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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8 **Introduction**

9   The study of community ecology has developed from a study of how species affect each

10 other in terms of resource competition to the study of how that competition over evolutionary

11 history; i.e. how the ability of species to extract resources impacted the interactions between

12 species historically, and to the community structure we observe at the present. This historical

13 shift can be traced back to the models that formed the study of trophic cascades, and with that the

14 birth of the predator-prey dynamics research group. Naturally this group continued to focus and

15 narrow the research, eventually leading to the study of non-consumptive effects of predators on

16 entire communities colloquially named "the ecology of fear".

17   While the ecology of fear continued to focus on means by which the community structure

18 impacts specific species behaviors, some of the researchers involved chose to broaden the study

19 onto a system level. These researchers began to assess ecosystem health using the trophic

20 cascades as the basis for a new theory of behavioral cascades reverberating down the food chain

21 and affecting habitat selection of species along the chain.

22   John Laundré (2001) called this effect "Landscapes of fear" (LOF), and it has gained

23   dominance in studies ever since (Figure 1). This review is directed to analyze how the LOF has

24   changed from a theory based in trophic cascades and became a useful tool for conservation and a

25   measurable attribute of population behavior. This review is intended to build on the previous

26   review (Laundre *et al.*, 2010) and will guide the reader through three major sections: (1) the

27   historical background leading to the development of the ecology of fear research group and

28   segue to the early applications of the LOF. (2) It will discuss the methods by which researchers

29   worldwide have measured the LOF and how they applied the theory. And lastly, (3) this review

30   will make predictions for the directions in which the study of the LOF is developing and identify

31   possible applications for future use.

32   **Historical base: Trophic cascades**

33   The world is green because predators manage the populations of grazing species

34   concluded Hairston (Hairston, Smith & Slobodkin, 1960) in what later became known as the

35   "Green World Hypothesis". Since this ground breaking paper a large focus in community

36   ecology was directed at the study of trophic cascades, i.e. the idea that through direct predation

37   the size of a population impacts multiple trophic levels below it and the size of the population of

38   prey dictates the availability of resources that sustain the predators above them.

39   The textbook example used to teach these interactions is population fluxes in Lotka-

40   Volterra of lynx-hare (and mastings) predator-prey cycles in Canadian boreal forests (Hewitt,

41   1921; Fox & Bryant, 1984; Krebs et al., 1995; Lima, 1998). This example highlights the trophic

42   cascades from a bottom-up perspective, i.e. how the availability of resources influences the

43   populations of predators. Resource availability dictates the availability of niches for species to

44   occupy in the community; however, the top-down interactions greatly dictate the traits the

45   species must have to survive within those niches. Robert Paine pioneered the study of the

46   predation implications on prey when he described how a diverse predator community results in

47   diverse prey community (Paine, 1963). In this example, the predation pressure from multiple

48   intertidal zone predators (sea stars) removed the competitive ability of the dominant barnacles

49   and allowed for higher mollusk diversity. More recently, Schmitz and Price (2011) showed a

50   strong positive correlation between the biomass of arachnid predators on the vegetation biomass

51   in an agricultural system. In this system, spiders feed on grasshoppers that damage vegetation.

52   The biomass of spiders thus positively correlates with the health of the vegetation crop. These

53   examples show that the predators negatively affect the prey populations and thus indirectly have

54   positive effects on the vegetation. However a few questions remained unanswered: (1) Do

55   predators manage the populations of prey solely by consuming them? And (2) would the

56   evolution of prey species to manage the risk of predation not overcome the negative impacts

57   these predators have on their prey populations? Thus a study of non-consumptive predator

58   effects was created, i.e. the "ecology of fear".

59   **Non- Consumptive Effects of Predators: an "Ecology of Fear"**

60   One does not have to study wildlife behavior to understand the effects predation risk has on

61   animal behavior. All one has to do, is think of our own body's response to a risky situation. Our

62   bodies instinctively respond to the risk in the environment by producing stress hormones. This

63   production results in increased blood pressure, pulse and sensory sensitivity. In essence, our

64   bodies tell us to get out of harm's way as fast as we can. In this example of our own day-to-day

65   life we find the evidence for the millions of years evolutionary race between predators and prey

66   to maintain the energetic needs of both groups. Prey evolve mechanisms to avoid the risk, and

67   predators find ways to out-gun these defense mechanisms.

68   In non-human examples we expect that predators would have to find a balance between over-

69   hunting a naïve food resource into extinction and starvation from aiming to hunt over vigilant

70   prey (Brown & Vincent, 1992; Lima, 1998, 2002; Wolf & Mangel, 2007; Brown, 2010). The

71   predators must manage the fear in the prey into an optimal state of vigilance (Embar, Mukherjee

72   & Kotler, 2014) and the prey counteracts the predator management through a variety of

73   behavioural strategies, or choices. I will examine a few case studies of such strategies.

74   Many species choose their habitat based on the risk which this habitat poses to them. For

75   *e*xample, heteromyid rodents choose habitat based on the density of vegetation. Species

76   (kangaroo rats) that can hop out of harm's way prefer *the* un-encumbered open, and species that

77   are limited in predator evasion strategies (pocket mice) find shelter under thick vegetation

78   (Rosenzweig, 1973; Bleicher, 2014). In kangaroo rats specifically the presence of vipers was

79   shown to be a driver of the choice of the open habitat (Bouskila, 1995). In another example,

80   Gerbilline rodents responded to owls with clear preference for sheltered microhabitats (Kotler,

81   Blaustein & Brown, 1992; Abramsky et al., 1996; Rosenzweig, Abramsky & Subach, 1997;

82   Kotler et al., 2002; St. Juliana et al., 2011; Embar et al., 2014). Habitat fragmentation, or edge

83   effect, has been shown to affect the habitat use (predominantly in the form of avoidance) by song

84   birds (Storch, Woitke & Krieger, 2005; Fischer & Lindenmayer, 2007). The final example is of

85   larger animals (ungulates and primates) selecting habitat where the sightlines allow good

86   visibility of approaching predators (Tadesse, 2012; Abu Baker & Brown, 2013; Sandford, 2013;

87   Coleman & Hill, 2014).

88   Other strategic choices of prey driven by the predator-prey dynamics can include dietary

89   selection and movement patterns. For example (again in the Heteromyid rodents), foragers better

90   equipped for risk management (kangaroo rats) have a more diverse diet than the foragers less

91   well equipped for predator management (pocket mice) who forage what they can (Davidson,

92   Brown & Inouye, 1980). In another example, in the Simpson Desert, dasyurid marsupials avoid

93   risk by covering large distances to search for refuge. These small mammals (20 grams on

94   average) inhabit burrows in the swale of sand dunes located away from the resource dense

95   habitats at the dune crests (Haythornthwaite, 2005; Haythornthwaite & Dickman, 2006). All of

96   these adaptations clearly suggest that a trade-off between resources and predation risk occurs

97   within a spatial dynamic, and as such these predator-prey games can and should be studied using

98   a spatial analysis, a "landscape of fear".

99   **Spatial Analysis of Risk and Resources: A "landscape of fear"**

100   **A. Theory**

101   Two major research labs (Brown and Laundré), cooperatively pioneered the development of

102   theory of the LOF (Laundre, Hernandez & Ripple, 2010). Initially, the landscapes of fear were

103   proposed as metaphor for the implications of the predators on prey behavior on a landscape level.

104   It was used to predict the implications of reintroduction of predators such as wolves on the

105   populations of elk and bison (Laundré, Hernández & Altendorf, 2001). Only a relatively low

106   proportion of the literature actually develops the theory (Figure 2) and further information on its

107   development may be found in Laundré (2010). The theory was expanded to study the effects of

108   landscape heterogeneity (Brown & Kotler, 2004) culminating in measured maps combining

109   vegetation, refuge, resource availability and risk. In an example with cape ground squirrels

110   (*Xerus inauris*), the LOF was interpreted as a cost benefit analysis of energetic values over

111   change in the landscape (Joules/ meter) (Van Der Merwe & Brown, 2008). This conversion

112   allowed researchers to weigh the study of energetic gain from food patches and compare those

113   gains to the cost of risk avoidance (*cf.* Brown 1988)

114   It is important to draw attention to a common misinterpretation on the LOF theory. The LOF

115   is not the study of how the features in the landscape cause the organisms to assess risk

116   differently, but rather how a population of organisms sense the risk in the environment as a

117   continuous variable of the landscape itself. This virtual, spatially dependent, variable is

118   influenced by multiple factors: (1) the intensity of predation the population senses in the

119   environment (predator community structure and activity); (2) the population size (safety in

120   numbers); (3) inter-species competition (competition may embolden populations when resources

121   are scarce) and (4) the energetic state of the population (hungry animals will take more risk).

122   Some features of physical environment influence the LOF (e.g. blocked sightlines). However

123   given the dependency on all the above, one should observe these separately, or combine these

124   features with a spatial analysis.

125   Descriptive attributes of the LOF began taking increased priority in the literature as the

126   variety of applications increased (see section on applications below). The various attributes of

127   the LOF drew inspiration from other ecological and evolutionary theories to describe the zones

128   of different risk characteristics. In a study of striped mice, the features of risky habitat was

129   described as "islands" of fear, a reference to the island biogeography theory and the SLOSS

130   debate, emphasizing the impacts of both borders and edges and the distribution of safety zones in

131   the environment (Abu Baker & Brown, 2010). In the previous review Laundré et al. (2010)

132   prefer to describe the landscape features as valleys (safe) and peaks (risky) in an aim to show

133   that risk assessment is a quantitative attribute and not a binomial characteristic (two distinct

134   outcomes of risk or safety). Lastly in an aim to quantify this rate of change, my own work has

135   developed an approach to measuring the rate of change of perceived risk in the LOF.

136   This measure can be described as the rugosity of the landscape (Bleicher, Kotler & Brown,

137   2012; Bleicher, 2014). A highly rugose landscape (highly variable with steep changes between

138   points) implies that the population perceives the risk as localized. In comparison, flat landscapes

139   can be interpreted as the result of one of two behavioral assessments (or strategies). (1) A flat

140   LOF may be the result of a very "fearful" population whereas the majority of the entire

141   environment "plateaus" on a high risk contour. In such a LOF, the major focus of the behavior

142   remains in contact with the locations of refuge in the landscape and the risk lessens gradually as

143   one moves near the refuge. Alternately, (2) a population that is "secure" in its management

144   ability of predation risk from the predators in the environment will have a very flat landscape. In

145   this scenario, the zones of risk are less focused and tangible and thus the change between

146   "riskier" and "safer" zones is gradual and not very distinct.

147   **B. Measuring a Landscape of Fear**

148   Fear has many definitions based on the field of biology in which it is studied. In behavioral

149   ecology, the most common definition is the assessment of risk based on a set of criteria

150   dependent on learned and inherited information that drives strategic decision- making (Vincent

151   & Brown, 2005). In most studies that includes information on the lethality of the predators a prey

152   animal may encounter. This variable combines (1) the likelihood a predator will be encountered,

153   (2) environmental factors (vegetation, illumination, resources, etc.) contributing to the likelihood

154   of falling prey and (3) the amount of energy that must be expended to avoid the predation risk

155   (Brown, 1988). Two major theories were derived from that definition (optimal patch use and

156   optimal vigilance), and from those theories tools were developed to measure the perceived risk in

157   the environment (Brown, 1999).

158   Risk assessment in wildlife traditionally has been quantified using measures of activity,

159 such as presence or absence of individuals of the species in a habitat. These activity measures

160 present significant difficulties in this type on interpretation. The two general methods that have

161 been used are mark-recapture surveys (Ritchie & Johnson, 2009) and diversity surveys (Rösner

162 et al., 2014) to estimate population density in different habitats. Additionally, in birds, counting

163 the number of active nest sites in different habitat types (Zanette & Jenkins, 2000) served a

164 similar function equivalent to that of mark-recapture surveys. These methods alone are likely not

165 the strongest measure of risk as they are confounded by multiple external factors. For instance,

166 nesting areas and foraging areas likely do not overlap to any significant degree. This can be seen

167 in the above mentioned examples of dunnarts in the Simpson Desert that exhibit a large daily

168 migration pattern. Studies found that these animals transverse a large distance between the

169 burrows they occupy during the day and the locations in which they forage (Dickman, Predavec

170 & Downey, 1995; Haythornthwaite & Dickman, 2006). As a result, the animals may be caught in

171 the path they transverse nightly. Similarly, if burrows (or nests) were counted in the dune crests

172 where the dunnarts forage, (and likely encounter the majority of predators,) we would conclude

173 that this habitat is avoided by the foragers when in fact it is the lack of burrows dug by other

174 species that drives the nightly migration. Thus caution is suggested in the use of surveys alone to

175 quantify a LOF. In addition to using these methods, a stronger (and more reliable) way to

176 measure perceived risk is to measure foraging for small animals and vigilance for larger species.

177 Both foraging behavior and vigilance can be used in ways that are independent of other spatially

178 dependent variables. Examples of such spatially dependent variables are the chance of being

179 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.*

203   1997; Kotler *et al.* 1998; Oyugi *et al.* 2012) and it is a matter of time before LOF are measured

204   using this tool in fish as well.

205   Foraging behavior is best used to measure the response of populations of small animals,

206   whereas in populations of species of greater biomass vigilance is best measured instead. The

207   theory of optimal vigilance states that an animal will spend a greater amount of time (and

208   energy) in vigilance behavior when the perceived risk of predation is higher in the habitat

209   occupied by that prey individual (Brown, 1999). This theory has been tested greatly in ungulates

210   (Ale & Brown, 2009; Tadesse & Kotler, 2011) small mammals (Rosenzweig, Abramsky &

211   Subach, 1997; Kotler et al., 2010) and birds (Elgar, 1989; Robinette & Ha, 2001). Vigilance,

212   measured in time, as a direct tool to measure effects of risk in the environment has been applied

213   in roe deer responding to hunting pressures (Benhaiem et al., 2008), duikers responding to

214   habitat heterogeneity (Abu Baker & Brown, 2013), mule deer responding to vegetation density

215   of fir trees compared with juniper bushes (Altendorf et al., 2001)[1] and more.

216   **C. Applications**

217   The use of LOF follows general trends in ecological research. Ecologists traditionally have

218   an attraction to large megafauna, and these trends carry to the LOF theory as well (Figure 3B).

219   The major group for which the LOF has been applied remains with the initial group for which it

220   was designed, the ungulates (Laundré *et al.*, 2001; Laundre *et al.*, 2010). Similarly, the research

221   has been developed on model organisms for behavioural ecology, species that are readily

222   available and of no particular conservation status, predominantly gerbils, squirrels, heteromyid

223   rodents, voles and lemmings (*e.g.* Brown & Kotler 2004; Bleicher 2014; Eccard & Liesenjohann

224   2014).

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[1] Mentioned as surveying behavior and not vigilance

225   Similar to the above, the focal study systems have been drawn to model systems (Figure 3C).

226   For ungulates in North America the predominant systems studied were alpine scrublands and

227   forests, the system in which the theory was developed (*e.g.* Altendorf *et al.* 2001; Laundré *et al.*

228   2001; Ripple & Beschta 2004; Creel *et al.* 2005; Hernández & Laundré 2005). In the small

229   mammals, arid (and tundra) zones (both arid grasslands and hyper-arid environments) have been

230   used largely because of their simplicity (*e.g.* Bleicher *et al.* 2012; Bleicher 2014; Dupuch *et al.*

231   2014; Eccard & Liesenjohann 2014). The use of the theory has been limited to simple systems

232   because of the ease of mapping a LOF on a two dimensional scale with the third being the

233   perception of risk. The one exception to this pattern is the study of habitat selection by primates

234   in which the third dimension of altitude (within trees) was added (Willems & Hill, 2009;

235   Emerson, Brown & Linden, 2011; Coleman & Hill, 2014).

236   On a side note, two trajectories can be expected in the way in which LOFs are being mapped.

237   Initially, three dimensional maps (with the three dimensions of space; longitude X latitude X

238   altitude) are likely to become more popular as landscapes of fear are applied to aquatic systems,

239   alpine ranges, tropical forests and avian species where the populations are not limited in two

240   dimensional vector movement. Similarly, a temporal dimension in the form of time series should

241   gain popularity to study the temporal changes observed in behavior influenced by seasonal,

242   competitive and predation pressures.

243   How have the LOF been applied to research? Given the history of the theory in conservation,

244   the LOF continue to have a significant proportion of manuscripts dedicated to this topic (Figure

245   2). The surprising observation is the small proportion of the research using the LOF that remains

246   in that field. In the conservation literature that used LOF analysis we find a pattern and a trend

247   for future applications. The majority of the papers were using the LOF to monitor the changes in

248   community habitat use and the resulting vegetation changes that occur in the landscape. One

249   example includes the success of willow regeneration in Yellowstone National Park (Ripple &

250   Beschta, 2004a,b, 2006). Other examples study the impact on health of the prey populations

251   through diet quality (Hernández & Laundré, 2005). I believe the LOF, as a population attribute

252   and assessment tool, should be used to a much greater extent in conservation. I found that

253   dasyurid marsupials, during a period of population bust, used artificial shelters only when these

254   were adjacent to natural refuges (Bleicher & Dickman, 2016). The ability to map out the habitat

255   use of species of conservation interest, provides an ability to assess the effectiveness of

256   conservation treatments aimed to increase habitat use by these species. This makes the LOF a

257   powerful conservation tool, which has potential to revolutionize the way in which species of

258   conservation concern are surveyed.

259   Despite the LOF being based in conservation, the majority of applications of the LOF (33

260   manuscripts) appear to be directed towards understanding habitat use and the influence that these

261   have on population and community dynamics (31 of those manuscripts). How are these

262   applications used to interpret population and community dynamics? For example, two competing

263   lemming species showed that the competition for resources in shared habitats had a greater

264   impact on their foraging than did the relative risk of predation (Dupuch et al., 2014). The

265   changes in the LOF of competing rodents from two systems (gerbils and heteromyid) showed

266   how predation risk, and the resulting habitat use, provide a mechanism of coexistence between

267   competing species (Bleicher, 2014). From another example (of many more), predation risk in

268   forest fragments in Australia limited the nest site selection in birds (Zanette & Jenkins, 2000).

269   The last application, not well developed at this stage, is the transcendence of environmental

270   risk into a measurable impact on neurologically manifested stress syndromes. Ecologically, when

271   an animal is under stress (risk of predation), the neurological registering of the risk cues causes

272   an increase in stress hormones to be released in the body of the animal (Gross & Canteras,

273   2012).The physiological responses to these stress hormones are energetically costly (Apfelbach

274   et al., 2005) and influence a lowered productivity (*e.g.* Mukherjee *et al.* 2014). An example of

275   the research in the neuro-ecology field showed that sparrows respond with an increase of a

276   variety of stress hormones (plasma total corticosterone, corticosteroid binding globulin (CBG)

277   and free corticosterone) in response to an increase in the risk of predation in the environment

278   (Zanette et al., 2011). In their work, Clinchy *et al.* (2013) suggest that this connection of

279   environmental stress and neurological responses are a fertile ground for research, moving away

280   from the chronic stress studied in laboratory animals.

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

282   The LOF as a tool, can be applied to understanding the dynamics of change in habitat

283   selection for populations, and how these can be related to ecosystem functions and community

284   structure. The LOF also provides a means of comparison between species on the same physical

285   landscape (or within similar constraints). This tool can, in the future, be used in three major

286   ways.

287   (1) The LOF can reveal spatial intricacies that are driven by the evolutionary games

288   between competitors and between predator and prey species. As a result, I believe that we should

289   study the mechanisms by which both predator and prey interact using a spatial analysis that can

290   highlight the intricacies of the decision-making process (in both players). (2) I would like to

291   encourage the data mining of previous experiments that measured behaviour in vigilance and

292   GUDs. In experiments that used grid formations, a common normalization of the data is usually

293   performed, averaging the GUDs along treatments. These data sets could be reused to explore the

294 spatial distribution of habitat use. I expect many of these old experiments will confirm their

295 findings using the LOF approach; however, many novel patterns are likely to emerge and further

296 our understanding of behavioural patterns on a spatial scale. (3) I expect (stated above) the

297 infiltration of this tool as a measure of conservation success. (4) Last, some experiments have

298 begun to mend the gap between ecological and neurological pathways to the study of fear on the

299 spatial scale (Clinchy et al., 2011). Directly measuring the neurological impacts of risk in the

300 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.=

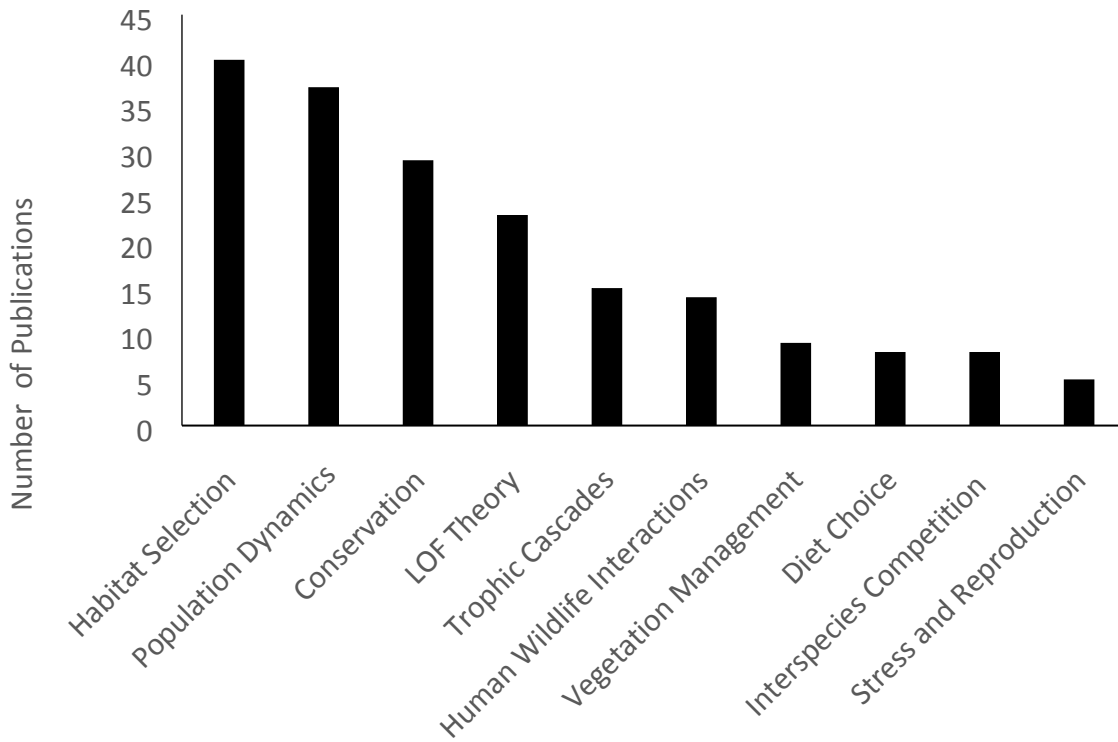508   vegetation l. and s. (mammal) = large and small.
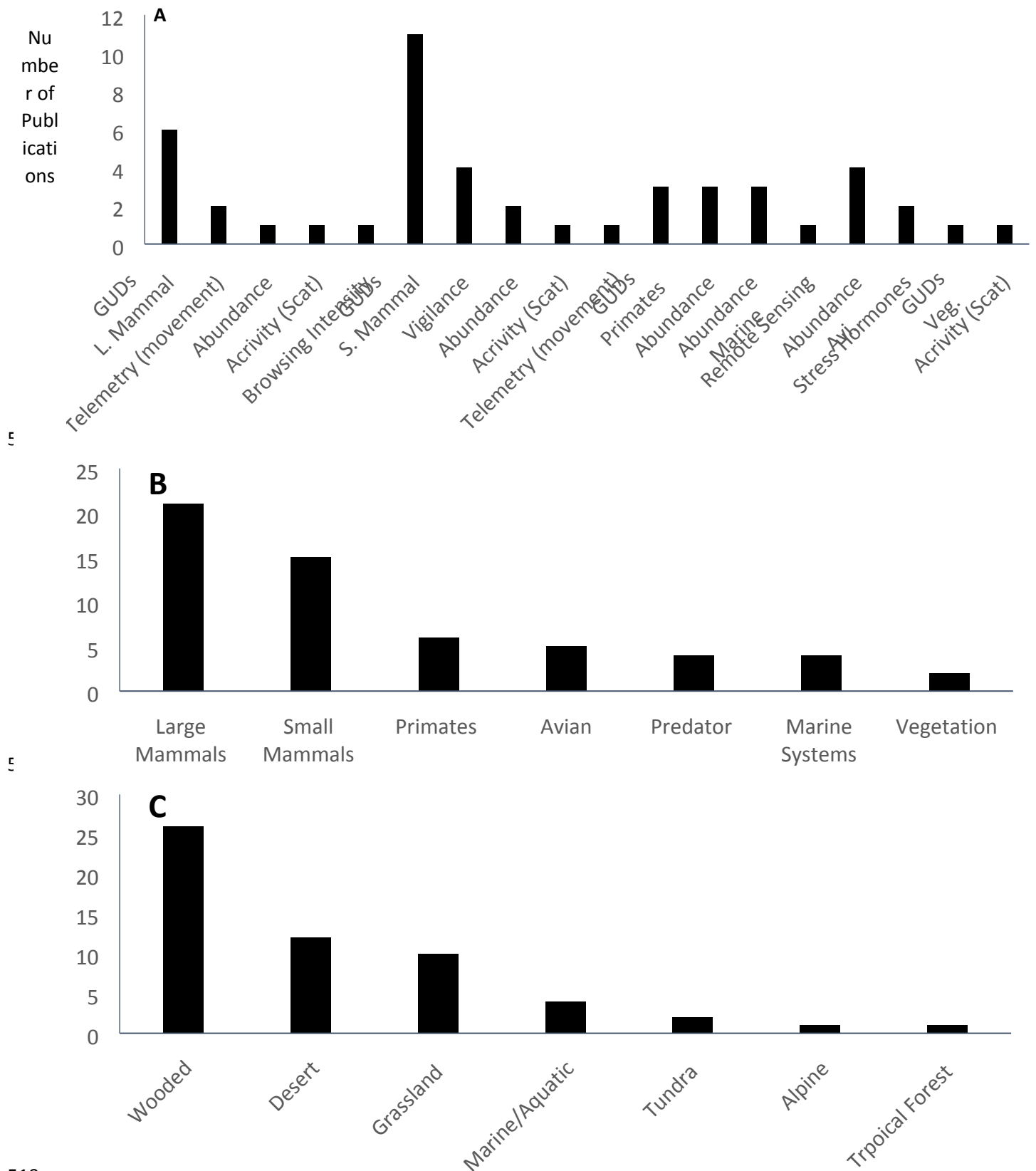
509
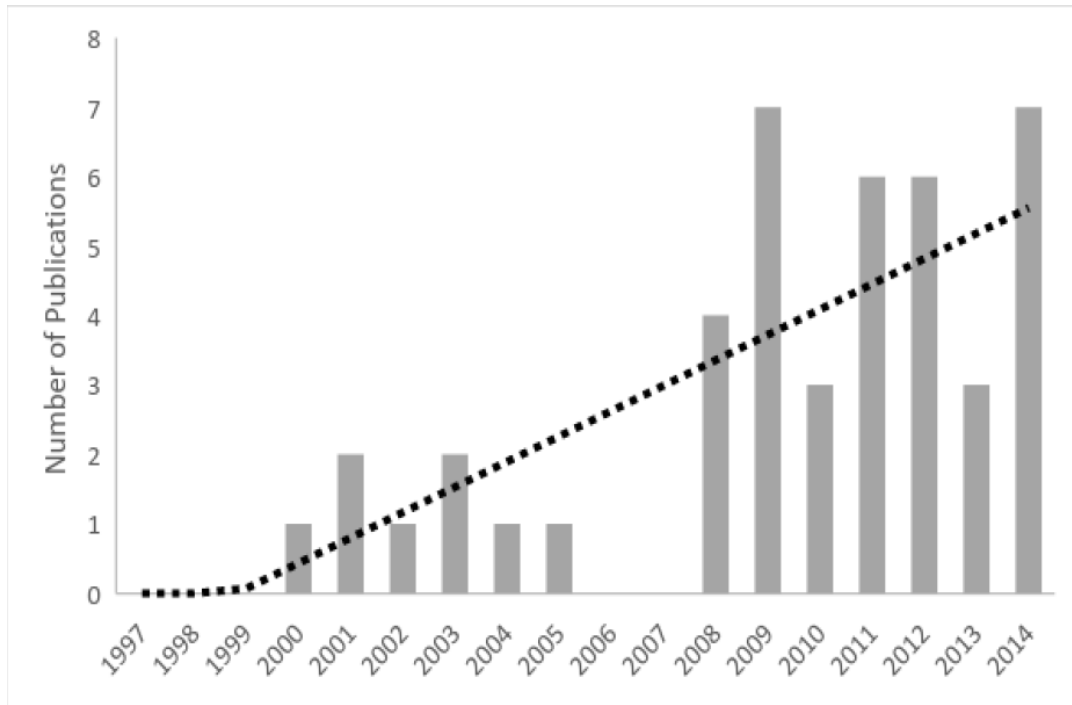
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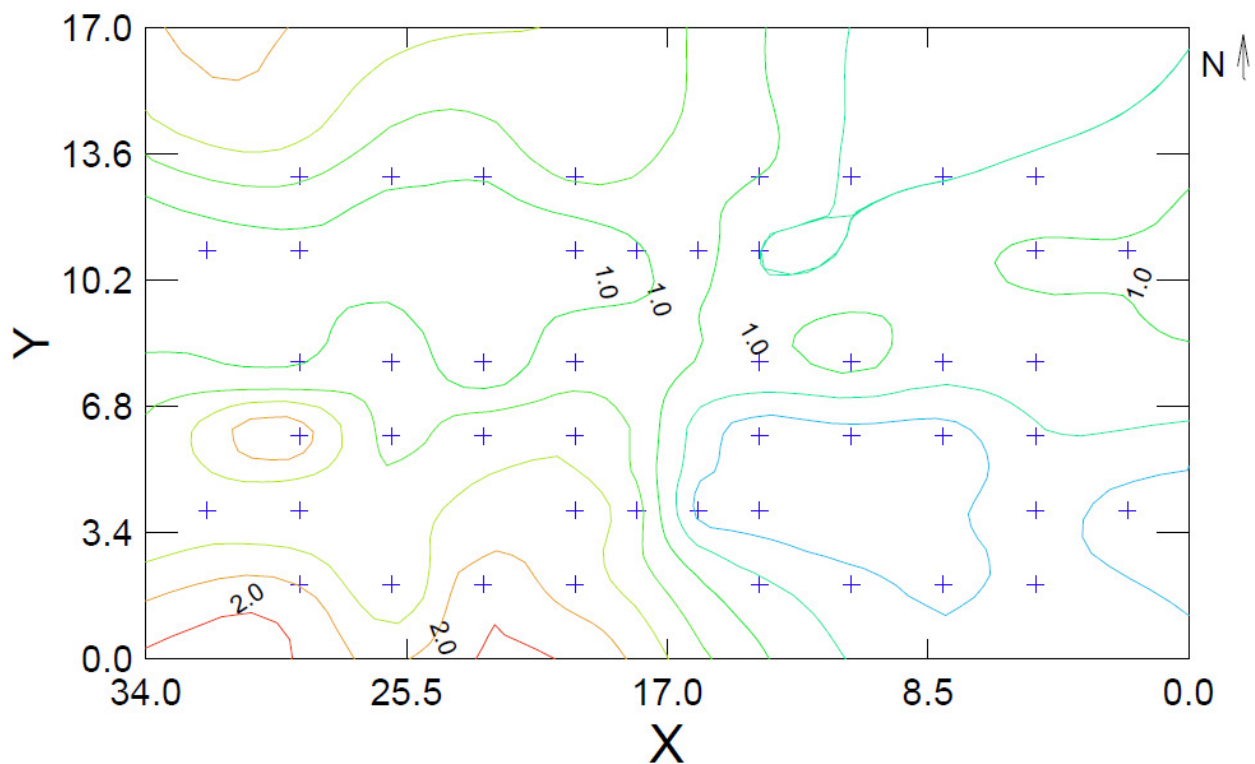511 **Figure 1.**

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515   **Figure 2**.

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520   **Figure 3.**

521   Appendix I. Example of Landscape of Fear Map using a dataset adapted from Bleicher et al.

522   (2016). The map shows the distribution of risk using giving up densities (GUDs) for a population

523   of Allenby's gerbils (*G. andersoni allenbyi*) in a controlled enclosure in Sde Boker, Israel. The

524   contour lines are derived using the distance weighted least squares (DWLS) smoothing function

525   at a tension of 0.5. GUD values above 2.0g (orange and red) reflect areas that are perceived as

526   dangerous by the gerbils while areas below 1.0g (green and blue) reflect zones of safety. The +

527   signs are the locations in which the data was collected and both *x* and *y*-exes are measuring the

528   enclosure in meters.

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