat was described as “islands” of fear, a reference to the island biogeography theory and the SLOSS debate, emphasizing the impacts of both borders and edges and the distribution of safety zones in the environment (Abu Baker & Brown, 2010). In the previous review Laundré et al. (2010) prefer to describe the landscape features as valleys (safe) and peaks (risky) in an aim to show that risk assessment is a quantitative attribute and not a binomial characteristic (two distinct outcomes of risk or safety). Lastly in an aim to quantify this rate of change, my own work has developed an approach to measuring the rate of change of perceived **risk** in the LOF.



This measure can be described as the rugosity of the landscape (Bleicher, Kotler & Brown, 2012; Bleicher, 2014). A highly rugose landscape (highly variable with steep changes between points) implies that the population perceives the risk as localized. In comparison, flat landscapes can be interpreted as the result of one of two behavioral assessments (or strategies). (1) A flat LOF may be the result of a very “fearful” population whereas the majority of the entire environment “plateaus” on a high risk contour. In such a LOF, the major focus of the behavior remains in contact with the locations of refuge in the landscape and the risk lessens gradually as one moves near the refuge. Alternately, (2) a population that is “secure” in its management ability of predation risk from the predators in the environment will have a very flat landscape. In this scenario, the zones of risk are less focused and tangible and thus the change between “riskier” and “safer” zones is gradual and not very distinct.

B. Measuring a Landscape of Fear

Fear has many definitions based on the field of biology in which it is studied. In behavioral ecology, the most common definition is the assessment of risk based on a set of criteria dependent on learned and inherited information that drives strategic decision- making (Vincent & Brown, 2005). In most studies that includes information on the lethality of the predators a prey animal may encounter. This variable combines (1) the likelihood a predator will be encountered, (2) environmental factors (vegetation, illumination, resources, etc.) contributing to the likelihood of falling prey and (3) the amount of energy that must be expended to avoid the predation risk (Brown, 1988). Two major theories were derived from that definition (optimal patch use and optimal vigilance), and from those theories tools were developed to measure the perceived risk in the environment (Brown, 1999).



Risk assessment in wildlife traditionally has been quantified using measures of activity, such as presence or absence of individuals of the species in a habitat. These activity measures present significant difficulties in this type of interpretation. The two general methods that have been used are mark-recapture surveys (Ritchie & Johnson, 2009) and diversity surveys (Rösner et al., 2014) to estimate population density in different habitats. Additionally, in birds, counting the number of active nest sites in different habitat types (Zanette & Jenkins, 2000) served a similar function equivalent to that of mark-recapture surveys. These methods alone are likely not the strongest measure of risk as they are confounded by multiple external factors. For instance, nesting areas and foraging areas likely do not overlap to any significant degree. This can be seen in the above mentioned examples of dunnarts in the Simpson Desert that exhibit a large daily migration pattern. Studies found that these animals transverse a large distance between the burrows they occupy during the day and the locations in which they forage (Dickman, Predavec & Downey, 1995; Haythornthwaite & Dickman, 2006). As a result, the animals may be caught in the path they transverse nightly. Similarly, if burrows (or nests) were counted in the dune crests where the dunnarts forage, (and likely encounter the majority of predators,) we would conclude that this habitat is avoided by the foragers when in fact it is the lack of burrows dug by other species that drives the nightly migration. Thus caution is suggested in the use of surveys alone to quantify a LOF. In addition to using these methods, a stronger (and more reliable) way to measure perceived risk is to measure foraging for small animals and vigilance for larger species. Both foraging behavior and vigilance can be used in ways that are independent of other spatially dependent variables. Examples of such spatially dependent variables are the chance of being trapped for mark-recapture surveys and nest site availability for nests or borrows.

180 Aldo Leopold in observation on the Kaibab Plateau in Arizona proclaims that one can tell the
 181 stress (hunger state) on mule deer population by the height of the browse lines on the white pines
 182 (Leopold 1949, pg. 56). From this, and many other observations, ecologists have derived that
 183 foraging behavior can explain much of the state of the population that left the marks behind:
 184 Leopold states: “one need no doubt the unseen” (pg. 57), meaning that one does not need to
 185 observe the animal in action to infer what its state was. Brown (1988) suggested the Optimal
 186 patch use theory which deduces that the foraging activity of an animal within a resource patch is
 187 dictated by the metabolic costs involved in foraging in that patch, the predation risk within that
 188 patch and a missed opportunity cost (the value of all other patches in the environment in
 189 comparison to the patch the forager is in). From this theory a tool for measuring the perceived
 190 risk in the environment was developed, the giving up density (GUD). This tool has been used in
 191 hundreds of research projects (Bedoya-Perez et al., 2013), and is the dominant tool that has been
 192 used to quantify the LOF (Figure 3A) (Jacob & Brown 2000; Altendorf *et al.* 2001; Van Der
 193 Merwe & Brown 2008; Druce *et al.* 2009; Abu Baker & Brown 2010; Baker & Brown 2011;
 194 Emerson *et al.* 2011, and more). When the perceived energetic gain is diminished in comparison
 195 to the costs (mentioned above), the animal ceases foraging in a patch and the density of food left
 196 behind (GUD) becomes a quantifiable measure of these costs. The GUD as a measure for the
 197 LOF has proved itself useful for study in small mammals (Appendix I). Examples of studies
 198 include the cape ground squirrels mentioned above (Van Der Merwe & Brown, 2008), two
 199 competing lemming species in the Canadian tundra (Dupuch et al., 2014), striped mice and
 200 elephant voles in African grasslands (Abu Baker & Brown, 2010; Baker & Brown, 2011) and
 201 small carnivorous marsupials in the Australian Desert (Bleicher and Dickman, in preparation).
 202 GUDs have successfully been applied to measuring risk perception in birds (*e.g.* Brown *et al.*

1997; Kotler *et al.* 1998; Oyugi *et al.* 2012) and it is a matter of time before LOF are measured using this tool in fish as well.

Foraging behavior is best used to measure the response of populations of small animals, whereas in populations of species of greater biomass vigilance is best measured instead. The theory of optimal vigilance states that an animal will spend a greater amount of time (and energy) in vigilance behavior when the perceived risk of predation is higher in the habitat occupied by that prey individual (Brown, 1999). This theory has been tested greatly in ungulates (Ale & Brown, 2009; Tadesse & Kotler, 2011) small mammals (Rosenzweig, Abramsky & Subach, 1997; Kotler *et al.*, 2010) and birds (Elgar, 1989; Robinette & Ha, 2001). Vigilance, measured in time, as a direct tool to measure effects of risk in the environment has been applied in roe deer responding to hunting pressures (Benhaïem *et al.*, 2008), duikers responding to habitat heterogeneity (Abu Baker & Brown, 2013), mule deer responding to vegetation density of fir trees compared with juniper bushes (Altendorf *et al.*, 2001)¹ and more.

C. Applications

The use of LOF follows general trends in ecological research. Ecologists traditionally have an attraction to large megafauna, and these trends carry to the LOF theory as well (Figure 3B). The major group for which the LOF has been applied remains with the initial group for which it was designed, the ungulates (Laundré *et al.*, 2001; Laundré *et al.*, 2010). Similarly, the research has been developed on model organisms for behavioural ecology, species that are readily available and of no particular conservation status, predominantly gerbils, squirrels, heteromyid rodents, voles and lemmings (*e.g.* Brown & Kotler 2004; Bleicher 2014; Eccard & Liesenjohann 2014).

¹ Mentioned as surveying behavior and not vigilance

Similar to the above, ~~the~~ focal study systems have been drawn to model systems (Figure 3C). For ungulates in North America the predominant systems studied were alpine scrublands and forests, the system in which the theory was developed . Altendorf *et al.* 2001; Laundré *et al.* 2001; Ripple & Beschta 2004; Creel *et al.* 2005; Hernández & Laundré 2005). In ~~the~~ small mammals, arid (and tundra) zones (both arid grasslands and hyper-arid environments) have been used largely because of their simplicity (*e.g.* Bleicher *et al.* 2012; Bleicher 2014; Dupuch *et al.* 2014; Eccard & Liesenjohann 2014). The use of the theory has been limited to simple systems because of the ease of mapping a LOF on a two dimensional scale with the third being the perception of risk. The one exception to this pattern is the study of habitat selection by primates in which the third dimension of ~~altitude~~  (within trees) was added (Willems & Hill, 2009; Emerson, Brown & Linden, 2011; Coleman & Hill, 2014).

On a side note, two trajectories can be expected in the way in which LOFs are being mapped. Initially, three dimensional maps (with the three dimensions of space; longitude X latitude X altitude) are likely to become more popular as landscapes of fear are applied to aquatic systems, alpine ranges, tropical forests and avian species where the populations are not limited in two dimensional vector movement. Similarly, a temporal dimension in the form of time series should gain popularity to study the temporal changes observed in behavior influenced by seasonal, competitive and predation pressures.

How ~~have the~~  LOF been applied to research? Given the history of the theory in conservation, the LOF continue to have a significant proportion of manuscripts dedicated to this topic (Figure 2). The surprising observation is the small proportion of the research using the LOF that remains in that field. In the conservation literature that used LOF analysis we find a pattern and a trend for future applications. The majority of the papers were using the LOF to monitor the changes in

community habitat use and the resulting vegetation changes that occur in the landscape. One example includes the success of willow regeneration in Yellowstone National Park (Ripple & Beschta, 2004a,b, 2006). Other examples study the impact on health of the prey populations through diet quality (Hernández & Laundré, 2005). I believe the LOF, as a population attribute and assessment tool, should be used to a much greater extent in conservation. I found that dasyurid marsupials, during a period of population bust, used artificial shelters only when these were adjacent to natural refuges (Bleicher & Dickman, 2016). The ability to map out the habitat use of species of conservation interest, provides an ability to assess the effectiveness of conservation treatments aimed to increase habitat use by these species. This makes the LOF a powerful conservation tool, which has potential to revolutionize the way in which species of conservation concern are surveyed.

Despite the LOF being based in conservation, the majority of applications of the LOF (33 manuscripts) appear to be directed towards understanding habitat use and the influence that these have on population and community dynamics (31 of those manuscripts). How are these applications used to interpret population and community dynamics? For example, two competing lemming species showed that the competition for resources in shared habitats had a greater impact on their foraging than did the relative risk of predation (Dupuch et al., 2014). The changes in the LOF of competing rodents from two systems (gerbils and heteromyid) showed how predation risk, and the resulting habitat use, provide a mechanism of coexistence between competing species (Bleicher, 2014). From another example (of many more), predation risk in forest fragments in Australia limited the nest site selection in birds (Zanette & Jenkins, 2000).

The last application, not well developed at this stage, is the transcendence of environmental risk into a measurable impact on neurologically manifested stress syndromes. Ecologically, when

an animal is under stress (risk of predation), the neurological registering of the risk cues causes an increase in stress hormones to be released in the body of the animal (Gross & Canteras, 2012). The physiological responses to these stress hormones are energetically costly (Apfelbach et al., 2005) and influence a lowered productivity (*e.g.* Mukherjee *et al.* 2014). An example of the research in the neuro-ecology field showed that sparrows respond with an increase of a variety of stress hormones (plasma total corticosterone, corticosteroid binding globulin (CBG) and free corticosterone) in response to an increase in the risk of predation in the environment (Zanette et al., 2011). In their work, Clinchy *et al.* (2013) suggest that this connection of environmental stress and neurological responses are a fertile ground for research, moving away from the chronic stress studied in laboratory animals.

No longer a theory, now a measurable attribute (Prospectus)

The LOF as a tool, can be applied to understanding the dynamics of change in habitat selection for populations, and how these can be related to ecosystem functions and community structure. The LOF also provides a means of comparison between species on the same physical landscape (or within similar constraints). This tool can, in the future, be used in three major ways.

(1) The LOF can reveal spatial intricacies that are driven by the evolutionary games between competitors and between predator and prey species. As a result, I believe that we should study the mechanisms by which both predator and prey interact using a spatial analysis that can highlight the intricacies of the decision-making process (in both players). (2) I would like to encourage the data mining of previous experiments that measured behaviour in vigilance and GUDs. In experiments that used grid formations, a common normalization of the data is usually performed, averaging the GUDs along treatments. These data sets could be reused to explore the

spatial distribution of habitat use. I expect many of these old experiments will confirm their findings using the LOF approach; however, many novel patterns are likely to emerge and further our understanding of behavioural patterns on a spatial scale. (3) I expect (stated above) the infiltration of this tool as a measure of conservation success. (4) Last, some experiments have begun to mend the gap between ecological and neurological pathways to the study of fear on the spatial scale (Clinchy et al., 2011). Directly measuring the neurological impacts of risk in the environment is still in its infancy state Clinchy et al (2011, 2013).

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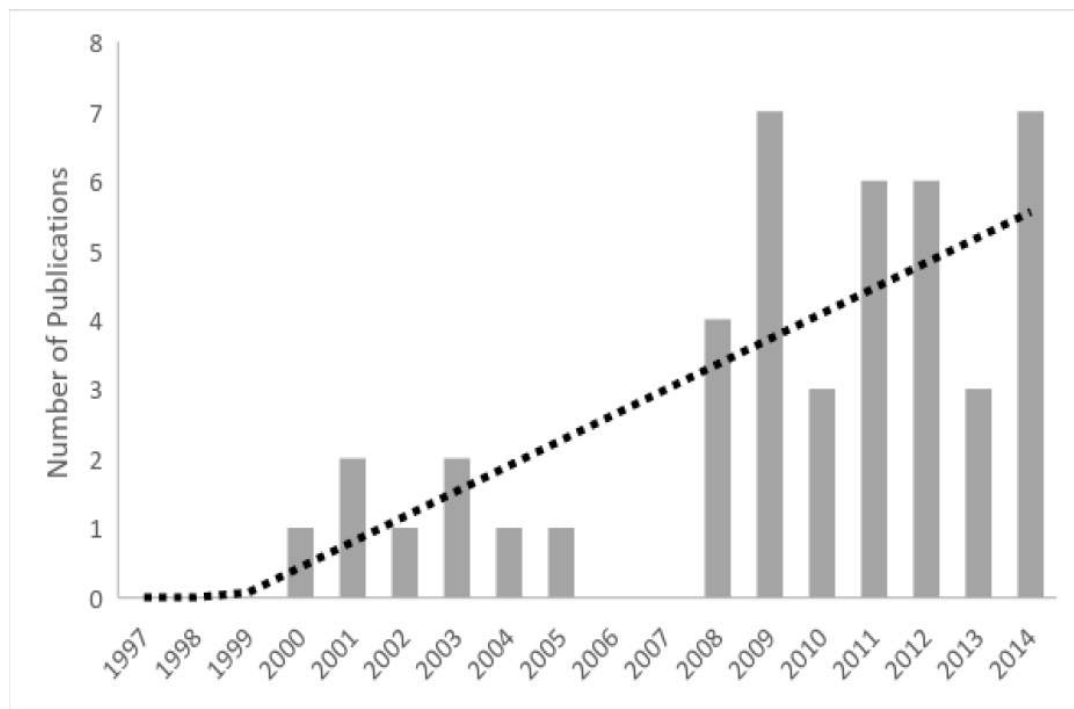
494 Figure Legends

495 **Figure 1.** Cumulative number of manuscripts publishing empirical analysis supporting the theory
 496 of LOFs in ecological journals (total of 58). The application of the theory is increasing in
 497 applications and use showing higher rate of publication with pulses of increasing magnitude
 498 2009, 2012 and 2014 (15 manuscripts). The trend line is for visual emphasis of the increase in
 499 use. At the time of writing 4 manuscripts were published in 2015.

500 **Figure 2.** Cumulative number of publications testing the theory of LOF using empirical data
 501 organized through the focus of the manuscripts. * A manuscript may be represented in more than
 502 one column if the manuscript discusses more than one aspect of the LOF theory.

503 **Figure 3.** Cumulative number of publications testing the theory of LOF using empirical data
 504 organized through: (A)* per species group the methods used to quantify fear, (B) the subject
 505 species classification (of the author's categorical choice), and (C) the system in which the
 506 experiment was performed. * A manuscript may be represented in more than one column if the
 507 manuscript uses more than one measurement variable. Abbreviations: avi. = avian, veg.=
 508 vegetation l. and s. (mammal) = large and small.

509

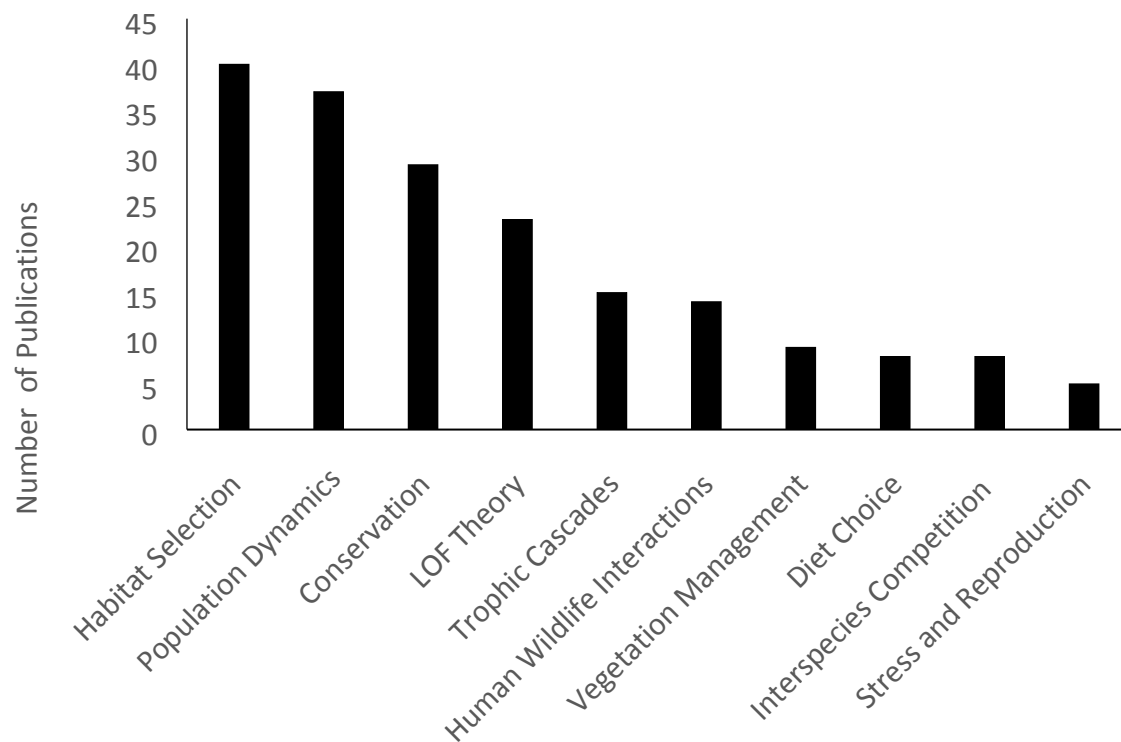


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511 **Figure 1.**

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515 **Figure 2.**

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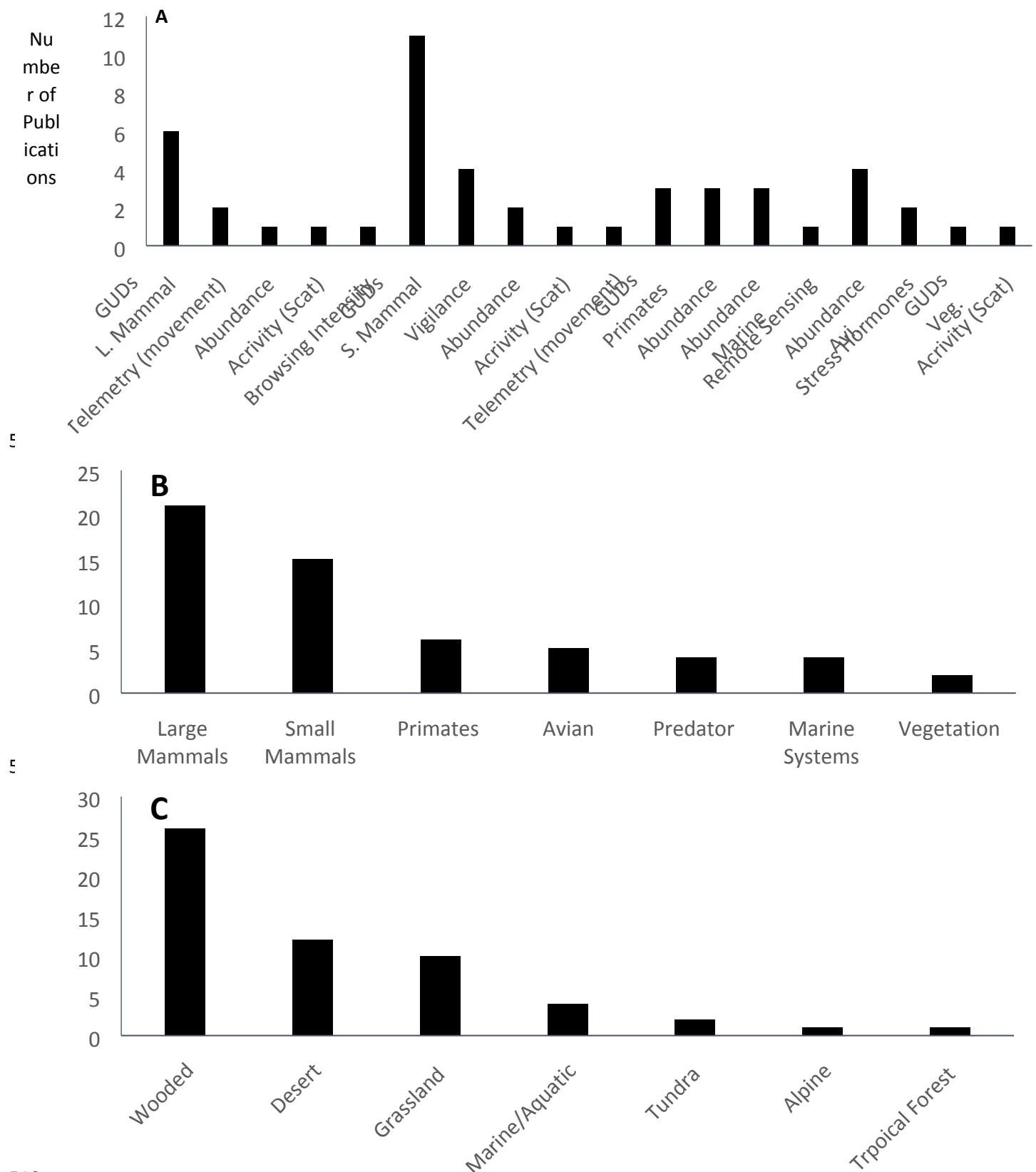


Figure 3.

Appendix I. Example of Landscape of Fear Map using a dataset adapted from Bleicher et al. (2016). The map shows the distribution of risk using giving up densities (GUDs) for a population of Allenby's gerbils (*G. andersoni allenbyi*) in a controlled enclosure in Sde Boker, Israel. The contour lines are derived using the distance weighted least squares (DWLS) smoothing function at a tension of 0.5. GUD values above 2.0g (orange and red) reflect areas that are perceived as dangerous by the gerbils while areas below 1.0g (green and blue) reflect zones of safety. The + signs are the locations in which the data was collected and both x and y -axes are measuring the enclosure in meters.

