

RISKY BUSINESS: DEALING WITH RISK IN A  
PREDATOR – PREY  
COMMUNITY

by

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DEDICATION

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## ABSTRACT

The Liuwa ecosystem has several ecological properties that affect interactions among large predators, with lions and hyaenas as dominant species and African wild dog and cheetah as subordinate species, and between predator and prey. First, the vegetation structure is highly uniform and typified by open grasslands with good visibility over long distances. Secondly the prey community is heavily dominated by wildebeest, with much lower numbers of zebra, oribi and other species. These characteristics combined with GPS data on a fine spatial scale, and a large observational dataset on both predators and prey enabled us to focus on several little-studied questions about the effects of predation risk in the wild.

Interspecific competition between predators can be a strongly limiting force for subordinate predators like cheetahs and African wild dogs. Both species use niche partitioning to reduce the risk of dangerous interactions in different ways that appear to have ramifications for coexistence. Wild dogs showed more dietary and temporal overlap with dominant competitors while cheetahs combine divergence in diet, temporal avoidance and reactive local spatial avoidance to coexist with lions and hyenas in areas of high prey density, even in open habitats. These results provide new insight into the conditions under which partitioning may not allow for coexistence of African wild dog, while it does for cheetah, with dominant predators making wild dogs more prone to competitive exclusion (local extirpation), particularly in open, uniform ecosystems with simple prey communities.

Focusing on predator-prey relationships the overall the conclusion is that the assessment of risk by animals is a very fine-tuned process. Our results confirm that both the *risky places hypothesis* (LT risk) and the *risky times hypothesis* (ST risk) are important, leading to both reactive and proactive responses. Critically, these effects do not act independently in their effects on the strength of antipredator responses. This interaction presents challenges for the design of research on risk effects. An effect of ST risk could be masked by unmeasured variation in LT risk (or vice versa), and an effect of ST risk might be caused by unmeasured variation in LT risk (or vice versa).

## CHAPTER ONE

## INTRODUCTION TO DISSERTATION

Overview of Dissertation

Virtually all species are exposed to predation risk. Considerable research has examined the effect of these risks on ecology and demography, both within predator communities (Palomares & Caro 1999; Creel 2001; Creel, Spong & Creel 2001; Caro & Stoner 2003; Cozzi et al. 2012; Broekhuis et al. 2013; Périquet, Fritz & Revilla 2014; Périquet et al. 2015), and in the context of predator-prey interactions (Creel, Schuette & Christianson; Creel *et al.* 2007; Creel, Schuette & Christianson 2014; Werner *et al.* 1983; Peckarsky *et al.* 1993; Boonstra *et al.* 1998; Creel & Winnie 2005; Christianson & Creel 2008, 2010; Sheriff, Krebs & Boonstra 2009; Valeix *et al.* 2009a; Courbin *et al.* 2015; Schuette *et al.* 2016; LaManna, Martin & Letters 2016). This work has convincingly demonstrated that behavioral responses of prey to predation risk (or responses to direct competitive interactions within carnivore guilds) often carry costs that influence growth, survival, reproduction, population dynamics, habitat selection, and community structure. To date, most of this work has focused on a single aspect of risk, considering either spatial or temporal variation in risk (but not both), or considering short term or long term variation in risk (but not both). In addition, the focus of research to date has been on single predator-predator or predator-prey pairs, and much has been learned from this approach, but this approach cannot fully describe the limiting effect of predation risk for species that interact with predator guilds that include several species.

Interference competition between predators affects virtually all predator species (Schoener 1974; Pianka 1981; Sinclair 1985; Ziv *et al.* 1993), and is widely recognized as an important force structuring large carnivore guilds (Palomares & Caro 1999; Creel *et al.* 2001; Caro & Stoner 2003). This risk is expressed as predation risk and kleptoparasitism, where predators steal prey killed by other predators. To reduce the effects of interference competition, subordinate species typically respond to dominant competitors through some combination of diet partitioning, spatial segregation or temporal segregation (Crooks, Vuren & Crooks 1995; Hayward & Slotow 2009; Cozzi *et al.* 2013; Périquet *et al.* 2014). In recent years the role of large predators in shaping ecosystems and maintaining biodiversity has become increasingly clear (Baum & Worm 2009; Ritchie & Johnson 2009; Ripple *et al.* 2014), concurrent with global declines in large predator populations (Estes *et al.* 2011). Thus there is considerable need to better understand the ecological consequences of large carnivore declines and extirpations. The ecological effects of terrestrial large predators remain strong in Africa relative to most other parts of the world, and large protected areas in Eastern and Southern Africa have retained ecologically intact large predator guilds including lion (*Panthera leo*), leopard (*Panthera pardus*), spotted hyena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*) populations.

All of these species prey primarily on ungulates, often with substantial dietary overlap, thereby creating the potential for exploitative or interference competition (Creel & Creel 1996; Hayward *et al.* 2006). Within the large carnivore guild, interference competition can be particularly strong because kleptoparasitism is common, probably

because it reduces the energetic costs of hunting by eliminating the costs of locating and killing prey (though stealing carcasses also entails some costs and risks). Furthermore, morphological adaptations to kill large prey also present increased dangers in competitive encounters and increase the cost of interactions (Palomares & Caro 1999; Creel *et al.* 2001). In direct interactions between species, lions and hyenas are dominant competitors, while cheetahs, leopards and African wild dogs are subordinates. The two dominant competitors have both beneficial and detrimental effects on each other (Périquet *et al.* 2014). Each can steal kills from the other, each can kill the other, and the net effect on each other's population dynamics or fitness is often not obvious. Due to asymmetry in body size, the two subordinate carnivores rarely kill lions or hyenas but are known to be killed by both (Caro & Laurenson 1994; Creel & Creel 1998), and lose kills to kleptoparasitism more often than they obtain them (Ginsberg *et al.* 1995; Creel & Creel 1996, 1998). Consequently, the net effect of lions and hyenas on the dynamics of subordinate competitors is usually negative, as revealed by a negative correlation in the densities of subordinate and dominant competitors across ecosystems (Creel & Creel 2002; Swanson *et al.* 2014) and by negatively correlated changes in density through time within ecosystems (Creel & Creel 2002; Swanson *et al.* 2014).

Natural selection favors adaptations, including behavioral responses, which reduce the cost of competitive interactions. Mechanisms of niche partitioning have seen substantial prior study in African large carnivores (Creel & Creel 1996; Durant 2000; Hayward & Slotow 2009; Cozzi *et al.* 2012, 2013; Broekhuis *et al.* 2013; Vanak *et al.* 2013). Carnivores can respond to the risk of costly competitive interactions pro-actively

or reactively. Reactive responses typically take place on small spatial and temporal scales as a result of direct interaction between the species, and are likely to be clear-cut (*e.g.*, wild dogs fleeing after a direct encounter with lions). Pro-active avoidance between animals utilizing the same resources takes place on larger spatial (home-range size or larger) and temporal (seasonal or annual) scales, in response to cues of risk that are usually less obvious to the human observer, and are likely to be subtle (*e.g.*, cheetahs avoiding locations commonly used by lions). When dominant competitors occupy areas of high prey concentration, proactive avoidance of dominant competitors can force subordinate competitors to trade food for safety.

For prey, the risks posed by predators are obvious, and studies with many prey species have shown that exposure to predation risk induces responses by prey that can carry costs affecting growth, reproduction, survival, and population dynamics (Werner *et al.* 1983; Peckarsky *et al.* 1993; Boonstra *et al.* 1998; Pangle *et al.* 2007; Sheriff *et al.* 2009; LaManna *et al.* 2016). Despite this, we have a very limited understanding of the magnitude of these ‘risk effects’ in the wild, at least in part because field studies are rarely designed in a manner that allows risk effects to be disentangled from simple bottom-up limitation by food (Creel & Christianson 2008; Christianson & Creel 2014). Our understanding has also been limited by a lack of studies that (1) measure responses of prey to risk from complete predator guilds, (2) relate the intensity of antipredator responses to the magnitude of direct predation, and (3) employ methods that quantify risk at more than one spatiotemporal scale.

The first point is conceptually obvious: different predators typically create risks at different places and times (Cresswell & Quinn 2010, 2013; Dröge *et al.* 2017). We have learned a great deal by quantifying the responses of prey to a single predator, particularly in cases where one predator is the dominant threat to a given prey species (Creel *et al.* 2007; Valeix *et al.* 2009b), but in many systems this approach is likely to provide an incomplete assessment of the constraints imposed by predation risk (Relyea 2001a). However, studies of responses by prey to the risks presented by complete predator guilds remain uncommon (Thaker *et al.* 2011).

The second point is also conceptually simple, but surprisingly few studies have tested how the strength of antipredator response relates to the magnitude of direct predation (Relyea 2001a), particularly under natural circumstances (Thaker *et al.* 2011; Creel *et al.* 2014; LaManna *et al.* 2016). While it is logical to hypothesize that prey will respond most strongly to the predators that kill them most often (Relyea 2001b; Thaker *et al.* 2011), it is also logical to hypothesize that a low level of direct predation might be the consequence of effective responses by the prey, rather than low ‘risk’ (Lank & Ydenberg 2003; Lind & Cresswell 2005). Clearly, describing this relationship is necessary to understand the relative importance of direct predation and risk effects as determinants of the total limiting effect of predators on prey (Creel & Christianson 2008).

The third point is conceptually more subtle: selection should favor prey that assess and respond to risk at more than one scale. In studies of ungulate prey responding to long term risk from large predators, studies have used GPS radiocollars to describe long-term variation in risk as areas of greater and lesser density of predator re-locations

(Valeix *et al.* 2009b) or kill sites (Moll *et al.* 2016), or as habitat types that vary in use by predators (Thaker *et al.* 2011). Responses to long-term variation in risk have also been assessed by comparison of study sites with variation in predator presence or density (Creel *et al.* 2007) or by comparing sites before and after predator colonization (Cherry *et al.* 2016). Other studies have used direct observations to measure short-term variation in risk as the immediate presence/absence or proximity of predators or kills (Winnie *et al.* 2007; Creel *et al.* 2014), and some have used data from GPS collars to determine responses to short-term risk (Valeix *et al.* 2009b; Basille *et al.* 2015). From such studies, it is clear that prey can respond to both short term variation in risk (the ‘risky times’ hypothesis) and spatial variation in the long term risks associated with a site (the ‘risky places’ hypothesis).

Behavioral studies have focused mainly on risky times (Creel *et al.* 2014), while ecological research has focused mainly on risky places (Hebblewhite, Pletscher & Paquet 2002; Kauffman *et al.* 2007; Creel *et al.* 2008). Common responses to risk include increased vigilance and reduced foraging (Winnie *et al.* 2007; Périquet *et al.* 2012; Broekhuis *et al.* 2013), changes in the speed of movement (Basille *et al.* 2015), movement to safe habitats (Creel *et al.* 2005; Valeix *et al.* 2009b) and increases or decreases in group size (Elgar 1989; Fitzgibbon 1990; Creel & Winnie 2005). Considerable evidence suggests that prey can detect and respond to both short term and long term variation in risk (Brown *et al.* 2014), but research has only begun to consider how responses might differ in response to short term and long term risks.

In chapter two of this thesis, I focus on mechanisms to reduce the intraguild competition between predators through spatial, temporal and dietary niche partitioning. To simultaneously examine all three aspects of niche partitioning one needs to couple location data with direct observation, which is rarely accomplished for a complete large predator guild. The dataset in our study is unique because it couples location data from GPS collars with extensive direct observations of both predators and prey, and thus has good power to analyze long-term spatial relationships, short-term activity patterns and dietary overlap/partitioning of all large carnivore species in a single area. Additionally, inferences are often complicated by the difficulty inherent in determining whether differences in space use are due to competition or simply reflect differences in habitat selection (Cozzi *et al.* 2013, but see Mills & Gorman 1997; Creel & Creel 2002;), but the ecosystem we studied is highly uniform with respect to habitat (see below) and supports a simple ungulate prey community dominated by only three species (M'Soka *et al.* in press), simplifying the interpretation of spatial and temporal overlaps.

The focus in chapter three is on risk posed to the main prey species by the complete predator guild in Liuwa Plain National Park. As described above, prior research has generally focussed on one of two hypotheses, (i) the *risky places* hypothesis, focusing on responses of prey to long-term exposure to risk (LT risk) and which lead to the proposal of the 'landscape of fear', and (ii) the *risky times* hypothesis, focusing on responses of prey to short-term exposure to risk (ST risk). Even though early on in the development of risk studies it was theorized that antipredator behavior depends on both the immediate and background level of predation risk (Lima & Bednekoff 1999), this

interaction has rarely been a focus of studies under natural conditions, simply because of the logistical difficulties involved. However, if responses to LT and ST risk interact (as we report here for ungulate prey in Liuwa), serious challenges arise for the design of research on risk effects. A real effect of ST risk could easily be masked by unmeasured variation in LT risk (or vice versa), and an apparent effect of ST risk might actually be caused by unmeasured variation in LT risk (or vice versa).

Chapter four focuses on adjustments in movement patterns of wildebeest in relation to LT and ST risk from the complete predator guild in LPNP. As discussed in Chapter 2, few studies have simultaneously examined the response of prey behavior to both LT and ST risk. Here, we hypothesized that prey movement patterns, in particular, should respond differently to LT risk and ST risk. For example, in response to cues of elevated LT risk (e.g., cues or memories that predators often use an area), selection might favor slow movements that allow careful assessment of ST risk during foraging movements. In response to elevated ST risk (e.g., direct encounter with a predator), selection might favor fast movements that reduce exposure to risks that are already assessed to be acute (at the extreme, full-speed flight once attacked). We further hypothesize that slow movement, to allow more careful assessment in response to LT risk, is likely to be a general response, but that the optimal response to ST risk is likely to vary in a manner that depends on the behavioral details of predator-prey interaction. For example, stalking predators that rely on short, ambush hunts typically pose little threat if they are detected prior to attack, so increased vigilance may be more effective than altered movement in response to ST risk from a detected stalker. In contrast, coursing

predators that rely on open pursuit remain dangerous once detected, so moving away while still at a relatively safe distance is likely to reduce ST risk from a detected courser. Thus, again, we focus on both ST risk (risky times hypothesis) and LT risk (risk places hypothesis) by focusing if wildebeest movement patterns, in particular, respond differently to LT risk and ST risk.

### Study Area and Populations

For all of the chapters, the data were gathered in a 1200 km<sup>2</sup> study area in the southern part of the 3660 km<sup>2</sup> Liuwa Plain National Park (LPNP) in Zambia. The vegetation in the study area is very homogenous and dominated by short and intermediate grasslands with occasional tree islands. The ungulate community is dominated by migratory wildebeest (*Connochaetes taurinus*) at densities ranging from 6.2 – 60.8 individuals/km<sup>2</sup>, migratory zebra (*Equus quagga*) at densities ranging from 1.8 – 8.1 individuals/km<sup>2</sup>, and non-migratory oribi (*Ourebia ourebi*) at densities ranging from 1.1 – 14.5 individuals/km<sup>2</sup>. These densities were estimated from distance sampling (which allowed correction for each species' probability of detection) on a systematic transect grid, several times in each year of the study (M'Soka *et al.* in press). Hyenas greatly outnumbered other predators within the study area, with 151 hyenas in four clans (M'Soka *et al.* 2016), 6 lions in one pride, 22 wild dogs in two packs and 17 known cheetahs.

Literature Cited

- Basille, M., Fortin, D., Dussault, C., Bastille-Rousseau, G., Ouellet, J.P. & Courtois, R. (2015) Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, **96**, 2622–2631.
- Baum, J.K. & Worm, B. (2009) Cascading predator and effects of changing oceanic predator abundances. *Journal of Animal Ecology*, **78**, 699–714.
- Boonstra, R., Hik, D., Singleton, G.R. & Tinnikov, A. (1998) The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs*, **68**, 371–394.
- Broekhuis, F.C., Cozzi, G., Valeix, M., McNutt, J.W. & Macdonald, D.W. (2013) Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology*, **82**, 1098–1105.
- Brown, G.E., Chivers, D.P., Elvidge, C.K., Jackson, C.D. & Ferrari, M.C.O. (2014) Background level of risk determines the intensity of predator neophobia in juvenile convict cichlids. *Behavioral Ecology and Sociobiology*, **68**, 127–133.
- Caro, T.M. & Laurenson, M.K. (1994) Ecological and genetic factors in conservation: A cautionary tale. *Science*, **263**, 485–486.
- Caro, T.M. & Stoner, C.J. (2003) The potential for interspecific competition among African carnivores. *Biological Conservation*, **110**, 67–75.
- Cherry, M.J., Morgan, K.E., Rutledge, B.T., Conner, L.M. & Warren, R.J. (2016) Can coyote predation risk induce reproduction suppression in white-tailed deer? *Ecosphere*, **7**, e01481.
- Christianson, D.A. & Creel, S. (2008) Risk effects in elk : sex-specific responses in grazing and browsing due to predation risk from wolves. *Behavioral Ecology*, 1258–1266.
- Christianson, D.A. & Creel, S. (2010) A nutritionally mediated risk effect of wolves on elk. *Ecology*, **91**, 1184–1191.
- Christianson, D. & Creel, S. (2014) Ecosystem scale declines in elk recruitment and population growth with wolf colonization: A before-after-control-impact approach. *PLoS ONE*, **9**, e102330.
- Courbin, N., Loveridge, A.J., Macdonald, D.W., Fritz, H., Valeix, M., Makuwe, E.T. & Chamaillé-jammes, S. (2015) Reactive responses of zebras to lion encounters shape their predator-prey space game at large scale. *Oikos*, **125**, 829–838.

- Cozzi, G., Broekhuis, F.C., McNutt, J.W. & Schmid, B. (2013) Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation. *Biodiversity and Conservation*, **22**, 2937–2956.
- Cozzi, G., Broekhuis, F.C., McNutt, J.W., Turnbull, L.A. & David, W. (2012) Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, **93**, 2590–2599.
- Creel, S. (2001) Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology*, **15**, 271–274.
- Creel, S. & Christianson, D. (2008) Relationships between direct predation and risk effects. *Trends in Ecology and Evolution*, **23**, 194–201.
- Creel, S., Christianson, D., Liley, S. & Winnie, J.A. (2007) Predation risk affects reproductive physiology and demography of elk. *Science*, **315**, 960–960.
- Creel, S. & Creel, N.M. (1996) Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, **10**, 526–538.
- Creel, S. & Creel, N.M. (1998) Six ecological factors that may limit African wild dogs, *Lycaon pictus*. *Animal Conservation*, **1**, 1–9.
- Creel, S. & Creel, N.M. (2002) *The African Wild Dog: Behavior, Ecology and Conservation*. Princeton University Press, Princeton.
- Creel, S., Schuette, P. & Christianson, D.A. *Direct Predation Rates and the Foraging Costs of Increased Vigilance in Five African Ungulates*.
- Creel, S., Schuette, P. & Christianson, D. (2014) Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, **25**, 773–784.
- Creel, S., Spong, G. & Creel, N.M. (2001) Interspecific competition & population biology of extinction-prone carnivores. *Carnivore Conservation* (eds J.L. Gittleman, S.M. Funk, D.W. MacDonald & R.K. Wayne), pp. 35–61. Cambridge University Press, Cambridge.
- Creel, S. & Winnie, J.A. (2005) Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour*, **69**, 1181–1189.
- Creel, S., Winnie, J.A., Christianson, D. & Liley, S. (2008) Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour*, **76**, 1139–1146.

- Creel, S., Winnie Jr, J.A., Maxwell, B., Hamlin, K., Creel, M., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M. (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**, 3387–3397.
- Cresswell, W. & Quinn, J.L. (2010) Attack frequency, attack success and choice of prey group size for two predators with contrasting hunting strategies. *Animal Behaviour*, **80**, 643–648.
- Cresswell, W. & Quinn, J.L. (2013) Contrasting risks from different predators change the overall nonlethal effects of predation risk. *Behavioral Ecology*, **24**, 871–876.
- Crooks, K.R., Vuren, D. Van & Crooks, K.R. (1995) Resource utilization by two insular endemic mammalian carnivores, the island fox and island spotted skunk. *Oecologia*, **104**, 301–307.
- Dröge, E.D., Creel, S., Becker, M.S. & M’Soka, J.L.J. (2017) Spatial and temporal avoidance of risk within a large carnivore guild. *Ecology and Evolution*, **7**, 189–199.
- Durant, S.M. (2000) Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, **11**, 624–632.
- Elgar, M.A. (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biology Reviews*, **64**, 13–33.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pkitch, E.K., Ripple, W.J., Sandin, S. a, Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. & Wardle, D.A. (2011) Trophic downgrading of planet earth. *Science*, **333**, 301–306.
- Fitzgibbon, C.D. (1990) Mixed-species grouping in Thomson’s and Grant’s gazelles : the antipredator benefits. *Animal Behaviour*, **39**, 1116–1126.
- Ginsberg, J.R., Alexander, K.A., Creel, S., Kat, P.W., McNutt, J.W. & Mills, M.G.L. (1995) Handling and survivorship of African wild dog (*Lycaon pictus*) in five ecosystems. *Conservation Biology*, **9**, 665–674.
- Hayward, M.W., O’Brien, J., Hofmeyr, M. & Kerley, G.I.H. (2006) Prey preferences of the African wild dog *Lycaon pictus* (Canidae: Carnivora): Ecological requirements for conservation. *Journal of Mammalogy*, **87**, 1122–1131.
- Hayward, M.W. & Slotow, R. (2009) Temporal partitioning of activity in large African carnivores: Tests of multiple hypotheses. *South African Journal of Wildlife Research*, **39**, 109–125.

- Hebblewhite, M., Pletscher, D.H. & Paquet, P.C. (2002) Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology*, **80**, 789–799.
- Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R. & Boyce, M.S. (2007) Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters*, **10**, 690–700.
- LaManna, J.A., Martin, T.E. & Letters, E. (2016) Costs of fear: Behavioural and life-history responses to risk and their demographic consequences vary across species. *Ecology Letters*, **19**, 403–413.
- Lank, D.B. & Ydenberg, R.C. (2003) Death and danger at migratory stopovers: Problems with “predation risk.” *Journal of avian biology*, **34**, 225–228.
- Lima, S.L. & Bednekoff, P.A. (1999) Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *The American Naturalist*, **153**, 649–659.
- Lind, J. & Cresswell, W. (2005) Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, **16**, 945–956.
- M’Soka, J.L.J., Creel, S., Becker, M.S., Droge, E.D., Jassiel, M., Creel, S., Becker, M.S. & Droge, E.D. (2016) Spotted hyaena survival and density in a lion depleted ecosystem: the effects of prey availability, humans and competition between large carnivores in African savannahs. *Biological Conservation*, **201**, 348–355.
- M’Soka, J.L.J., Creel, S., Becker, M.S. & Murdoch, J.D. Ecological and anthropogenic effects on the density of migratory and resident ungulates in a human-inhabited protected area (in press). *African Journal of Ecology*, 1–14.
- Mills, M.G.L. & Gorman, M.L. (1997) Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology*, **11**, 1397–1406.
- Moll, R.J., Killion, A.K., Montgomery, R.A., Tambling, C.J. & Hayward, M.W. (2016) Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores. *Ecology*, **97**, 1123–1134.
- Palomares, F. & Caro, T.M. (1999) Interspecific killing among mammalian carnivores. *The American Naturalist*, **153**, 492–508.
- Pangle, K.L., Peacor, S.D., Johannsson, O.E. & Johannsson, O.E. (2007) Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology*, **88**, 402–412.

- Peckarsky, B.L., Cowan, C.A., Penton, M.A., Cowan, C.A., Penton, M.A. & Anderson, C. (1993) Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology*, **74**, 1836–1846.
- Périquet, S., Fritz, H. & Revilla, E. (2014) The lion king and the hyaena queen: large carnivore interactions and coexistence. *Biological Reviews*, **90**, 1197–1214.
- Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., Madzikanda, H., Fritz, H., Macdonald, D.W., Loveridge, A.J. & Lyon, C.B. (2012) Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology*.
- Périquet, S., Valeix, M., Claypole, J., Drouet-Hoguet, N., Salnicki, J., Mudimba, S., Revilla, E. & Fritz, H. (2015) Spotted hyaenas switch their foraging strategy as a response to changes in intraguild interactions with lions. *Journal of Zoology*, **297**, 245-254.
- Pianka, E.R. (1981) Competition and niche theory (ed RM May). *Theoretical Ecology*, **8**, 167–196.
- Relyea, R.A. (2001a) Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology*, **82**, 523–540.
- Relyea, R.A. (2001b) The Relationship between predation risk and antipredator responses in larval anurans. *Ecology*, **82**, 541–554.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343**, 1241484.
- Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**, 982–998.
- Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, **185**, 27–39.
- Schuette, P., Creel, S., Christianson, D. & Hayward, M.W. (2016) Ungulate distributions in a rangeland with competitors, predators and pastoralists. *Journal of Applied Ecology*, **53**, 1066–1077.
- Sheriff, M.J., Krebs, C.J. & Boonstra, R. (2009) The sensitive hare: Sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology*, **78**, 1249–1258.

- Sinclair, A.R.E. (1985) Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology*, **54**, 899–918.
- Swanson, A., Caro, T.M., Davies-Mostert, H., Mills, M.G.L., Macdonald, D.W., Borner, M., Masenga, E., Packer, C., David, W., Borner, M., Masenga, E., Packer, C., Paul, S., Africa, S., Conservation, W. & Centre, R. (2014) Cheetahs and wild dogs show contrasting patterns of suppression by lions. *The Journal of Animal Ecology*, **83**, 1418–1427.
- Thaker, M., Vanak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M. & Slotow, R. (2011) Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, **92**, 398–407.
- Valeix, M., Fritz, H., Loveridge, A.J., Davidson, Z., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. (2009a) Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology*, **63**, 1483–1494.
- Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. (2009b) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, **90**, 23–30.
- Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C. & Greatwood, S. (2013) Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology*, **94**, 2619–2631.
- Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.
- Winnie, J., Creel, S., Winnie Jr, J.A. & Creel, S. (2007) Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Animal Behaviour*, **73**, 215–225.
- Ziv, Y., Abramsky, Z., Kotler, B.P. & Subach, A. (1993) Interference competition and temporal habitat partitioning in two gerbil species. *Oikos*, **66**, 237–246.

CHAPTER TWO

SPATIAL AND TEMPORAL AVOIDANCE OF RISK WITHIN A LARGE  
CARNIVORE GUILD – PREDATOR AVOIDANCE BY PREDATORS

Contribution of Authors and Co-Authors

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Abstract

Within a large carnivore guild, subordinate competitors (African wild dog, *Lycaon pictus*, and cheetah, *Acinonyx jubatus*) might reduce the limiting effects of dominant competitors (lion, *Panthera leo*, and spotted hyena, *Crocuta crocuta*) by avoiding them in space, in time, or through patterns of prey selection. Understanding how these competitors cope with one other can inform strategies for their conservation. We tested how mechanisms of niche partitioning promote coexistence by quantifying patterns of prey selection and the use of space and time by all members of the large carnivore guild within Liuwa Plain National Park in western Zambia. Lions and hyenas specialized on wildebeest, whereas wild dogs and cheetahs selected broader diets including smaller and less abundant prey. Spatially, cheetahs showed no detectable avoidance of areas heavily used by dominant competitors, but wild dogs avoided areas heavily used by lions. Temporally, the proportion of kills by lions and hyenas did not detectably differ across four time periods (day, crepuscular, early night, and late night), but wild dogs and especially cheetahs concentrated on time windows that avoided nighttime hunting by lions and hyenas. Our results provide new insight into the conditions under which partitioning may not allow for coexistence for one subordinate species, the African wild dog, while it does for cheetah. Because of differences in responses to dominant competitors, African wild dogs may be more prone to competitive exclusion (local extirpation), particularly in open, uniform ecosystems with simple (often wildebeest dominated) prey communities, where spatial avoidance is difficult.

Keywords: carnivore, conservation, interspecific competition, intraguild predation, niche partitioning, risk effect

### Introduction

Interference competition affects virtually all species (Schoener 1974; Pianka 1981; Sinclair 1985; Ziv *et al.* 1993), and is widely recognized as an important force structuring large carnivore guilds (Palomares & Caro 1999; Creel, Spong & Creel 2001; Caro & Stoner 2003). The limiting effect of competition between large carnivores can be strong (Estes & Goddard 1967; Mills & Biggs 1993; Creel & Creel 1996; Mills & Gorman 1997), and to reduce these effects, subordinate species typically respond to dominant competitors through some combination of diet partitioning, spatial segregation or temporal segregation (Crooks, Vuren & Crooks 1995; Hayward & Slotow 2009; Cozzi *et al.* 2013; Périquet, Fritz & Revilla 2014). In recent years, the role of large carnivores in shaping ecosystems and maintaining biodiversity has become increasingly clear (Baum & Worm 2009; Ritchie & Johnson 2009; Ripple *et al.* 2014), along with global declines in large carnivore populations (Estes *et al.* 2011). The ecological effects of terrestrial large carnivores remain strong in Africa relative to most other parts of the world, and large protected areas in Eastern and Southern Africa have retained ecologically intact large carnivore guilds including lion (*Panthera leo*), leopard (*Panthera pardus*), spotted hyena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*) populations.

All of these species prey primarily on ungulates, often with substantial dietary overlap, thereby creating the potential for exploitative or interference competition within the large carnivore guild (Creel & Creel 1996; Hayward *et al.* 2006). Interference competition can be particularly strong because kleptoparasitism among these species is common, probably because it reduces the energetic costs of hunting by eliminating the costs of hunting and killing prey (although stealing carcasses also entails some costs and risks).

Furthermore, the morphological adaptations used to kill large prey also present dangers in competitive encounters and increase the cost of direct interactions (Palomares & Caro 1999; Creel *et al.* 2001). During direct interactions between species, lions and hyenas are dominant competitors, while cheetahs, leopards, and African wild dogs are subordinates. The two dominant competitors have both beneficial and detrimental effects on each other (Périquet *et al.* 2014). Each can steal kills from the other, each can kill the other, and the net effect on each other's population dynamics or fitness is often not obvious. Due to asymmetry in body size, cheetahs and wild dogs rarely kill lions or hyenas but are known to be killed by both (Caro & Laurenson 1994; Creel & Creel 1998), and lose kills to kleptoparasitism more often than they obtain them (Ginsberg *et al.* 1995; Creel & Creel 1996, 1998). Consequently, the net effect of lions and hyenas on the dynamics of subordinate competitors is usually negative, as revealed by a negative correlation in the densities of subordinate and dominant competitors across ecosystems (Creel & Creel 2002; Swanson *et al.* 2014) and by negatively correlated changes in density through time within ecosystems (Creel & Creel 2002; Swanson *et al.* 2014).

Natural selection favors adaptations (including behavioral responses) that reduce the cost of competitive interactions. Mechanisms of niche partitioning have seen substantial prior study in African large carnivores (Creel & Creel 1996; Durant 2000a; Hayward & Slotow 2009; Cozzi *et al.* 2012; Broekhuis *et al.* 2013; Vanak *et al.* 2013). As with antipredator responses of prey, carnivores can respond to the risk of costly competitive interactions proactively or reactively. Reactive responses typically take place on small spatial and temporal scales as a result of direct interaction between the species, and are likely to be clear-cut (e.g., wild dogs fleeing after a direct encounter with lions). Proactive avoidance between animals utilizing the same resources takes place on larger spatial (significant part of home range size or larger) and temporal (seasonal or annual) scales, in response to cues of risk that are subtle and usually less obvious to the human observer (e.g., cheetahs avoiding locations commonly used by lions). When dominant competitors occupy areas of high prey concentration, proactive avoidance of dominant competitors can force subordinate competitors to trade food for safety. Several studies have found that African wild dogs are negatively affected by hyena kleptoparasitism (Estes & Goddard 1967; Kruuk 1972; Creel & Creel 1996; Gorman *et al.* 1998; Speakman *et al.* 2015), and studies in an overlapping set of ecosystems show that lions can limit African wild dogs in numbers and distribution, through a combination of direct predation and competitive exclusion from areas of high prey density (Ginsberg *et al.* 1995; Creel & Creel 1996; Mbizah, Marino & Groom 2012; Vanak *et al.* 2013). Mills & Gorman (1997) found that African wild dogs in Kruger National Park avoided lions and thus did not favor habitats with high impala density, even though impala comprised 71%

of their prey. Similarly, wild dogs in the Selous Game Reserve avoided areas heavily used by lions, and consequently hunted disproportionately often in habitats where they had significantly reduced rates of encounter with prey (Creel *et al.* 2001).

In contrast to these results for wild dogs, Vanak *et al.* (2013) found substantial spatial overlap in the ranges of lions and cheetahs (while confirming low overlap between lions and wild dogs). Broekhuis *et al.* (2013) examined the effects of both lions and hyenas on cheetahs. Similar to the results of Vanak *et al.* (2013), space use by cheetahs was highly similar to that of lions and hyenas over long timescales, but within these areas of shared use, cheetahs avoided risk on short timescales by positioning themselves further from the nearest lions and hyenas than expected by chance Broekhuis *et al.* (2013). Durant (1998, 2000) also found that cheetahs avoided both lions and hyenas and concluded that ability to hunt within local “competition refuges” was critical for their persistence within an ecosystem.

In addition to (or alternative to) spatial avoidance, subordinate competitors can avoid dominant competitors temporally, by hunting when dominant competitors are less active. Darnell *et al.* (2014) found that in Hluhluwe–iMfolozi Park, African wild dogs showed both spatial and temporal avoidance of lions, particularly during denning periods, but did not show any avoidance of hyenas. Durant (1998) found that cheetahs avoided lions and hyenas in both space and time. In contrast, Cozzi *et al.* (2012) found a high degree of overlap in activity signals from GPS collars on African wild dogs, cheetahs, lions, and hyenas, concluding that overlaps in activity patterns were driven by food limitation that constrained avoidance in that ecosystem. Despite this result, data from

most ecosystems show that the majority of hunts by wild dogs and (especially) cheetahs are typically diurnal or crepuscular (Estes & Goddard 1967; Mills & Biggs 1993; Creel & Creel 2002), which reduces the likelihood of direct interference competition with more nocturnal lions and (especially) hyenas (Mills & Biggs 1993; Kolowski *et al.* 2007; Cozzi *et al.* 2012). While some authors suggest that crepuscular activity of primarily nocturnal carnivores could perhaps increase their hunting success (Hayward & Slotow 2009), temporal partitioning of activity has generally been interpreted as a mechanism by which subordinate carnivores can reduce the frequency of both food loss and the risk of injury or death by direct interactions with lions and hyenas at contested kill sites.

As mentioned above, the relationship between the two dominant competitors, lions and hyenas, is a complex mixture of facilitation and competition (Périquet *et al.* 2014). In a comprehensive review of hyena–lion interactions, Périquet *et al.* (2014) found strong evidence for costs to both species through exploitation and interference competition through diet overlap, intraguild predation, and kleptoparasitism, but also identified benefits to both species from scavenging opportunities, and mechanisms that reduce costs such as differences in prey selection (Pereira, Owen-Smith & Moleón 2014; Périquet *et al.* 2014). In contrast, Trinkel & Kastberger (2005) found no benefits of lions for hyenas.

Prior studies of competition within the large carnivore guild have often focused on a single pair of species (but see Mills & Biggs 1993; Creel & Creel 2002; Cozzi *et al.* 2012; Broekhuis *et al.* 2013; Vanak *et al.* 2013). Camera trapping studies have been used to study niche partitioning within broader guilds, mainly to analyze broad patterns of

spatial overlap (Ngoprasert *et al.* 2012; Steinmetz, Seuaturien & Chutipong 2013). However, the frequency of detection on camera traps for most large carnivores is generally too low to meaningfully analyze patterns of spatial or temporal avoidance (Ngoprasert *et al.* 2012). For example, in an intensive camera trapping study to estimate leopard population density and survival, individuals known to be present often went undetected for a month or more (Rosenblatt *et al.* 2016), implying low power to detect patterns of interaction or spatial avoidance on the relevant timescale, and somewhat limited power to detect temporal avoidance. Spatial data from GPS collars can provide strong inferences about proactive spatial avoidance, but typically do not provide samples adequate for inferences about reactive avoidance (Creel, Winnie & Christianson 2013). Neither camera trapping nor GPS collars provide information on dietary overlap or partitioning. To simultaneously examine these three aspects of niche partitioning, one needs to couple location data with direct observation, which has rarely been accomplished for a complete large carnivore guild. The dataset in this study is unique because it couples extensive location data with extensive direct observations, and thus has good power to analyze long-term spatial relationships, short-term activity patterns, and dietary overlap/partitioning of all large carnivore species present within an ecosystem. Finally, inferences about spatial avoidance are often complicated by the difficulty inherent in determining whether differences in space use are due to competition or simply reflect differences in habitat selection that would occur without competitive constraints (Cozzi *et al.* 2013; but see Mills & Gorman 1997; Creel & Creel 2002): Because the ecosystem we studied is highly uniform with respect to

habitat (Figure 2.2) and supports a simple ungulate guild dominated by only three species (M'Soka 2015), the interpretation of spatial and temporal overlaps is simplified considerably.

We examined the use of space and time by the large carnivore guild of Liuwa Plain National Park (LPNP) in western Zambia, consisting of hyenas, lions, cheetahs, and African wild dogs. Leopards are absent from LPNP. Historically, they occupied woodland areas along rivers, but have not been recorded in LPNP for the last 50 years. Based on prior studies, we hypothesized that African wild dogs and cheetahs would avoid lions and hyenas in both space and time to reduce kleptoparasitism and direct predation. We hypothesized a negative relationship between space use of subordinate competitors (African wild dogs and cheetahs) and dominant competitors (lions and spotted hyenas). We hypothesized that subordinate competitors would make a majority of their kills during time periods in which dominant competitors were least active. We hypothesized that hyenas and lions would not show such patterns with regard to each other. Finally, we hypothesized that hyenas and lions would show strong dietary overlap by specializing on the most abundant prey and that cheetahs and wild dogs would reduce dietary overlap by preying on a wider range of species.

## Methods

### Study Area and Populations

All of our data were gathered from a 1,200-km<sup>2</sup> study area within Zambia's 3,660-km<sup>2</sup> LPNP (Figure 2.1).

This area holds Africa's second largest wildebeest migration, within LPNP and areas immediately northwest. Our study area is in the southern portion of LPNP, dominated by short and intermediate grasslands with occasional tree islands (Figure 2.2), and supports an ungulate community dominated by migratory wildebeest (*Connochaetes taurinus*) at densities ranging from 6.2 to 60.8 individuals/km<sup>2</sup>, migratory zebra (*Equus quagga*) at densities ranging from 1.8 to 8.1 individuals/km<sup>2</sup>, and nonmigratory oribi (*Ourebia ourebi*) at densities ranging from 1.1 to 14.5 individuals/km<sup>2</sup>. These densities were estimated from distance sampling on a systematic transect grid two to three times in each year of the study, with a total transect length of 1,280 km (M'Soka *et al.* in press). and structure within our study area simplified interpretation of differences between species in their use of space.

Other species that were occasionally killed occurred at much lower densities, including common duiker (*Sylvicapra grimmia*), red lechwe (*Kobus leche*), steenbok (*Raphicerus campestris*), common reedbuck (*Redunca arundinum*), and scrub hare (*Lepus saxatilis*). Hyenas greatly outnumbered other carnivores within the study area, with populations of 151 hyenas in four clans (M'Soka *et al.* 2016), six lions in one pride, 22 wild dogs in two packs, and 17 known cheetahs.

### Location Data

Locations of African wild dogs, hyenas, and lions were collected between 24 June 2010 and 23 December 2015 using GPS and VHF radio collars fit to individuals in all but one group known to reside wholly or largely within the study site (details below). From 07 January 2012 to 13 April 2013, the alpha female of a resident African wild dog pack

was fitted with a GPS collar taking a location every 5 hr. A second resident pack was fitted with VHF collars and was monitored from 25 June 2010 to 30 May 2014 after which the last members of the pack left the study area permanently following the death of the alpha male and subsequent dissolution of the breeding pack. From 24 October 2010 to 13 May 2012, five hyenas (in three of the four resident clans) were fitted with GPS collars (recording a location every 2 or 3 hr). During the course of the study, one of these clans split into two, but frequent resightings of known individuals confirmed that the two newly formed clans remained largely within the source clan's area. The remaining clan was monitored with VHF collars on five clan members, which provided a total of 318 locations (two hyenas in this clan were fitted with GPS collars, but the GPS function failed in both). The lion population in LPNP was actively restored after only one lioness remained in 2009. Several females and males were reintroduced and a maximum of six lions were present in the study area during the study period, consisting of one coalition of two males, and one pride of females and cubs. Between 24 June 2010 and 28 May 2015, at least one male and one female were fitted with a GPS satellite collar or GPS remote download collar (recording a location every 3 or 4 hr). The lions formed cohesive groups (males were never recorded without each other), and the home ranges of males and females largely overlapped (see section 3). All cheetah locations came from observations from four cheetahs fitted with VHF collars between 02 August 2012 and 23 December 2015. These included single locations from opportunistic observations, and multiple locations from hunt follows in which cheetahs were observed continuously through complete periods of activity. When moving, a GPS location was recorded at 15-minute

intervals, and while stationary only one location was recorded, with the start time and end time at that location. Cheetahs were followed in 50 periods between 12 November 2012 and 23 December 2015 for up to 7 days. Although the methods for cheetahs provided fewer locations than GPS collars on the other species, this sampling was representative for cheetahs within the study site, as all known groups included a collar. Locations for all four species were used to fit utilization distributions (UDs) that were resampled in an identical manner for each species to compare space use (as described below). All immobilization procedures to fit animals with collars were conducted with permission, following animal welfare standards and protocols required by the Zambia Department of Veterinary and Livestock Services and the Department of National Parks and Wildlife. The location data for the four species come from overlapping periods from 2010 to 2015, but the interval sampled was not identical for all species. However, data from GPS collars show that the ranging patterns of lions and hyenas changed very little year to year. Thus, the species for which we have the most locations are the dominant competitors, both with temporally stable spatial distributions, providing a good basis for tests of avoidance by the subordinate competitors during the period that they were sampled.

### Utilization Distributions

Location data were used to calculate UD for each species using the `adehabitatHR` package (Calenge 2006) in R (R Core Team, 2016, version 3.1). The UD reflects the relative intensity of use for a location, represented by a grid cell, within the home range of a species or group of animals. We used a grid cell size of 1,000 m. This spatial scale was fine enough to resolve variation in space use, and we had enough

locations for every species to examine utilization at this scale. Standard methods for bandwidth selection (e.g., least-squares cross-validation) did not converge, probably due to very large home range sizes for some, and the standard reference bandwidth (href) yielded rather discontinuous UD. In such cases, several authors (Silverman 1986; Wand & Jones 1994) recommend using a subjective visually chosen bandwidth as smoothing parameter. We used a more objective approach by calculating the daily distance moved for each individual animal by summing the distances between consecutive locations within a day, for individuals fitted with GPS collars or observed during hunt follows. We then examined the frequency distribution of daily distances for each species and selected the 90th percentile (95th for cheetahs, with sparser data) as the bandwidth. This procedure yielded largely continuous UD, occasionally keeping some clustered locations separate in a plausible manner. Because the home ranges of the two wild dog packs and the four hyena clans had little overlap, UD were calculated separately for each group, and then combined and rescaled to result in a total utilization of 1 for the combined UD. This process properly resolved areas of low use between home ranges. For cheetahs and lions, individual ranges overlapped very substantially, so we calculated a single UD for each species.

To test for correlations in the use of space for each pair of species, we sampled the calculated UD for each species using a grid of points separated by 1,000 m in both dimensions. The starting point of the grid was generated randomly in a 25-km<sup>2</sup> area outside of the study area (oriented N–S). We selected 1,000-m grid spacing to balance an unavoidable trade-off between spatial autocorrelation and sample size. To ensure

coverage of the study area, we preferred sampling the UDs with a grid, rather than random location, and tested whether our inferences were affected by the choice of grid cell size (they were not). We recorded locations outside of our 1,200-km<sup>2</sup> study site for all species, but our analysis is based only on locations within the focal study area. This restricted the analysis to an area within which we had good data on utilization by all four species, avoiding problems of interpretation that arise with a patchy distribution of sampling effort (i.e., where low utilization can be an artifact of sampling). The UD values within the study area for each species were scaled from 0 to 1 for ease of interpretation as “relative use”. However, it should be recognized that absolute intensity of utilization, and thus the potential strength of interference competition, also depends on the population density of each species, and as noted above, hyenas greatly outnumbered the other carnivores.

In addition to restricting our analysis to the well-sampled focal study area, we restricted our analysis to areas known to be used within the focal area. Thus, we extracted UD values for each carnivore species at each grid location and tested the correlations between species with data restricted to locations with nonzero values for both species. In this way, we tested for spatial avoidance in areas of shared use for all possible pairs except for wild dog and cheetah, which have not been observed to interact strongly in any ecosystem.

Following Zuur, Ieno & Elphick (2009), we used quasibinomial generalized linear models fit with the `glm` function in R to test the relationship for each species pair, in a manner that accounted for extrabinomial variation. We assessed the fit of all models

using Q–Q and scale–location plots, which confirmed good fits. Heteroscedasticity was apparent in most cases, but the effect of heteroscedasticity is to reduce power. Because we did detect effects where they were expected (see section 3), heteroscedasticity was “not a reason to throw out an otherwise good model” (Mankiw 1990). Maps of the UDs were created in QGIS 2.10.1-Pisa (QGIS Development Team 2015). Our a priori hypotheses and thus our initial tests were for linear relationships, but we tested whether other plausible functional forms provided a better fit. For the relationships of African wild dogs, hyenas, and cheetahs to lions, drop-in-deviance tests supported second-order polynomial and exponential relationships (see section 3).

#### Activity Data

To analyze whether carnivores avoided each other temporally, we recorded the time at which kills were made by each species. For this analysis, we considered only kills that were directly observed and probable kills (judged to be less than one hour old, with only a single carnivore present and no evidence of attendance by other carnivores from spoor). We never detected lions losing kills. If a kill made within the hour by cheetahs or African wild dogs was lost to lions or hyenas, we were likely to detect them nearby, because all African wild dog packs and cheetah groups were collared. We never detected hyenas losing kills to cheetahs or African wild dogs. They did lose kills to lions, as detected by direct observation, presence at kills, and spoor. To obtain representative data for all species, hunt follows were conducted by direct observation over complete hunting periods. A hunt follow consisted of a complete follow of an animal from the time it started hunting to the time it stopped hunting. Often these follows were performed for

several consecutive hunt periods for the same species. While not all species were followed for an equal number of hours, this affects only the precision of estimates of the proportion of kills made per time period (but does not produce bias): The precision obtained was adequate for all species (see section 3). There were a total of 453 carcasses with a well-described time of death, between 03 December 2010 and 07 December 2015. Within our sample, 77.5% of kills were directly observed, with the remaining 22.5% judged to be less than one hour old, and carcasses judged to be older than one hour not included. Times of kills were grouped into four periods of the day, the crepuscular period (5–7 a.m. and 5–7 p.m.), daytime (8 a.m.–4 p.m.), early night (8 p.m.–12 p.m.), and late night (1 a.m.–4 a.m.). The percentage of kills made by each carnivore in each period was calculated and the exact binomial confidence intervals calculated to compare activity patterns across species.

### Prey Selection

Patterns of prey selection and the processes that yield them will be analyzed in detail elsewhere, but briefly, we examined dietary overlap using the set of kills just described, plus 101 kills (a total of 554) that could be ascribed to a carnivore but could not be assigned a time of death with sufficient precision for the analysis of temporal activity patterns. The densities of prey species have been estimated (M'Soka *et al.* in press), but these data are not directly relevant to a comparison of prey selection by each carnivore species from a single prey community available to them all. Restated, use of each prey species could be converted to use/availability, but the same denominator would be applied to all carnivores, so differences among carnivores would not be affected.

## Results

### Prey Selection

Predation by all four carnivores concentrated on the most common ungulate species, particularly wildebeest (Figure 2.3). Wildebeest were the most important prey for three of the four carnivores, comprising 92% of hyena kills (95% CI: 85%–96%), 90% of lion kills (95% CI: 85%–96%), 59% of wild dog kills (95% CI: 52%–65%), and 30% of cheetah kills (95% CI: 20%–42%). Lions and hyenas preyed almost exclusively on wildebeest, while cheetahs and wild dogs had broader diets that commonly included oribi, which were very rarely killed by lions or hyenas. Together, wildebeest and oribi comprised 77% of wild dog kills and 74% of cheetah kills.

Thus within LPNP, there is substantial overlap between the diets of all large carnivores, and the potential for interference competition is high, particularly when hunting wildebeest, which are by far the most abundant prey species within the study site.

### Spatial Niche Partitioning

Figure 2.4 shows overlaps between UDs for each pair of species that we examined, within the 1,200-km<sup>2</sup> study area. All species concentrated their activities in grasslands in the western portion of the study area (see Figure 2.2), and rarely used wooded areas to the east.

African wild dog utilization densities were best described by a quadratic response to increasing lion utilization densities (Figure 2.5a), rather than a linear relationship (drop-in-deviance = 8.01,  $df = 1$ ,  $p < .0001$ ). The linear component of this relationship

was positive ( $b = 6.45$ , 95% CI: 5.07–7.85,  $t(484) = 9.125$ ,  $p < .0001$ ), but there was an equally strong negative quadratic effect ( $b = -8.14$ , 95% CI: -6.76 to -3.42,  $t(484) = -5.979$ ,  $p < .0001$ ), indicating some degree of avoidance of the areas most heavily used by lions. African wild dog utilization densities increased linearly with increasing hyena utilization densities (Figure 2.5d,  $b = 2.81$ , 95% CI: 2.61–3.01,  $t(780) = 27.38$ ,  $p < .0001$ ), providing no evidence of spatial avoidance.

Cheetah utilization densities increased linearly with increasing hyena utilization densities (Figure 2.5e,  $b = 2.67$ , 95% CI: 2.36–2.98,  $t(347) = 17.07$ ,  $p < .0001$ ), and exponentially with increasing lion utilization density (Figure 2.5b,  $b = 2.61$ , 95% CI: 2.45–2.77,  $t(282) = 13.575$ ,  $p < .0001$ ), providing no evidence of spatial avoidance of either species.

Hyena utilization densities were quadratically related to lion utilization densities (Figure 2.5c). The linear component of this relationship was positive, as seen above for the effect of lions on African wild dogs ( $b = 6.55$ , 95% CI: 5.05–8.07,  $t(381) = 8.513$ ,  $p < .0001$ ), with a weaker negative quadratic effect ( $b = -3.90$ , 95% CI: -5.71 to -2.05,  $t(381) = -4.195$ ,  $p < .0001$ ) when compared to the responses of wild dogs to lions.

### Temporal Niche Partitioning

Cheetahs made most of their kills during daylight hours (figure 2.6, 0.70, 95% CI 0.61–0.78), and they had by far the highest proportion of daytime kills of all species. Cheetahs also made a considerable proportion of their kills in the crepuscular periods (0.29, 95% CI 0.21–0.37) with very few kills early in the night (0.01, 95% CI 0.0002–0.04) or late at night (0.01, 95% CI 0.0002–0.040). The largest proportion of kills (0.42,

95% CI 0.34–0.51) by African wild dogs was during the crepuscular periods, and wild dogs made a larger proportion of kills in this period than any of the other species. African wild dogs also made a considerable proportion of their kills during the day (0.30, 95% CI 0.22–0.38) and the early night (0.18, 95% CI 0.12–0.25) but made few kills late at night (0.10, 95% CI 0.059–0.16). The proportion of kills for lions and hyenas were spread more evenly over the time periods. Lions kills were most common in the crepuscular periods (0.36, 95% CI 0.20–0.55) and both night periods (early night 0.24, 95% CI 0.11–0.42, late night 0.24, 95% CI 0.11–0.42), with fewer kills in the daytime (0.15 95% CI 0.05–0.32). Hyenas had their highest proportions of kills during the late-night period (0.35, 95% CI 0.27–0.43), and the proportion of kills during the crepuscular, early night, and daytime periods were 0.26 (95% CI 0.19–0.34), 0.23 (95% CI 0.16–0.30), and 0.16 (95% CI 0.11–0.23), respectively.

To summarize, the proportion of kills made by lions and hyenas did not detectably differ across time periods, with appreciable killing rates throughout the entire 24 hr, but with half or more of their kills made in full darkness. Wild dogs and particularly cheetahs each concentrated their hunting into windows that avoided the nighttime hunting window, when both lions and hyenas were still highly active. Cheetahs also had a very low proportion of kills during the early night, when wild dogs, lions, and hyena all showed substantial activity. Thus, the temporal niches of the dominant competitors were broad, while the niches of both the subordinate competitors (particularly cheetahs) reduced nocturnal overlap.

## Discussion

Niche partitioning is expected to reduce the effects of interspecific competition (particularly for subordinate competitors), and can potentially be accomplished through spatial avoidance, temporal avoidance, or prey selection. We found evidence for all of these mechanisms, with differences among species pairs that yield insights about coexistence and competitive exclusion.

All of the species in LPNP's large carnivore guild show substantial overlap in prey selection with other guild members. Such dietary niche overlap creates the potential for interspecific competition, which for these species can manifest as aggressive interference competition sufficient to cause serious injury or death. As predicted by niche theory, subordinate competitors persist within LPNP in part by widening their dietary niche to avoid the narrower niches of the dominant competitors (Hayward & Kerley 2008), which specialize almost exclusively on the most abundant resource, wildebeest. Alternatively, (or additionally), small prey species such as oribi may provide a higher benefit/cost ratio for the smaller wild dog and cheetah than they do for larger hyenas and lions. Even this mechanism might be related to interspecific competition, because smaller prey species are more likely to be consumed before dominant competitors can detect and aggregate at a kill. The patterns of dietary niche overlap within the carnivore guild of LPNP conform to patterns described across ecosystems, with subordinates showing a "decreasing preference for [common] prey species and increase in number of prey species killed" to reduce niche overlap with dominants (Hayward & Kerley 2008).

The Liuwa ecosystem has several important ecological properties that affect interactions among large carnivores. First, the vegetation structure is highly uniform within the area we studied, and is typified by open grasslands with good visibility over long distances (Figure 2.2). Under these conditions, large carnivores can detect one another relatively easily and spatial avoidance is not easily accomplished, particularly when dominant competitors seek out opportunities to steal kills. Second, the ungulate prey community has a simple structure that is highly dominated by wildebeest, with much lower numbers of zebra, oribi, and other species. All of the large carnivore species prey heavily on wildebeest, although oribi are also critical prey for wild dogs and especially cheetahs. We suggest that open environments with a simple prey set constrain the options for subordinate species like wild dogs and cheetahs, promoting competitive exclusion. Aligning with this inference, wild dogs have been competitively excluded from ecologically similar areas in Serengeti National Park and the Ngorongoro Crater (Estes & Goddard 1967; Malcolm & Marten 1982; Creel & Creel 1996), and have not been resident within the LPNP study site for more than a year. Our data also suggest that cheetahs may coexist with dominant competitors under these conditions because of more complete temporal niche partitioning to heavily exploit the daylight hours (Swanson *et al.* 2014).

#### Relationships of African Wild Dogs to Dominant Competitors

Like hyenas and lions, wild dogs relied most heavily on wildebeest in LPNP, but the dominant competitors specialized almost completely on wildebeest, while the dietary niche of wild dogs was much broader, particularly due to predation on oribi. This pattern

might be explained by differences in the cost/benefit ratio of hunting smaller prey (Creel & Creel 2002), but it also aligns with a basic prediction of competition theory, that a subordinate competitor can persist by adopting a generalist strategy that reduces niche overlap with dominant competitors that specialize on the most profitable niche space. Contrary to expectation, space use by African wild dogs was positively related to utilization by lions and hyenas, a result that contrasts sharply with prior comparisons both across ecosystems (Creel & Creel 1996; Swanson *et al.* 2014) and within ecosystems (Mills & Gorman 1997; Creel & Creel 2002; Vanak *et al.* 2013; Masenga *et al.* 2015). In these ecosystems, African wild dogs persisted stably over long periods, while they disappeared from LPNP and other open grassland systems dominated by wildebeest (Estes & Goddard 1967; Fanshawe & Fitzgibbon 1993), suggesting that spatial niche partitioning may be critical for competitive coexistence of wild dogs with dominant competitors. Despite the generally positive correlation in space use by wild dogs and dominant competitors, the relationship to relative use by lions was asymptotic while the relationship to relative use by hyenas was linear, even though hyenas outnumbered lions 40-fold. To some degree, this result aligns with prior studies showing that African wild dogs avoid areas with a high probability of encountering lions.

The difference in spatial relationships of wild dogs to lions and hyenas could perhaps be explained by the fact that a small number of lions in a single pride could be avoided more easily and effectively than the much larger number of hyenas in several clans. The difference might also be explained by recognizing that intraguild predation on wild dogs is more commonly due to lions than to hyenas (Mills & Biggs 1993; Creel &

Creel 1998) and that wild dogs can dominate hyenas in competitive interactions if they outnumber them (Estes & Goddard 1967; Fanshawe & Fitzgibbon 1993; Creel & Creel 1996). Nonetheless, our results suggest that on a per-capita basis, the limiting effect of lions on the use of space by wild dogs is strong. We suggest that in an open landscape, it might be impossible for African wild dogs to establish themselves permanently in the face of unavoidable competitors. In other open, relatively intact ecosystems in Africa (Serengeti, Etosha, Ngorongoro), African wild dogs have also been present only intermittently. Wild dogs showed appreciable overlap with their dominant competitors in temporal patterns of hunting, but were more active during the crepuscular period and less active in full darkness, as in most other systems (Mills & Gorman 1997; Creel & Creel 2002; Cozzi *et al.* 2012; Rasmussen & Macdonald 2012).

#### Relationships of Cheetahs to Dominant Competitors

Cheetahs were the only species that did not prey primarily on wildebeest, preferring the much less abundant oribi, and cheetahs had the broadest diets of the four carnivores. As with African wild dogs, these differences can partially be explained by differences in the cost/benefit ratio of hunting small prey, but also align with the hypothesis that cheetahs' dietary niche has evolved to reduce limitation by dominant competitors. Cheetahs focused their activity in areas heavily used by lions in data aggregated over the long term, as has been found elsewhere (Broekhuis *et al.* 2013; Swanson *et al.* 2014), and their space use showed a positive linear relationship with that of hyenas. Broekhuis *et al.* (2013) found that cheetahs avoid lions in space, but in a reactive way (on a short timescale), by positioning themselves further from lions than

predicted by a random distribution within areas of shared use (also see Durant 2000b). For cheetahs, avoidance of both lions and hyenas is typically more clearly related to temporal patterns rather than spatial patterns (Mills & Biggs 1993). Cheetahs made about 70% of their kills during full daylight, and thereby avoided hunting in the crepuscular and nighttime periods in which the other species made approximately three quarters of their kills, and when surprise encounters at close range are more likely to occur and more likely to escalate.

#### Relationships Between the Dominant Competitors, Hyena and Lion

Space use by hyenas was positively correlated to space use by lions, but the relationship was asymptotic, suggesting avoidance of areas most heavily used by lions. Lions and hyenas also showed very similar temporal distributions of hunts. In general, these results align with the inferences from a recent review by Périquet *et al.* (2014) who noted that these species have both negative and positive influences on each other, so that the net effect is complex and avoidance is weak. Périquet *et al.* (2014) suggested that finer patterns in selection of prey age–sex classes and processes affecting scavenging opportunities facilitate coexistence between hyenas and lions, allowing both species to concentrate their hunting in areas of high prey availability.

It is increasingly clear that within Africa's large carnivore guild, interspecific competition can be a strongly limiting force for cheetahs and especially African wild dogs. Both species use niche partitioning to reduce the risk of dangerous interactions, but in different ways that appear to have ramifications for coexistence. Wild dogs show more dietary and temporal overlap with dominant competitors. Cheetahs combine divergence

in diet, temporal avoidance, and reactive local spatial avoidance to coexist with lions and hyenas in areas of high prey density, even in open habitats. Our results provide new insight into the conditions under which partitioning may not allow for coexistence for one subordinate species, the African wild dog, while it does for cheetah. Because of differences in mechanisms of response, African wild dogs may be more prone to competitive exclusion (local extirpation), particularly in open, uniform ecosystems with simple (often wildebeest dominated) prey communities, where spatial avoidance is difficult.

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Figure 2.1 Location of Liuwa Plain National Park within Zambia and Africa



Figure 2.2 The 1,200-km<sup>2</sup> focal study area is dominated by open grasslands heavily used by migratory wildebeest and zebra and resident oribi. The homogeneity of habitat type and structure within our study area simplified interpretation of differences between species in their use of space.

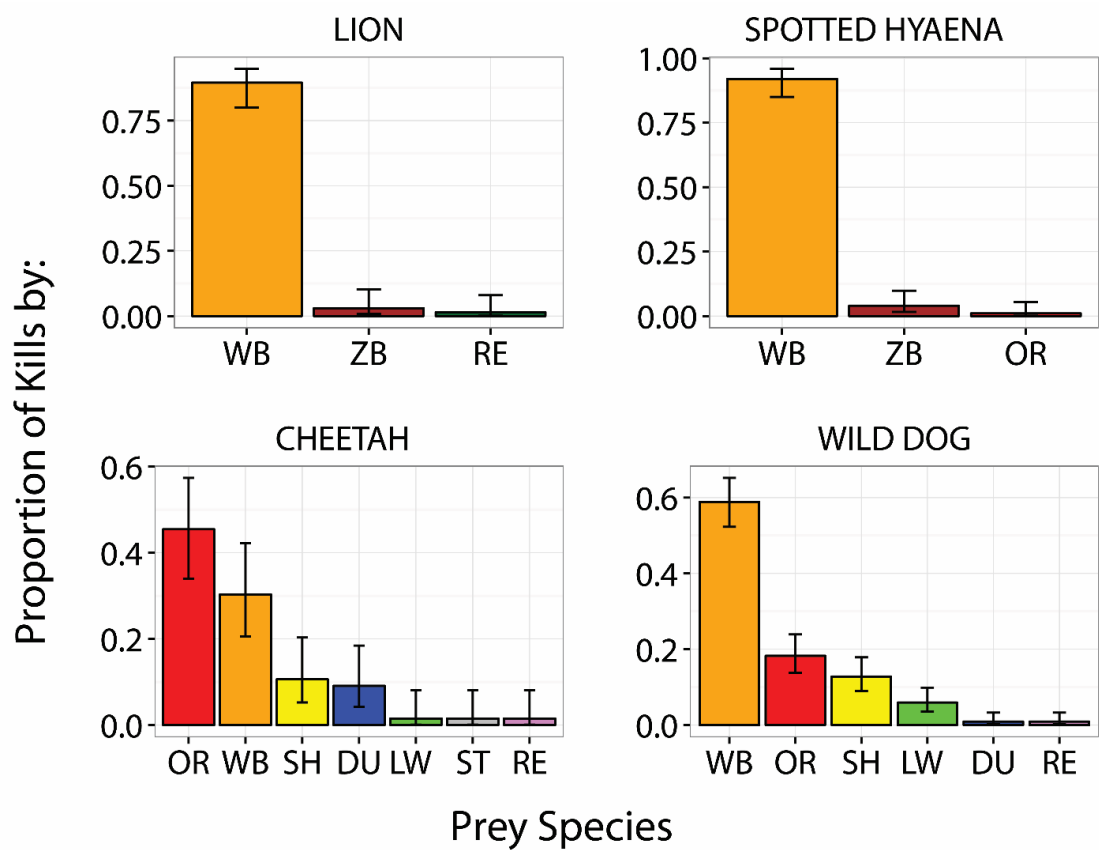


Figure 2.3 Patterns of prey selection by each of the large carnivore species. WB, wildebeest; ZB, zebra; OR, oribi; SH, springhare; DU, duiker; LW, red lechwe; ST, steenbok; RE, reedbuck.

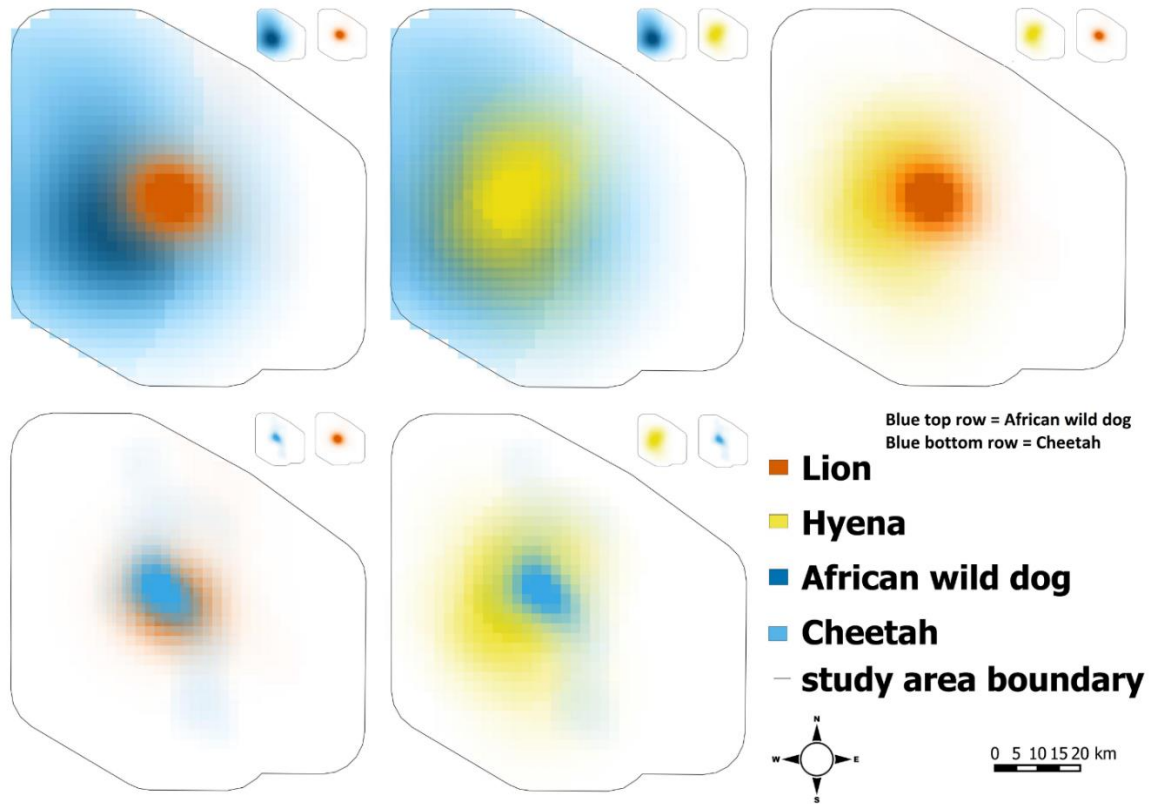


Figure 2.4 Utilization distributions for each pair of species for which we tested associations. In each panel, the outline denotes the boundaries of the 1,200-km<sup>2</sup> focal study area, and the intensity of color indicates intensity of use.

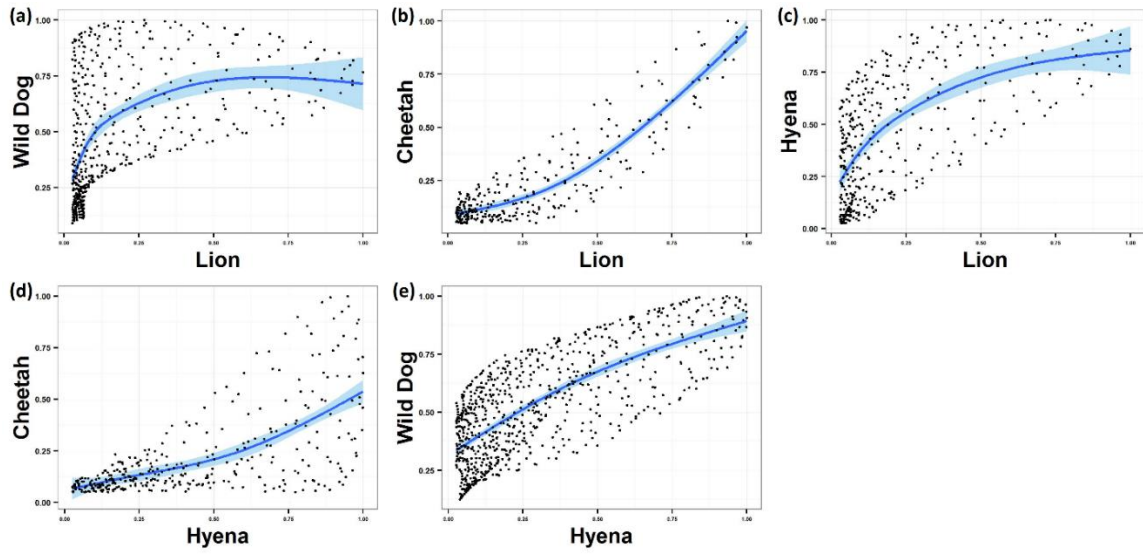


Figure 2.5 Correlations between space use by species pairs within areas used by both species. (a) wild dog and lion; (b) cheetah and lion; (c) hyena and lion; (d) wild dog and hyena; (e) cheetah and hyena

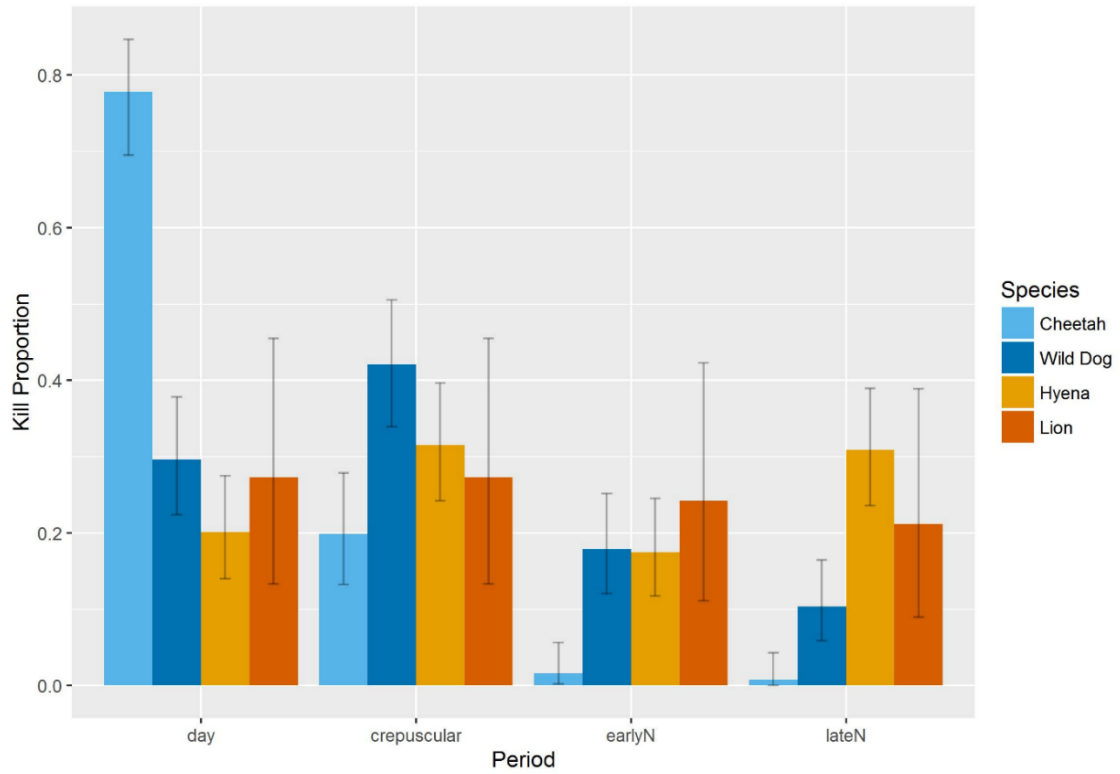


Figure 2.6 The proportion of kills made by each carnivore species per time window. EarlyN and LateN denote early and late night: See Chapter 2: Activity Data for details. Species color codes are the same as in Figure 2.4.

Literature Cited

- Baum, J.K. & Worm, B. (2009) Cascading predator and effects of changing oceanic predator abundances. *Journal of Animal Ecology*, **78**, 699–714.
- Broekhuis, F.C., Cozzi, G., Valeix, M., McNutt, J.W. & Macdonald, D.W. (2013) Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology*, **82**, 1098–1105.
- Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.
- Caro, T.M. & Laurenson, M.K. (1994) Ecological and genetic factors in conservation: A cautionary tale. *Science*, **263**, 485–486.
- Caro, T.M. & Stoner, C.J. (2003) The potential for interspecific competition among African carnivores. *Biological Conservation*, **110**, 67–75.
- Cozzi, G., Broekhuis, F.C., McNutt, J.W. & Schmid, B. (2013) Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation. *Biodiversity and Conservation*, **22**, 2937–2956.
- Cozzi, G., Broekhuis, F.C., McNutt, J.W., Turnbull, L.A. & David, W. (2012) Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, **93**, 2590–2599.
- Creel, S. & Creel, N.M. (1996) Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, **10**, 526–538.
- Creel, S. & Creel, N.M. (1998) Six ecological factors that may limit African wild dogs, *Lycaon pictus*. *Animal Conservation*, **1**, 1–9.
- Creel, S. & Creel, N.M. (2002) *The African Wild Dog: Behavior, Ecology and Conservation*. Princeton University Press, Princeton.
- Creel, S., Spong, G. & Creel, N.M. (2001) Interspecific competition & population biology of extinction-prone carnivores. *Carnivore Conservation* (eds J.L. Gittleman, S.M. Funk, D.W. MacDonald & R.K. Wayne), pp. 35–61. Cambridge University Press, Cambridge.
- Creel, S., Winnie, J.A. & Christianson, D. (2013) Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: An example with wolves and elk. *Ecology and Evolution*, **3**, 5189–5200.

- Crooks, K.R., Vuren, D. Van & Crooks, K.R. (1995) Resource utilization by two insular endemic mammalian carnivores, the island fox and island spotted skunk. *Oecologia*, **104**, 301–307.
- Darnell, A.M., Graf, J.A., Somers, M.J., Slotow, R., Szykman Gunther, M. & Gunther, M.S. (2014) Space use of African wild dog in relation to other large carnivores. *Plos One*, **9**, e98846.
- Durant, S.M. (1998) Competition and coexistence : refuges an example from carnivores Serengeti. *Journal of Animal Ecology*, **67**, 370–386.
- Durant, S.M. (2000a) Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, **11**, 624–632.
- Durant, S.M. (2000b) Predator avoidance, breeding experience and reproductive success in endangered cheetahs (*Acinonyx jubatus*). *Animal Behaviour*, **60**, 121–130.
- Estes, R.D. & Goddard, J. (1967) Prey selection and hunting behavior of the African wild dog. *The Journal of Wildlife Management*, **31**, 52–70.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pickett, E.K., Ripple, W.J., Sandin, S. a, Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. & Wardle, D.A. (2011) Trophic downgrading of planet earth. *Science*, **333**, 301–306.
- Fanshawe, J.H. & Fitzgibbon, C.D. (1993) Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour*, **45**, 479–490.
- Ginsberg, J.R., Alexander, K.A., Creel, S., Kat, P.W., McNutt, J.W. & Mills, M.G.L. (1995) Handling and survivorship of African wild dog (*Lycaon pictus*) in five ecosystems. *Conservation Biology*, **9**, 665–674.
- Gorman, M.L., Mills, M.G.M.G.L., Raath, J.P.J.P., Speakman, J.R., Mills, M.G.M.G.L., Raath, J.P.J.P. & Speakman, J.R. (1998) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature*, **852**, 1992–1994.
- Hayward, M.W. & Kerley, G.I.H. (2008) Prey preferences and dietary overlap amongst Africa's large predators. *South African Journal of Wildlife Research*, **38**, 93–108.
- Hayward, M.W., O'Brien, J., Hofmeyr, M. & Kerley, G.I.H. (2006) Prey preferences of the African wild dog *Lycaon pictus* (Canidae: Carnivora): Ecological requirements for conservation. *Journal of Mammalogy*, **87**, 1122–1131.

- Hayward, M.W. & Slotow, R. (2009) Temporal partitioning of activity in large African carnivores: Tests of multiple hypotheses. *South African Journal of Wildlife Research*, **39**, 109–125.
- Kolowski, J.M., Katan, D., Theis, K.R. & Holekamp, K.E. (2007) Daily patterns of activity in the spotted hyena. *Journal of Mammalogy*, **88**, 1017–1028.
- Kruuk, H. (1972) *The Spotted Hyena: A Study of Predation and Social Behaviour*. University of Chicago Press, Chicago.
- M'Soka, J.L.J. (2015) *Spotted Hyaena Survival and Density in a Lion Depleted Ecosystem: The Effects of Competition between Large Carnivores African Savannahs*. Montana State University.
- M'Soka, J.L.J., Creel, S., Becker, M.S., Droge, E.D., Jassiel, M., Creel, S., Becker, M.S. & Droge, E.D. (2016) Spotted hyaena survival and density in a lion depleted ecosystem: the effects of prey availability, humans and competition between large carnivores in African savannahs. *Biological Conservation*, **201**, 348–355.
- M'Soka, J.L.J., Creel, S., Becker, M.S. & Murdoch, J.D. Ecological and anthropogenic effects on the density of migratory and resident ungulates in a human-inhabited protected area (in press). *African Journal of Ecology*, 1–14.
- Malcolm, J.R. & Marten, K. (1982) Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behavioral Ecology and Sociobiology*, **10**, 1–13.
- Mankiw, N.G. (1990) A quick refresher course in macroeconomics. *Journal of Economic Literature*, **28**, 1645–1660.
- Masenga, E.H., Jackson, C.R., Mjingo, E.E., Jacobson, A., Riggio, J., Lyamuya, R.D., Fyumagwa, R.D., Borner, M. & Roskaft, E. (2015) Insights into long-distance dispersal by African wild dogs in East Africa. *African Journal of Ecology*, **54**, 95–98.
- Mbizah, M.M., Marino, J. & Groom, R.J. (2012) Diet of four sympatric carnivores in Save Valley Conservancy, Zimbabwe: implications for conservation of the African wild dog (*Lycaon pictus*). *South African Journal of Wildlife Research*, **42**, 94–103.
- Mills, M.G.L. & Biggs, H.C. (1993) Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. *Mammals as Predators* (eds N. Dunstone & M.L. Gorman), pp. 253–268. Zoological Society of London, London.

- Mills, M.G.L. & Gorman, M.L. (1997) Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology*, **11**, 1397–1406.
- Ngoprasert, D., Lynam, A.J., Sukmasuang, R., Tantipisanuh, N., Chutipong, W., Steinmetz, R., Jenks, K.E., Gale, G.A., Grassman, L.I., Kitamura, S., Howard, J., Cutter, P., Cutter, P., Leimgruber, P., Songsasen, N. & Reed, D.H. (2012) Occurrence of three felids across a network of protected areas in Thailand: Prey, intraguild, and habitat associations. *Biotropica*, **44**, 810–817.
- Palomares, F. & Caro, T.M. (1999) Interspecific killing among mammalian carnivores. *The American Naturalist*, **153**, 492–508.
- Pereira, L.M., Owen-Smith, N. & Moleón, M. (2014) Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Review*, **44**, 44–55.
- Périquet, S., Fritz, H. & Revilla, E. (2014) The lion king and the hyaena queen: large carnivore interactions and coexistence. *Biological Reviews*, **90**, 1197–1214.
- Pianka, E.R. (1981) Competition and niche theory (ed RM May). *Theoretical Ecology*, **8**, 167–196.
- QGIS Development Team. (2015) QGIS Geographic Information System.
- R Core Team. (2016) R: A language and environment for statistical computing.
- Rasmussen, G.S.A. & Macdonald, D.W. (2012) Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *Journal of Zoology*, **286**, 232–242.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343**, 1241484.
- Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**, 982–998.
- Rosenblatt, E., Creel, S., Becker, M.S., Merkle, J., Mwape, H., Schuette, P. & Simpamba, T. (2016) Effects of a protection gradient on carnivore density and survival: an example with leopards in the Luangwa valley, Zambia. *Ecology and Evolution*, **6**, 3772–3785.
- Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, **185**,

27–39.

Silverman, B. (1986) *Density Estimation for Statistics and Data Analysis*. CRC Press, Harvard.

Sinclair, A.R.E. (1985) Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology*, **54**, 899–918.

Speakman, J.R., Gorman, M.L., Mills, M.G.L. & Raath, J.P. (2015) Wild dogs and kleptoparasitism: some misunderstandings. *African Journal of Ecology*, **54**, 125–127.

Steinmetz, R., Seuaturien, N. & Chutipong, W. (2013) Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. *Biological Conservation*, **163**, 68–78.

Swanson, A., Caro, T.M., Davies-Mostert, H., Mills, M.G.L., Macdonald, D.W., Borner, M., Masenga, E., Packer, C., David, W., Borner, M., Masenga, E., Packer, C., Paul, S., Africa, S., Conservation, W. & Centre, R. (2014) Cheetahs and wild dogs show contrasting patterns of suppression by lions. *The Journal of Animal Ecology*, **83**, 1418–1427.

Trinkel, M. & Kastberger, G. (2005) Competitive interactions between spotted hyenas and lions in the Etosha National Park, Namibia. *African Journal of Ecology*, **43**, 220–224.

Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C. & Greatwood, S. (2013) Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology*, **94**, 2619–2631.

Wand, M.P. & Jones, M.C. (1994) *Kernel Smoothing*. CRC Press, London.

Ziv, Y., Abramsky, Z., Kotler, B.P. & Subach, A. (1993) Interference competition and temporal habitat partitioning in two gerbil species. *Oikos*, **66**, 237–246.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2009) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology & Evolution*, **1**, 3–14.

CHAPTER THREE

MEASURING THE ‘LANDSCAPE OF FEAR’: RISKY TIMES AND RISKY PLACES  
INTERACT TO AFFECT THE RESPONSE OF PREY

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Abstract

Both short-term and long-term cues about the risk of predation can have strong effects on the behavior of prey, thus affecting growth, reproduction, survival, and population dynamics. Inferences about the factors that affect the strength of such ‘risk effects’ in the wild have been limited by the lack of studies that (i) relate antipredator responses to the magnitude of direct predation, (ii) measure responses of prey to risk from complete predator guilds, and (iii) employ methods that quantify risk in more than one way. Here, we quantified behavioral responses of a complete ungulate prey guild to variation in both long-term and short-term risks from all of the large predators present in Liuwa Plain National Park (Zambia), with known patterns of direct predation. Our analysis allowed the first direct test for interaction between responses to long-term and short-term risk in the wild, and revealed that prey vigilance responded strongly to locations with high long-term risk when short-term risk was high, but not when short-term risk was low. This result has broad ramifications for the design and interpretation of field studies of antipredator behavior, its costs, and its consequences for population and community dynamics.

Keywords: Risk-effects, predator-prey relationship, landscape of fear, spatial risk, temporal risk.

## Introduction

Experiments with many species have shown that exposure to predation risk induces responses by prey that can carry costs affecting growth, reproduction, survival, and population dynamics (Werner *et al.* 1983; Peckarsky *et al.* 1993; Boonstra *et al.* 1998; Pangle *et al.* 2007; Sheriff, Krebs & Boonstra 2009; LaManna, Martin & Letters 2016). Despite this, we have a very limited understanding of the magnitude of these ‘risk effects’ in the wild, at least in part because field studies are rarely designed in a manner that allows risk effects to be disentangled from simple bottom-up limitation by food (Creel & Christianson 2008; Christianson & Creel 2014). Our understanding has also been limited by a lack of studies that (i) measure responses of prey to risk from complete predator guilds, (ii) relate the intensity of antipredator responses to the magnitude of direct predation, and (iii) employ methods that quantify risk at more than one spatiotemporal scale.

The first point is conceptually obvious: different predators typically create risks at different places and times (Cresswell & Quinn 2010, 2013; Dröge *et al.* 2017). We have learned a great deal by quantifying the responses of prey to a single predator, particularly in cases where one predator is the dominant threat to a given prey species (Creel *et al.* 2007; Valeix *et al.* 2009), but in many systems this approach is likely to provide an incomplete assessment of the constraints imposed by predation risk (Relyea 2001a). Despite this, studies of responses by prey to the risks presented by complete predator guilds remain uncommon (Thaker *et al.* 2011).

The second point is also conceptually simple, but surprisingly few studies have tested how the strength of antipredator response relates to the magnitude of direct predation (Relyea 2001a), particularly under natural circumstances (Thaker *et al.* 2011; Creel, Schuette & Christianson 2014; LaManna *et al.* 2016). While it is logical to hypothesize that prey will respond most strongly to the predators that kill them most often (Relyea 2001b; Thaker *et al.* 2011), it is also logical to hypothesize that a low level of direct predation might be the consequence of effective responses by the prey, rather than low 'risk' (Lank & Ydenberg 2003; Lind & Cresswell 2005). Clearly, describing this relationship is necessary to understand the relative importance of direct predation and risk effects as determinants of the total limiting effect of predators on prey (Creel & Christianson 2008).

The third point is conceptually more subtle: selection should favor prey that assess and respond to risk at more than one scale, but most field studies (including our own Creel *et al.* 2007) have quantified risk in just one way. In studies of ungulate prey responding to risk from large predators, many studies have used GPS radiocollars to describe long-term variation in risk as peaks and valleys in the distribution of predator locations (Valeix *et al.* 2009) or kill sites (Moll *et al.* 2016), or as habitat types that vary in use by predators (Thaker *et al.* 2011). Responses to long-term variation in risk have also been assessed by comparison of study sites with variation in predator presence or density (Creel *et al.* 2007) or by comparing sites before and after predator colonization (Cherry *et al.* 2016). Other studies have used direct observations to measure short-term variation in risk as the immediate presence/absence or proximity of predators or kills

(Winnie *et al.* 2007; Creel *et al.* 2014), and some have used data from GPS collars to determine responses to short-term risk (Valeix *et al.* 2009; Basille *et al.* 2015). From such studies, it is clear that prey can respond to both short term variation in risk (the ‘risky times’ hypothesis) and spatial variation in the long term risks associated with a site (the ‘risky places’ hypothesis). Behavioral studies have focused mainly on risky times, while ecological research has focused mainly on risky places (Creel *et al.* 2008). Surprisingly, the hypothesis that these two aspects of risk have interactive effects on prey behavior remains untested in the wild.

Here, we used a combination of data from GPS collars on predators and direct observation of prey under conditions of known immediate risk to examine the behavioral responses of a complete ungulate guild to both long-term and short-term variation in risk from all of the large predators in the ecosystem. We also used direct observation of each predator species to quantify direct predation on each of the ungulate species. We considered several alternative measures of long-term risk. These data allowed the first test (to our knowledge) for interaction between responses to long-term (LT) and short-term (ST) risk under natural conditions, as predicted by Lima & Bednekoff 1999 and as detected in laboratory settings (Brown *et al.* 2013; Joyce *et al.* 2016) and field experiments (Brown *et al.* 2013). Finally, because long term risk is often described indirectly through habitat variables (Ripple *et al.* 2001; Ripple & Beschta 2003), we tested whether measures of vegetation structure improved the model’s description of prey behavior.

## Methods

### Study Area and Populations

Our data were gathered in a 1200 km<sup>2</sup> study area in the southern part of the 3660 km<sup>2</sup> Liuwa Plain National Park (LPNP) in Zambia. The area has little topography (no rivers flow within the study site) and the vegetation is dominated by uniform short and intermediate grasslands with occasional tree islands (Fig 3.1). The ungulate community is dominated by migratory wildebeest (*Connochaetes taurinus*) at densities ranging from 6.2 – 60.8 individuals/km<sup>2</sup>, migratory zebra (*Equus quagga*) at densities ranging from 1.8 – 8.1 individuals/km<sup>2</sup>, and non-migratory oribi (*Ourebia ourebi*) at densities ranging from 1.1 – 14.5 individuals/km<sup>2</sup>. These densities were estimated from distance sampling (which allowed correction for each species' probability of detection) on a systematic transect grid, several times in each year of the study (M'Soka *et al.* in press). Hyenas greatly outnumbered other predators within the study area, with 151 hyenas in four clans (M'Soka *et al.* 2016), 6 lions in one pride, 22 wild dogs in two packs and 17 known cheetahs. Leopards are not present in LPNP, nor is there any record of their presence in recent times (M'Soka *et al.* 2016).

### Predator Follows to Quantify Magnitude of Direct Predation

Patterns of prey selection by the four predators and the methods used to obtain these data have been described in detail elsewhere (Dröge *et al.* 2017). Briefly, radio-collared predators were followed for complete hunting periods (from when they became

active until they became inactive), typically for several consecutive hunting periods. During these follows, we recorded the species (and when possible the age and sex) of prey that were encountered, hunted and killed. These follows, combined with opportunistic observations, yielded a sample of 453 kills where the identity of the predator was directly observed (N = 351) or inferred with high confidence (N = 102). High confidence was assigned to kills that were not directly observed but were very fresh, with only one predator species present, no other predators detected nearby, and no signs of attendance by other predators. Patterns of prey selection did not differ detectably between the complete data set and the subset of kills that were directly observed.

#### Location Data from Predators

Locations of African wild dogs, hyenas and lions were collected between June 24, 2010 and December 23, 2015 using GPS and VHF radio collars fit to individuals in all but one predator group known to reside wholly or largely within the study site (details below). All immobilization procedures to fit animals with collars were conducted with permission of the Department of National Parks and Wildlife (DNPW, formerly ZAWA), following animal welfare standards and protocols required by the Zambia Department of Veterinary and Livestock Services and the DNPW. From January 07, 2012 to April 13, 2013 the alpha female of a resident African wild dog pack was fitted with a GPS collar taking a location every 5 hours for a total of 1354 locations. A second resident pack was fitted with VHF collars and was monitored from June 25, 2010 to May 30, 2014, when the pack dissolved into multiple dispersal groups following the death of the alpha male; a

total of 359 locations from this pack were used. From October 24, 2010 to May 13, 2012 5 hyenas (in three of the four resident clans) were fitted with GPS collars (recording a location every 2 or 3 hours for a total of 187, 725 and 3,493 locations for each clan). During the course of the study one of these clans split into two, but frequent re-sightings of known individuals confirmed that the two newly-formed clans remained largely within the source clan's area. The remaining clan was monitored with VHF collars on five clan members, which provided a total of 318 locations (two hyenas in this clan were fitted with GPS collars but the GPS function failed in both). The lion population in Liuwa consisted of 1 coalition of 2 males, and 1 pride of females and cubs that formed a cohesive social group totaling six individuals. Between June 24, 2010 and May 28, 2015 at least one male and one female lion was fitted with a GPS satellite collar (recording a location every 3 or 4 hours for a total of 11,018 locations) and one additional female was fitted with a VHF collar for the duration of the study. Cheetah locations came from observations of 4 cheetahs fitted with VHF collars (and their associates) between June 30, 2010 and December 23, 2015, with one collar in each group known to use the site. These included single locations from opportunistic observations, and multiple locations from hunt follows in which cheetahs were observed continuously through at least one complete period of hunting activity (and up to 7 days) on 50 occasions between November 11, 2012 and December 23, 2015. When moving, a GPS location was recorded at 15 minute intervals, and while stationary a single location was recorded; a total of 2,000 locations from cheetahs were used. Although the locations from cheetahs were not collected with

GPS collars, this sampling provided representative data for cheetah movements within the study site.

For each of the four species, these locations were used to fit a utilization distribution that was resampled in an identical manner for each species to compare space use (as described below). The location data for the four species come from overlapping periods from 2010 to 2015, but the interval sampled was not identical for all species. However, data from GPS collars showed that the ranging patterns of lions and hyenas changed little year to year, sampling of wild dogs was intensive for the entire period during which they used the site, and the locations of cheetahs showed no evidence of territorial partitioning of the study area, suggesting that the sampling provided representative data (Dröge *et al.* 2017).

#### Utilization Distributions Fit to Location Data to Quantify Spatial Variation in Long-term Risk

From the locations described above we calculated a utilization distribution (UD) for each species (Worton 1989; Seaman & Powell 1996) using the `adehabitatHR` package (Calenge 2006) in R (R Core Team 2016), with a grid cell size of 500 meters. This spatial scale was fine enough to provide a meaningful description of variation in space use, and the data for each species allowed us to fit UDs (shown in ref 11) at this scale. Randomly thinning the data for lions (with the most locations) to equal the sample size for wild dogs (with the fewest locations) yielded very little change in the estimated UD. Standard methods for selection of bandwidth as a smoothing parameter, e.g. least squares cross validation (Seaman & Powell 1996), did not always converge, and the standard reference

bandwidth ( $h_{ref}$ ) yielded rather discontinuous utilization distributions. In such cases, several authors (Silverman 1986; Wand & Jones 1994) recommend using a subjective visually chosen bandwidth. We adopted a more objective version of this approach, by calculating the daily distance moved for each individual animal (by summing the distances between consecutive locations within a day for individuals fitted with GPS collars or observed during continuous hunt follows, which are described below). We then selected the 90<sup>th</sup> percentile of the frequency distribution of daily distances (95<sup>th</sup> for cheetahs, with sparser data) as the smoothing parameter. This procedure yielded largely continuous UD<sub>s</sub>, occasionally keeping densely clustered locations separate in a reasonable manner. Because the home ranges of the two wild dog packs and the four hyena clans had little overlap, UD<sub>s</sub> were calculated separately for each group, then combined and rescaled to result in a total utilization of 1 for the combined UD. This process properly resolved areas of low use between home ranges. For cheetahs and lions, individual ranges overlapped very substantially, so we calculated a single UD for each species.

It is possible that prey respond primarily to predators on the basis of functional groups (e.g., stalkers vs. coursers) rather than species (Schmitz 2008; Thaker *et al.* 2011), though tests of this hypothesis have shown variable results (Thaker *et al.* 2011; Creel *et al.* 2014; Moll *et al.* 2016). To test this possibility we combined the UD<sub>s</sub> of the coursing predators, hyenas and wild dogs, and those of stalking predators, cheetahs and lions, and again rescaled them to a total utilization of 1. Finally, to calculate the utilization of the

study area by all of the predators, we combined the UDs of all four species and again rescaled to a total utilization of 1.

To more completely examine what factors drive variation in antipredator response, we also fit each of the UDs just described to a subset of the data restricted to kill sites, to test whether long term risk is better described by the locations at which predators made kills rather than the locations that predators used for all purposes.

### Ungulate Observations to Quantify Responses to Risk

To measure the behavioral response of prey to short-term and long-term variation in risk, we used 348 scan-sample observations of ungulate herds. For each observation we recorded the location, distance to the nearest known predator, predator species, presence/absence of a kill, and the date and time. We then recorded the species, number of animals in the herd, sex and age class (adult, sub-adult, juvenile), and its behavior at the moment of the observation. For this analysis, our primary response variable was the proportion of adults vigilant ( $\bar{X} = 0.09$ ), operationally defined as an ungulate being stationary and holding its head above shoulder height with the ears and eyes focused simultaneously, while not chewing (neither taking bites nor ruminating). This definition focuses on clear-cut attentiveness to the surroundings and excludes more ambiguous ‘routine’ vigilance (Creel *et al.*; Périquet *et al.* 2012; Blanchard & Fritz 2016). We focused on vigilance because it is the most common antipredator behavior for all three of these species (Creel *et al.*) and increased vigilance causes reduced feeding in these species (Creel *et al.*). We did not use data from herds that directed vigilance at the

observer. To sample behavior representatively, each of the 348 observations consisted of an average of 7 scans, performed at intervals of 2-10 minutes (depending on herd size, which determined the time required to scan the herd). To avoid pseudoreplication, the unit of analysis was the observation period, rather than scans within observation periods (i.e., we tested for effects on the mean proportion of adults vigilant, with one mean per observation period). Herds were observed from a stationary vehicle, with either binoculars or a spotting scope. Scans were conducted primarily around dusk and dawn when predators were still active but observation conditions were good. While we do not focus on group size in this analysis, we confirmed that the inferences reported here for the effects of long-term and short-term risk on vigilance were not altered by the inclusion of group size as a predictor.

To collect these data efficiently, we began by locating a predator, recording its location and searching for nearby ungulates. We recorded the location of the prey herd and determined the straight-line distance (in meters) between the predator and prey. We aimed to stratify observations across prey species and distance to the nearest predator, so that half ( $N = 176$ ) of the ungulate scans were within 500 meters of a predator and half ( $N = 172$ ) were at longer distances (of which 99 observations were for distances between 500 m and 1 km, and 73 were for distances between 1 km and 2 km). We also distributed ungulate observations across the entire study area, though ungulate observations were unavoidably more concentrated in areas with higher long-term use by predators (because predators were not often found within 2 km of prey in areas of low use). It is possible that another undetected predator was sometimes closer to the observed herd, but due to the

openness of the terrain this was probably uncommon. This inference was reinforced by taking care that no vigilance was observed towards unmonitored predators during the scans.

### Measures of Short Term and Long Term Variation in Predation Risk

We measured the risk of predation in two basic ways. *Short term* variation in the risk of predation ('ST risk') was measured by recording the distance to the nearest predator at the time of observation, and whether a kill was present at the predator's location. As described above, observations were made at dawn and dusk when predation risk remained high, but observations were linked to the presence of predators that were not actively hunting or moving, so that distance could be measured accurately. *Long term* variation in risk ('LT risk') was measured by determining the intensity of use by each predator (i.e., the height of its UD) at the location of the observation. We further tested whether antipredator behavior was related to the species of predator, the species of prey, and the frequency of predation on each prey species by each predator. Models that substituted predator functional type (stalker vs courser) for predator species were compared, and models that described long term risk by fitting UDs only to kill sites, rather than fitting UDs to all predator locations. Finally, we tested whether measures of short-term and long-term risk interacted in their effects on vigilance.

We used 453 kills for which the predator and prey species could be assigned with confidence to measure the proportion of predation by each of the four predators on each of the three prey species (Table 3.1). These same data were used to create an overall UD

of all kill sites, of kill sites for each species except for zebra (which were killed too infrequently to create a distribution of kill sites), of kill sites for each predator species, of kill sites for each predator functional type (stalker and courser), of kill sites for each predator-prey pair (restricted to those for which there were enough data: wild dog – wildebeest, wild dog – oribi, cheetah – wildebeest, cheetah – oribi, hyena – wildebeest, lion – wildebeest) and of kill sites for each predator functional type – prey species pair (stalker – wildebeest, stalker – oribi, courser – wildebeest, courser – oribi).

At the location of each ungulate observation, we extracted the value for each of the UDs just described as alternative measures of long term variation in risk, and then (as described below) identified which measures of LT and ST risk best predicted vigilance by prey.

### Model Identification

To identify the parameters that affected vigilance, we began with a quasibinomial generalized linear model that included effects of prey species, predator species (i.e., the species that was immediately nearest), the distance between the two (a measure of immediate, short term risk), the presence or absence of a recent kill at the predator's location (another possible measure of short term risk) and three measures of long term risk at the location of observation: 1.) The UD of predators (all species), 2.) The UD of carcasses (all species), and 3.) The proportion of kills that the observed prey species constituted for the nearest predator. We included three two-way interactions that we hypothesized (*a priori*) to be important: prey species x predator species, distance to the

nearest predator x predator species, and an interaction between long and short term risk (UD of all predators x distance to the nearest predator). We used all of the data to estimate the main effects of ST risk and LT risk, but it was not possible to collect a large sample of observations with high ST risk (i.e., a carnivore nearby) in areas with very low LT risk (i.e., where carnivores rarely go). In addition, for observations with low ST risk (i.e. the nearest carnivore was quite distance from the location of the prey), it is not clear that measures of LT and ST risk based on widely separated locations for the predator and prey would be meaningful. To address these issues when testing for an interaction between LT and ST risk, we assigned a value of 0 for LT risk to observations with the nearest predator more than 450m away, thus restricting the test for interaction between the effects of LT risk and ST risk to situations in which ST risk was appreciable (i.e., we tested whether LT risk interacted with ST risk when ST risk was known to be present).

We then used likelihood ratio tests for sequential deletion of weak effects from this model, but retained main effects that were part of strong interactions. As described previously, long term risk was measured in more than one way, and we used AIC scores to test whether the model's explanatory power was improved by replacing the UD of all predators with the UD for each of the predator species, the UD of each predator functional group (stalker and courser), or the UD for the predator that was immediately present. Similarly, we used AIC scores to test if explanatory power was increased by replacing the UD of kill sites for all prey species with the UD of kills sites only for the prey species observed. Lastly, we used AIC scores to check whether the distance between predator and prey had better explanatory power than a simple factorial presence/absence

parameter, where presence was defined as the predator being less than 450m from the prey based on the results of prior research (Creel *et al.* 2014).

With the quasibinomial GLM identified by these steps, we tested whether the addition of a vegetation structure parameter improved the explanatory power of the model, to test whether prey used attributes of the environment itself to assess risk, beyond assessments of the long and short term presence of predators. There was little variation in vegetation structure on our study site, which was > 90% open grassland, so we tested instead for effects of grass height, with three levels (<10 cm, 10 cm – 1 m, >1 m). We tested the addition of this effect to the model as a single parameter, as an interaction with ungulate species, as an interaction with predator species and as a three-way interaction with both ungulate species and predator species. This test was conducted as a final step because measurements of grass height were available only for a subset of the data (N = 334 observations).

Continuous predictor variables were centered and scaled prior to analysis so that effects could be compared directly.

## Results

From the initial model of vigilance, likelihood ratio tests eliminated weak effects of the proportion of kills of the observed prey species by the predator that was present (df=1,  $F = 0.003$ ,  $p$ -value 0.96), the presence or absence of a recent kill at the predator's location (df = 1,  $F = 0.6407$ ,  $p$ -value 0.42), the utilization distribution of kill sites (df = 1,  $F = 0.0003$ ,  $p$ -value =0.98) and the interaction between the predator species and distance

( $df = 3$ ,  $F = 1.2963$ ,  $p$ -value = 0.28). The resulting model (Table 3.2) included effects of prey identity, predator identity, interaction between predator and prey identity, ST risk (distance between the predator and the prey), LT risk (the UD of the predator that was present: see next paragraph), and interaction between ST risk and LT risk (see Table 3.2 for coefficients and their standard errors). As we have previously reported (Creel et al., in review) vigilance in LPNP was not detectably related to variation in herd size ( $b = -0.014 \pm 0.0001$  SE,  $t = 1.41$ ,  $P = 0.16$ ), or composition [proportion females]  $b = 0.004 \pm 0.006$  SE,  $t = 0.68$ ,  $P = 0.49$ ), probably because herd sizes are small in comparison to many savanna ecosystems ( $\bar{X} \pm SE$ : oribi  $2.47 \pm 0.09$ , zebra  $13.03 \pm 2.80$ , wildebeest  $6.46 \pm 1.42$ ), so that LPNP ungulates cannot depend on strong dilution of risk to provide safety.

Controlling for differences among predator and prey species, vigilance levels were much higher in locations of high LT risk, increasing by 139% with an increase of one standard deviation in LT risk (Fig 3.2, right panel,  $b = 1.39$ , S.E.M. = 0.39,  $t = 3.55$ ,  $P < 0.001$ ). LT risk was best described by the local intensity of use by the predator that was immediately closest at the time of observation rather than other measures of LT risk. As expected, vigilance tended to decrease as the distance to the nearest predator increased (i.e., as ST risk decreased), but the main effect of ST risk on vigilance was only  $1/10^{\text{th}}$  as strong as that of LT risk (Fig 3.2, left panel,  $b = -0.27$ , S.E.M. = 0.245,  $t = -1.13$ ,  $P = 0.26$ ), and the effect of ST risk was manifest primarily through a strong interaction with LT risk (Fig 3.2, middle panels,  $b = -0.66$ , S.E.M. = 0.33,  $t = -2.02$ ,  $P = 0.04$ ). When a predator was close ( $< 250$  m), vigilance increased strongly and consistently in locations

with high LT risk, but responses to LT risk were weak and variable when no predators were immediately nearby.

Substituting alternative measures of LT into the final model, AIC scores revealed that prey responded most strongly to the UD of the predator species that was immediately present. The next best model was the UD of all predators combined ( $\Delta\text{AIC} = 0.93$ ), with weaker support for models with the UDs of stalkers, coursers or individual species.

The addition of grass height did not improve the model's explanatory power. Confidence intervals for effects of grass height on vigilance greatly overlapped zero (grass 10 cm – 1 m:  $b = -0.14 \pm 1.01$  S.E.,  $t = -0.14$ ,  $P = 0.89$ ; grass > 1 m:  $b = -0.40 \pm 0.69$  S.E.,  $t = -0.59$ ,  $P = 0.56$ ; reference level was grass <10 cm), and confidence intervals overlapped zero for all but one of the interactions between grass height, predator species and prey species.

## Discussion

As expected, ungulates were more vigilant in places that were heavily used by predators over the long term. Contrary to expectation, there was little evidence that ungulates were more vigilant if they were closer to the nearest predator at the time of observation. This result came, however, from a model that allowed for interaction between LT and ST risk, and variation in ST risk did affect vigilance in a manner that depended on the LT risk of the location. Controlling for differences in mean vigilance among prey species and differences in their responses to the four predators, vigilance was greatest when high levels of ST risk (a predator immediately nearby) occurred in

locations with high LT risk (heavy use by that predator species). It is striking that the best measure of LT risk to describe this interaction was the UD of the predator that was immediately present, indicating a fine-tuned assessment by prey of the relationship between ST and LT risk, rather than a consistently stronger response to specific predator species or functional types. To summarize, prey responded most strongly when they encountered immediate risk in a place where they could have anticipated that very risk.

The result that prey responded more strongly to times of high ST risk in places with high LT risk has a parallel in the theory of Lima & Bednekoff (Lima & Bednekoff 1999), who emphasized that “antipredator behavior depends on both the immediate and the background level of predation risk”. Although Lima & Bednekoff (Lima & Bednekoff 1999) focused entirely on temporal variation in risk, while we quantified spatial and temporal variation in risk, both bodies of work suggest that responses to ST risk depend on patterns of LT risk. It has also been shown that the strength (and retention) of learned responses to risk are affected by past exposure to risk in laboratory studies with fish (Brown *et al.* 2013; Joyce *et al.* 2016), and tadpoles (Brown *et al.* 2013) and in a field experiment with fish (Brown *et al.* 2013). Our results confirm that both the *risky places hypothesis* (LT risk) and the *risky times hypothesis* (ST risk) are important (Creel *et al.* 2008) and that they do not act independently in their effects on the strength of antipredator responses. This interaction presents serious challenges for the design of research on risk effects. A real effect of ST risk could easily be masked by unmeasured variation in LT risk (or vice versa), and an apparent effect of ST risk might actually be caused by unmeasured variation in LT risk (or vice versa). Few (if any) prior field studies

have employed a design that addresses these complications, so our results have broad implications for the design and interpretation of studies of antipredator behavior, its costs, and its consequences for population and community dynamics.

Vegetation structure is often used as a proxy for LT risk (Ripple *et al.* 2001; Ripple & Beschta 2003). Because the vegetation on our study site was highly homogeneous open grassland, we did not include vegetation type in our original model, but we did test *post-hoc* if vegetation structure (grass height) improved the model appreciably, and it did not. With the accumulation of studies collecting location data over long periods from GPS collars, it will be an interesting question for further research (at sites with more complex structure) whether vegetation structure or predator utilization itself is a better predictor of risk effects (Hopcraft, Sinclair & Packer 2005). We suggest that variables such as vegetation structure and topography should be tested in addition to data on the predators themselves, and not as a proxy for such data.

Our analysis found that responses varied among predator-prey pairs, but not as expected if the strength of response was positively correlated to direct predation rate (Relyea 2001b). The strength of responses (Table 3.2) did align with the predictions of Preisser, Orrock & Schmitz (Preisser, Orrock & Schmitz 2007) who predicted that stalking predators, like lions and cheetahs, should have stronger effects on prey behavior than coursing predators, like wild dogs and hyenas. It is notable, however, that the effect of interactions between predator and prey identity tended to offset this difference (e.g. wildebeest responded very strongly to wild dogs: Table 3.2) and in fact models including LT risk from wild dogs, hyenas or both coursers performed better (AIC 1797.329-

1799.028) than models including LT risk from lions, cheetahs or both stalkers (AIC 1799.77-1800.70). Neither the immediate presence of a kill nor the long term distribution of kill sites had any detectable effect on vigilance, suggesting that kill locations (Kauffman *et al.* 2007) might be a weak proxy for data on the predators themselves when seeking to understand risk effects. In the short term, the presence of a kill could be an indicator of risk in systems where many individuals might be killed (e.g. some invertebrate systems Crowl & Covich 1990), but for ungulate-large carnivore systems, a kill decreases the short-term likelihood of a hunt and may be interpreted as a cue of safety.

It is becoming increasingly clear that predators can have strong effects on prey demography and dynamics through the costs of antipredator behavior, and that these effects might cascade to affect community structure and function. For a more complete understanding of the strength of these risk effects, we still require studies that measure responses of prey to risk from complete predator guilds, relate the intensity of antipredator responses to the magnitude of direct predation, quantify risk at more than one spatiotemporal scale, and test for interactions in these effects. Several field studies have simultaneously examined the effects on prey behavior of short term and long term variation in predation risk (Creel *et al.* 2008; Heithaus *et al.* 2009; Brook, Johnson & Ritchie 2012), but data from the wild do not yet provide an empirical basis to assess whether the interaction between short term and long term risk that we observed will prove to be a general pattern, as theory suggests it should be (Lima & Bednekoff 1999).

If so, then studies capable of describing this interaction will be critical for a proper understanding of risk effects.

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Conflicts of Interest: None declared

	Wildebeest	Oribi	Zebra
<b>Wild Dog</b>	0.76 (0.69 – 0.82)	0.23 (0.17 – 0.30)	--
<b>Cheetah</b>	0.22 (0.13 – 0.35)	0.64 (0.50 – 0.76)	--
<b>Hyena</b>	0.95 (0.87 – 0.98)	0.01 (0.00 – 0.07)	0.04 (0.01 – 0.07)
<b>Lion</b>	0.96 (0.88 – 0.99)	--	0.04 (0.01 – 0.12)

Table 3.1 The proportion of kills by each predator species that were comprised of each prey species. 95% binomial confidence interval in parentheses.

Effect <sup>3</sup>	Estimate	SE	<i>t</i>	<i>P</i>
<i>Intercept</i>	-3.49137	1.275	-2.738	0.007
<i>Risk</i>				
Short Term Risk (Distance)	-0.277	0.245	-1.129	0.26
Long Term Risk	1.389	0.391	3.554	<b>&lt;0.001</b>
ST X LT interaction	-0.663	0.327	-2.025	<b>0.044</b>
<i>Predator Species<sup>1</sup></i>				
Spotted hyena	-1.549	1.32	-1.173	0.241
Lion	2.844	2.032	1.399	0.163
African wild dog	-6.216	2.021	-3.076	<b>0.002</b>
<i>Prey Species<sup>2</sup></i>				
Wildebeest	-4.015	1.426	-2.813	<b>0.005</b>
Zebra	3.004	3.377	0.89	0.374
<i>Species Interaction</i>				
Wildebeest X Hyena	1.654	1.49	1.11	0.268
Zebra X Hyena	-1.494	3.43	-0.436	0.663
Wildebeest X Lion	-1.619	2.223	-0.728	0.467
Zebra X Lion	-4.342	4.031	-1.077	0.282
Wildebeest X Wild Dog	9.352	2.255	4.147	<b>&lt;0.001</b>
Zebra X Wild Dog	0.669	4.338	0.154	0.877

Table 3.2 Effects on prey vigilance levels from the final generalized linear model. Short term risk was described by the distance to the nearest predator at the time of observation. Long term risk was described by a kernel utilization distribution fit to carnivore locations for the complete study period.

1: Reference level is cheetah.

2: Reference level is oribi.

3: Multiplicative effects, with all continuous variables centered and scaled for direct comparison.

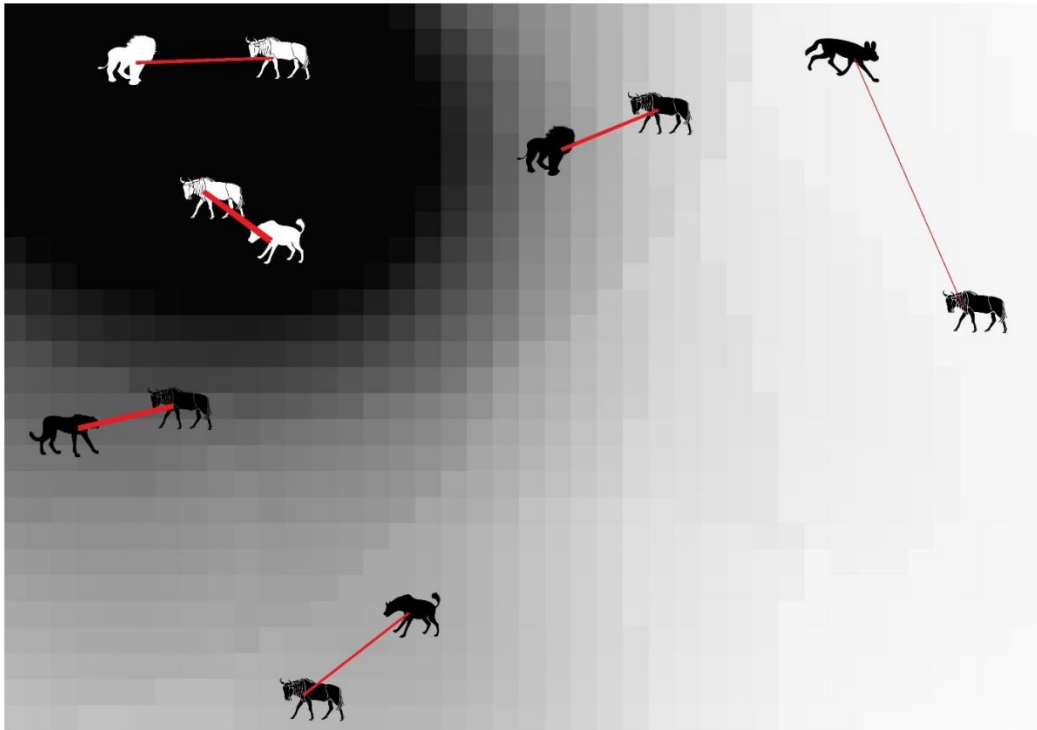


Figure 3.7 Schematic diagram for methods relating prey behavior to variation in short term and long term risk. A schematic diagram using wildebeest as an example to illustrate how the behavior of prey was related to short-term and long-term variation in risk. Background shading indicates long term risk, with darker areas indicating greater intensity of use by predators, as described by a kernel utilization distribution fit to predator locations for the entire study period. Comparison of models with prey utilization distributions fit to different subsets of data allowed us to test whether long term risks from all predators, from specific predators, from specific predator functional groups (stalker & courser) or from kill sites yielded more power to explain variation in prey behavior. Red lines indicate immediate short term risk, assessed by the distance to the nearest predator at the time of observation, its species, and whether a kill was present. We attempted to balance the data for all combinations of ST and LT risk, though some combinations (predator close in area of very low predator use) are not common.



Figure 3.2 The uniformly open vegetation structure and lack of topographic variation within the study site simplified interpretation of prey responses to the patterns just described.

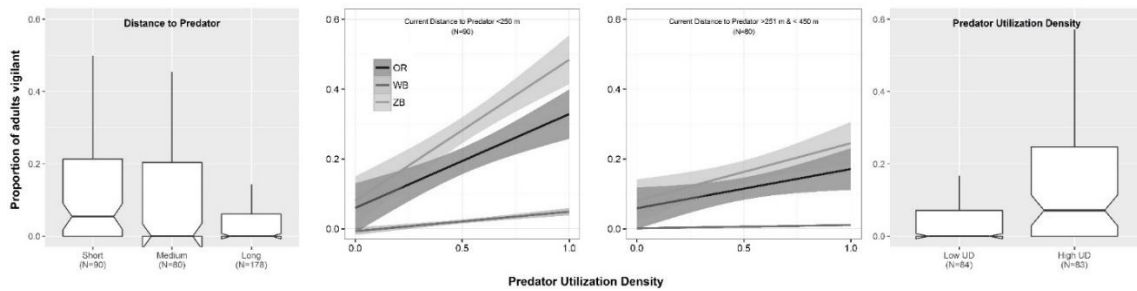


Figure 3.3 Interaction in the effects of short term and long term risk on prey behavior. The vigilance of prey was affected by short term risk (left panel, relating vigilance to the distance to the nearest predator at the time of observation), long term risk (right panel).

Literature Cited

- Basille, M., Fortin, D., Dussault, C., Bastille-rousseau, G., Ouellet, J.P., Courtois, R., Asille, M.A.B., Ortin, D.A.F., Ussault, C.H.D., Ousseu, G.U.B.A. & Ourtois, H.C. (2015) Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, **96**, 2622–2631.
- Blanchard, P. & Fritz, H. (2016) Induced or routine vigilance while foraging. *Oikos*, **116**, 1603–1608.
- Boonstra, R., Hik, D., Singleton, G.R. & Tinnikov, A. (1998) The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs*, **68**, 371–394.
- Brook, L.A., Johnson, C.N. & Ritchie, E.G. (2012) Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology*, **49**, 1278–1286.
- Brown, G.E., Ferrari, M.C.O., Elvidge, C.K., Ramnarine, I. & Chivers, D.P. (2013) Phenotypically plastic neophobia: a response to variable predation risk. *Proceedings of the Royal Society B*, **280**, 20122712.
- Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.
- Cherry, M.J., Morgan, K.E., Rutledge, B.T., Conner, L.M. & Warren, R.J. (2016) Can coyote predation risk induce reproduction suppression in white-tailed deer? *Ecosphere*, **7**, e01481.
- Christianson, D. & Creel, S. (2014) Ecosystem scale declines in elk recruitment and population growth with wolf colonization: A before-after-control-impact approach. *PLoS ONE*, **9**, e102330.
- Creel, S. & Christianson, D. (2008) Relationships between direct predation and risk effects. *Trends in Ecology and Evolution*, **23**, 194–201.
- Creel, S., Christianson, D., Liley, S. & Winnie, J.A. (2007) Predation risk affects reproductive physiology and demography of elk. *Science*, **315**, 960–960.
- Creel, S., Dröge, E.D., M'soka, J., Smit, D., Becker, M.S., Christianson, D.A. & Schuette, P.A. The relationship between direct predation and antipredator responses: a test with multiple predators and multiple prey (in review). *Ecology*.

- Creel, S., Schuette, P. & Christianson, D. (2014) Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, **25**, 773–784.
- Creel, S., Winnie, J.A., Christianson, D. & Liley, S. (2008) Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour*, **76**, 1139–1146.
- Cresswell, W. & Quinn, J.L. (2010) Attack frequency, attack success and choice of prey group size for two predators with contrasting hunting strategies. *Animal Behaviour*, **80**, 643–648.
- Cresswell, W. & Quinn, J.L. (2013) Contrasting risks from different predators change the overall nonlethal effects of predation risk. *Behavioral Ecology*, **24**, 871–876.
- Crowl, T.A. & Covich, A.P. (1990) Predator-induced life-history shifts in a freshwater snail. *Science*, **247**, 949–951.
- Dröge, E.D., Creel, S., Becker, M.S. & M'Soka, J.L.J. (2017) Spatial and temporal avoidance of risk within a large carnivore guild. *Ecology and Evolution*, **7**, 189–199.
- Heithaus, M.R., Wirsing, A.J., Burkholder, D., Thomson, J., Dill, L.M., Heithaus, R. & Wirsing, J. (2009) Towards the tactics a predictive of framework landscape for predator and risk effects: prey escape interaction features. *Journal of Animal Ecology*, **78**, 556–562.
- Hopcraft, J.G.C., Sinclair, A.R.E. & Packer, C. (2005) Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, **74**, 559–566.
- Joyce, B.J., Demers, E.E., Ferrari, M.C.O., Chivers, D.P. & Brown, G.E. (2016) Background predation risk and learned predator recognition in convict cichlids: Does risk allocation constrain learning? *Ethology*, **122**, 841–849.
- Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R. & Boyce, M.S. (2007) Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters*, **10**, 690–700.
- LaManna, J.A., Martin, T.E. & Letters, E. (2016) Costs of fear: Behavioural and life-history responses to risk and their demographic consequences vary across species. *Ecology Letters*, **19**, 403–413.
- Lank, D.B. & Ydenberg, R.C. (2003) Death and danger at migratory stopovers: Problems with “predation risk.” *Journal of avian biology*, **34**, 225–228.

- Lima, S.L. & Bednekoff, P.A. (1999) Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *The American Naturalist*, **153**, 649–659.
- Lind, J. & Cresswell, W. (2005) Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, **16**, 945–956.
- M'Soka, J.L.J., Creel, S., Becker, M.S., Droge, E.D., Jassiel, M., Creel, S., Becker, M.S. & Droge, E.D. (2016) Spotted hyaena survival and density in a lion depleted ecosystem: the effects of prey availability, humans and competition between large carnivores in African savannahs. *Biological Conservation*, **201**, 348–355.
- M'Soka, J.L.J., Creel, S., Becker, M.S. & Murdoch, J.D. Ecological and anthropogenic effects on the density of migratory and resident ungulates in a human-inhabited protected area (in press). *African Journal of Ecology*, 1–14.
- Moll, R.J., Killion, A.K., Montgomery, R.A., Tambling, C.J. & Hayward, M.W. (2016) Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores. *Ecology*, **97**, 1123–1134.
- Pangle, K.L., Peacor, S.D., Johannsson, O.E. & Johannsson, O.E. (2007) Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology*, **88**, 402–412.
- Peckarsky, B.L., Cowan, C.A., Penton, M.A., Cowan, C.A., Penton, M.A. & Anderson, C. (1993) Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology*, **74**, 1836–1846.
- Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., Madzikanda, H., Fritz, H., Macdonald, D.W., Loveridge, A.J. & Lyon, C.B. (2012) Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology*.
- Preisser, E.L., Orrock, J.L. & Schmitz, O.J. (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology*, **88**, 2744–2751.
- R Core Team. (2016) R: A language and environment for statistical computing.
- Relyea, R.A. (2001a) Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology*, **82**, 523–540.
- Relyea, R.A. (2001b) The Relationship between predation risk and antipredator responses in larval anurans. *Ecology*, **82**, 541–554.

- Ripple, W.J. & Beschta, R.L. (2003) Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management*, **184**, 299–313.
- Ripple, W.J., Larsen, E.J., Renkin, R.A. & Smith, D.W. (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation*, **102**, 227–234.
- Schmitz, O.J. (2008) Effects of predator hunting mode on grassland ecosystem function. *Science (New York, N.Y.)*, **319**, 952–4.
- Seaman, E.D. & Powell, R.A. (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, **77**, 2075–2085.
- Sheriff, M.J., Krebs, C.J. & Boonstra, R. (2009) The sensitive hare: Sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology*, **78**, 1249–1258.
- Silverman, B. (1986) *Density Estimation for Statistics and Data Analysis*. CRC Press, Harvard.
- Thaker, M., Vanak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M. & Slotow, R. (2011) Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, **92**, 398–407.
- Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. (2009) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, **90**, 23–30.
- Wand, M.P. & Jones, M.C. (1994) *Kernel Smoothing*. CRC Press, London.
- Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.
- Winnie, J., Creel, S., Winnie Jr, J.A. & Creel, S. (2007) Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Animal Behaviour*, **73**, 215–225.
- Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164–168.

## CHAPTER FOUR

RESPONSE OF WILDEBEEST (*CONNOCHAETES TAURINUS*) MOVEMENTS TO  
SPATIAL VARIATION IN LONG TERM RISKS FROM A  
COMPLETE PREDATOR GUILDContribution of Authors and Co-Authors

Manuscript in Chapter 4

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Abstract

Many studies have shown that behavioral responses to the risk posed by predators can carry costs for prey by reducing fecundity or survival, with consequent effects on population dynamics. Responses to risk include increased vigilance and reduced foraging, movement to safe habitats, increases or decreases in group size, and changes in patterns of movement. While we know that prey can detect and respond to both long term (LT) and short term (ST) variation in risk, field studies have only recently begun to consider how these responses might differ. Here, we hypothesize that prey movement patterns should respond differently to cues of LT and ST variation in risk. Specifically, cues of elevated LT risk might lead to decreased movement to improve the assessment of ST risk, while elevated ST risk might favor increased movement that reduces exposure to risks that are already assessed to be acute. We further hypothesize that decreases in movement are likely to be a general response to LT risk, while responses to ST risk are likely to vary in a manner that depends on the type of predator. Stalking predators rely on short, ambush hunts and typically pose little threat if detected prior to attack, so increased vigilance may be more effective than increased movement. In contrast, coursing predators that rely on open pursuit remain dangerous once detected, so moving away while still at a relatively safe distance is likely to reduce ST risk from a detected courser. Wildebeest movements responded to the local intensity of predator use (LT risk), after controlling for other seasonal, diurnal and bottom-up effects on movement. Step lengths decreased and turning angles increased, and both of these effects were considerable. These responses reveal that wildebeest are capable of assessing and responding to the

long term risk associated with an area. In contrast, immediate encounters with predators (ST risk) typically provoked fast, linear flight, particularly for encounters with coursers. The effect of long term risk was to cause wildebeest to move more slowly and less linearly, i.e. to slow down and turn around, as part of a suite of behavioral responses (also including increased vigilance that promote cautious assessment of ST risks when in locations with high levels of LT risk.

Keywords: Risk-effects, predator-prey relationship, landscape of fear, spatial risk, temporal risk, responses to risk

### Introduction

Many studies have shown that behavioral responses to the risk posed by predators can carry costs for prey by reducing fecundity or survival, with consequent effects on population dynamics (Werner *et al.* 1983; Peckarsky *et al.* 1993; Boonstra *et al.* 1998; Pangle *et al.* 2007; Sheriff, Krebs & Boonstra 2009; LaManna, Martin & Letters 2016). Responses to risk include increased vigilance and reduced foraging (Winnie *et al.* 2007; Périquet *et al.* 2012; Broekhuis *et al.* 2013), movement to safe habitats (Creel *et al.* 2005; Valeix *et al.* 2009), increases or decreases in group size (Elgar 1989; Fitzgibbon 1990; Creel & Winnie 2005), and changes in patterns of movement (Basille *et al.* 2015). Risk varies on many scales that are likely to be pertinent to optimal responses by prey, and studies to date have documented responses to both short term (ST) and long term (LT) variation in risk. Ecological studies often test responses of prey to long term variation, by quantifying how some measure of risk varies across space (with data aggregated over

time) (Hebblewhite, Pletscher & Paquet 2002; Kauffman *et al.* 2007). In contrast, behavioral studies often examine responses of prey to ST variation, by recording the immediate presence of a predator (with data aggregated over space) (*e.g.*, Creel, Schuette & Christianson 2014). These alternative approaches have been termed the ‘risky places’ and the ‘risky times’ hypotheses (Creel *et al.* 2008) and much has been learned from each. Considerable evidence now shows that prey can detect and respond to both ST and LT variation in risk (Brown *et al.* 2014), but research has only begun to consider how antipredator behavior might differ in response to ST and LT risks (Dröge *et al.*, accepted).

Here, we hypothesize that prey movement patterns, in particular, should respond differently to LT risk and ST risk. For example, in response to cues of elevated LT risk (*e.g.*, cues or memories that predators often use an area), selection might favor slower movements that allow more careful assessment of ST risk during foraging movements. In response to elevated ST risk (*e.g.*, direct encounter with a predator), selection might favor fast movements that reduce exposure to risks that are already assessed to be acute (at the extreme, full-speed flight once attacked). We further hypothesize that slower movement, to allow more careful assessment in response to LT risk, is likely to be a general response, but that the optimal response to ST risk is likely to vary in a manner that depends on the behavioral details of predator-prey interaction. For example, stalking predators that rely on short, ambush hunts are less successful if they are detected prior to attack (Fitzgibbon 1989), so increased vigilance may be more effective than altered movement in response to ST risk from a detected stalker. In contrast, coursing predators

that rely on open pursuit remain dangerous once detected, so moving away while still at a relatively safe distance is likely to reduce ST risk from a detected courser.

To date, experimental studies of the effect of risk on movement patterns have primarily examined responses to simulations of ST risk, including caged predators (Skelly *et al.* 2016), predators rendered incapable of killing prey (Schmitz 2012), and olfactory cues of predation events (the combined scents of predators and crushed prey: Sih & McCarthy (2002)). These experiments have yielded variable results. For example, snails responded to predatory crayfish by retreat to safe locations and reduced movement (Sih & McCarthy 2002), but mayflies respond to predatory caddisflies with rapid movement by drifting (Peckarsky *et al.* 1993). While these effects on the speed of movement are in opposite directions, the inference in both studies was that prey responded to immediate risk in a manner that reduced the likelihood of being attacked. McCarthy & Fisher (2000) compared the responses of snail prey to cues of LT risk and ST risk from crayfish, and found that LT risk (non-foraging crayfish scent) provoked increased movement to the surface, while ST risk (injured prey scent) provoked decreased movement and burial in the substrate.

Studies of ungulates facing predation risk from large carnivores (the focus of this study) have also found variable effects of ST risk on movement. Basille *et al.* (2015) found that woodland caribou moved faster when they were within 2.5 km of wolves (a coursing predator), and Proffitt *et al.* (2009) found that elk moved more quickly when they were within 5 km of wolves in a very open study area. In contrast, Creel *et al.* (2005) found that elk in a mosaic of forest and meadows tended to move more slowly on

days that wolves were within the same local drainage (for drainages with a mean radius of 4.9 km), though this effect was much weaker than simultaneous effects on habitat selection. Latombe *et al.* (2014) used a step selection function incorporating step lengths and turning angles to examine the response of moose and caribou movements to wolves, and found very similar results: the recent passage of wolves within 5 km had strong effects on habitat selection, but effects on the speed of movement varied between species and seasons in both strength and sign. Martin & Owen-Smith (2016) found that zebra and wildebeest both increased their rate of movement in the 2 hours after a probable encounter with lions, and that zebra moved more quickly over the subsequent 24 hours. Courbin *et al.* (2015) found that zebras moved more than twice as rapidly in the 24 hours after a probable encounter with lions, sometimes due to immediate flight over several kilometers, and sometimes due to ‘delayed flight’. In general, it seems clear that an increase in speed (due to flight) is common if prey is directly hunted, but the effect of elevated ST risk that does not involve a direct attack is not clear.

Very little is known about the response of ungulate movements to variation in LT risk. Fortin *et al.* (2005) used a step selection function to show that habitat selection by elk was affected by LT risk (the local intensity of use by wolves), but did not directly discuss the effect of LT risk on speed or turning angles. Frair *et al.* (2005) found that elk were more likely to make rapid, large movements (‘relocating’) in habitat types that had been more heavily used by wolves during a study conducted 15 years earlier. The inferences about risk from this study design are limited because habitat type typically has effects on movement that are independent of its use by predators, but to our knowledge,

this is the most direct test to date for an effect of natural variation in LT risk on the speed or linearity of ungulate movements. While we focus on a relationship between LT risk and movement patterns, variation in LT risk (or the ‘landscape of fear’: (Laundré, Hernández & Altendorf 2001) is known to affect many other aspects of ungulate behavior, ecology, physiology and demography (Creel *et al.* 2007; Valeix *et al.* 2009; Thaker *et al.* 2011; Périquet *et al.* 2012; Kuijper *et al.* 2013).

In this study, we used data from a 4-year field study to test how spatial variation in LT risk influenced the movement patterns of GPS-collared adult female wildebeest (*Connochaetes taurinus*) in Liuwa Plain National Park (LPNP), Zambia. We also tested how wildebeest movements responded to acute, ST risk during direct encounters with predators. LPNP is well suited for such a study because our 1200 km<sup>2</sup> study site is an unusually homogeneous, open, flat grassland with very little variation in vegetation structure or topography. The homogeneity of the area offers no structural refuges for prey, and forage for grazing wildebeest is relatively evenly distributed across the landscape. The predator guild consists of both cursorial (African wild dog *Lycaon pictus*, and spotted hyena *Crocuta crocuta*) and stalking (lion *Panthera leo*, and cheetah *Acinonyx jubatus*) predators, allowing a strong test for differences in response LT and ST risk from predators that hunt in different ways. We tested for effects of risk on both the speed and linearity of movement, controlling for other factors likely to affect movement, including the time of day, day of year, local forage quality and quantity, proximity to water, reproductive status and ‘inertia’ between consecutive movements autocorrelation).

## Methods

### Study Area and Populations

Our data were gathered in a 1200 km<sup>2</sup> study area in the southern part of the 3660 km<sup>2</sup> LPNP in Zambia. The vegetation in the study area is dominated by relatively homogeneous short and intermediate grasslands with occasional tree islands. The ungulate community is dominated by migratory wildebeest (*Connochaetes taurinus*) with local densities ranging from 6.2 – 60.8 individuals/km<sup>2</sup> and smaller populations of migratory zebra (1.8 – 8.1 individuals/km<sup>2</sup>) and non-migratory oribi (1.1— 14.5 individuals/km<sup>2</sup>) (M’Soka *et al.* in press). These densities were estimated from distance sampling (which allowed correction for each species’ probability of detection) on a systematic grid of transects spaced at 4 km intervals, surveyed several times in each year of the study (M’Soka *et al.* in press).

### Wildebeest Movement Data from GPS Collars

From 2010-06-24 to 2014-10-29, GPS collars from three manufacturers were fitted to 19 adult female wildebeest. Twelve of the collars reported locational errors (seven did not). In preliminary inspection of the data, five collars had large mean locational uncertainty (1,113m – 1,250m) and all five of these collars also had obviously erroneous locations. (i.e. multiple locations >1 km apart at near identical times) so they were removed from the dataset. Seven collars had an average locational uncertainty of 15.4m or less, and none of these seven collars had any obviously erroneous locations. The remaining 7 collars did not provide data on locational uncertainty, but none of these

showed biologically implausible movements, and they were retained in the dataset. Thus the final dataset included the movements of 14 adult female wildebeests, described by 10096 locations at 4 hour intervals between October 26, 2010 and October 29, 2014.

Collared wildebeest were directly observed about once a month, and more frequently at the time of calving. These observations were used to assess reproductive status and parturition date. At each sighting of a collared wildebeest cow a detailed record of herd composition was made, and special attention was paid to each collared wildebeest cow to determine if she had a calf. Especially during the first month after parturition, calves are typically found within meters of their mothers with an obvious association.

### Steps and Angles

We calculated the speed of movement (in km/h) between consecutive locations by dividing the distance between consecutive points (a *step*: Turchin 1998) by the time difference between those points. For each step, we associated this speed with the location of the starting point of the step. As shown in Figure 1, we determined two measures of the change in direction between consecutive steps. The *deflection angle* ( $\beta$ ) for a location was the difference between the bearings of the steps approaching and leaving that point. The *displacement angle* ( $\alpha$ ) for the location at time  $t$  was the angle between the bearing of the step leaving that point (from  $t$  to  $t+1$ ) and the bearing between  $t$  and  $t+2$ . Deflection angle is not affected by step length, but displacement angle is. Changes in direction to the left or right were considered equivalent, so that all angles fell between 0 and 180 degrees.

The speed and linearity of animal movements determined from GPS collars often show strong temporal autocorrelation, so to avoid pseudo-replication our linear models of effects on speed and angles of movement included a first order autoregression term. In Figure 4.1, the deflection angle  $\beta_1$  is the autoregressive predictor of  $\beta_2$  and the speed in Step 1 is the autoregressive predictor of speed in Step 2.

### Predator Data and Populations

The study area was occupied by 4 hyena clans, totaling about 150 animals (M'Soka *et al.* 2016), 6 lions forming 1 cohesive pride, two wild dog packs with a total of 22 individuals and 17 known cheetahs. Leopards are not present in LPNP. Wildebeest constituted  $\geq 90\%$  of kills by hyenas and lions, 59% of kills by wild dogs and 30% of kills by cheetahs (for which oribi were the most common prey) (Dröge *et al.* 2017). A detailed description of predator location data used in this study can be found in (Dröge *et al.* 2017). To summarize briefly, we obtained representative data on the use of space within the 1200 km<sup>2</sup> intensive study area by each of the large carnivores, using a combination of GPS and VHF radiocollars. We obtained 1713 locations for wild dogs, 4725 locations for hyenas, 2,000 locations for cheetahs and 11,018 locations for lions. At least one member of each group of each species was radio-collared, except for one hyena clan that split off from a collared clan during the study but remained within the same home range. All immobilization procedures to fit animals with collars were conducted with permission of the Department of National Parks and Wildlife (DNPW, formerly ZAWA), following animal welfare standards and protocols required by the Zambia Department of Veterinary and Livestock Services and the DNPW.

For each of the four species, these locations were used to fit a kernel utilization distribution for each species to compare space use (as described below). The location data for the four species come from overlapping periods from 2010 to 2015, but the interval sampled was not identical for all species. However, data from GPS collars showed that the ranging patterns of lions and hyenas changed little year to year, and the relocations of wild dogs were intensive for the period during which they used the site, while relocations of cheetahs showed no evidence of territorial partitioning of the study area, suggesting that the sampled individuals provided representative data (Dröge *et al.* 2017).

#### Utilization Distributions Fit to Location Data to Quantify Long-term Spatial Variation in Risk

From the locations of the predators we calculated a utilization distribution (UD) for each species (Worton 1989; Seaman & Powell 1996) using the `adehabitatHR` package (Calenge 2006) in R (R Core Team 2016), with a grid cell size of 500 meters. This spatial scale was fine enough to provide a meaningful description of variation in space use, and the data for each species allowed us to fit UDs at this scale. To objectively select a reference bandwidth ( $h_{ref}$ ) we used the same method as we successfully used in Dröge *et al.* (2017), where we selected the 90<sup>th</sup> percentile of the frequency distribution of daily distances moved (95<sup>th</sup> for cheetahs, with sparser data) as the smoothing parameter. Because the home ranges of the two wild dog packs and the four hyena clans had little overlap, UD's were calculated separately for each group, then combined and rescaled to result in a total utilization of 1 for the combined UD. This process properly resolved areas

of low use between home ranges. For cheetahs and lions, individual ranges overlapped very substantially, so we calculated a single UD for each species.

It is possible that wildebeests respond primarily to predators on the basis of functional groups (e.g., stalkers vs. coursers) rather than species (Schmitz 2008; Thaker *et al.* 2011), though tests of this hypothesis have shown variable results (e.g. Creel *et al.* 2014; Moll *et al.* 2016; Dröge *et al.* 2017). To test spatial responses of prey to functional groups of predators we combined the UD's of the coursing predators, hyenas and wild dogs, and those of stalking predators, cheetahs and lions, and again rescaled them to a total utilization of 1. Finally, to calculate the utilization of the study area by all of the predators, we combined the UD's of all four species and again rescaled to a total utilization of 1.

#### Wildebeest Responses to Direct Encounters with Predators

Data on direct encounters between predators and prey were obtained during carnivore 'follows' which are more extensively described elsewhere (Dröge *et al.* 2017). In short, radio-collared predators were followed for complete hunting periods (from when they became active until they became inactive), typically for several consecutive hunting periods. During these follows, we recorded the species (and when possible the age and sex) of prey that were encountered, hunted and killed. Here, we analyzed encounters of each predator species with wildebeests, to quantify the wildebeests' reaction (flight or no flight) and, if the encounter resulted in a chase, its distance. Confidence intervals for the proportion of encounters that provoked flight were calculated using the score method (Newcombe 1998). Chase distance was log transformed prior to analysis, and a Tukey

pairwise comparison test was used to test differences between predator species, while a two-sample t-test was used to test for a mean difference in chase distance between predator functional groups.

### Covariates of Wildebeest Movement Patterns

As described below (see *Model Construction*), we used beta regression models to test whether the speed or linearity of wildebeest movements was correlated with LT risk (as described by carnivore utilization distributions). Because ungulate movements respond to variables other than risk, we included the following parameters (in addition to risk and an autocorrelation term) in our models to control for their influence when testing for responses to risk.

### Reproductive Status

A growing fetus or a calf at heel might restrict the distance a wildebeest moved. We classified reproductive status in three categories: ‘Not Affected’, ‘Pre Parturition’ and ‘Post Parturition’. For each female, the estimated date of parturition was determined as the midpoint between the last direct observation of the wildebeest without calf, and the first observation with a calf. We assigned “Pre Parturition” to the 30 days prior to parturition and ‘Post Parturition’ to the 30 days immediately after parturition, thus assuming that any effects on movement would be strongest at the end of gestation when the energetic cost of gestation is highest, or immediately after birth when calves are least capable (though quite precocial). The rest of the days of the year were assigned to ‘Not Affected’.

### Distance to Water

As wildebeest need regular access to water, the distance from each wildebeest location to the nearest potential water source was calculated. The study area is flat with shallow depressions and is heavily inundated in the wet season, creating hundreds of pans (small ponds with no drainage). During field work the GPS coordinates of pans with water were always recorded. These were cross-referenced with images from Google Earth, and unobserved pans were added by inspecting the study area with Google Earth at high resolution. Some pans retain water year round, so water in Liuwa is never far in comparison to many ecosystems, but the distance to the nearest pan with water increases in the dry season as some pans dry out. Our analysis treats distance to water as a static variable (distance to the nearest location known to form a pan), because the data were not adequate to state which pans held water on a given date.

### Diet Quality

For grazing ungulates, dormant, senescent vegetation provided the least nutritional value while actively photosynthesizing tissue usually provides nutrients above maintenance levels (McNaughton 1979; Wilmshurst, Fryxell & Hudson 1995; Murray & Illius 2000; Shrader, Owen-Smith & Ogutu 2006). Annual photosynthetic cycles are conspicuous from leaf to landscape levels, and the influence of these cycles on diet quality can be measured by fecal chlorophyll concentration (Christianson & Creel 2009, 2014). We determined seasonal variation in diet quality from the fecal chlorophyll concentration of 180 fecal samples collected throughout the year. Fresh fecal samples were collected after observing a herd, collecting fresh samples (30 ml each) from

individual scats. These samples were frozen in liquid nitrogen until transportation (frozen) to the laboratory. Methods of assay have been described previously (Christianson & Creel 2009) but briefly, we extracted photosynthetic pigments by boiling a known mass of dry feces (~0.2 g) in 10 ml ethanol, drying under air in a water bath at 78.5 C and reconstituting in 1 ml methanol. Extracts were diluted 31-fold in methanol and scanned immediately on a 96-well microplate spectrophotometer. We determined optical density at 666 nm (peak absorption specific to chlorophylls, with correction for optical density at 750 nm to control for variation in turbidity) and expressed diet quality as optical density/0.2 g sample. To describe annual variation in diet quality, we identified the period for which fecal chlorophyll was above the median (Julian days 195-260) and below the median and defined these periods as ‘high’ and ‘low’ diet quality, respectively.

### Forage Quantity

The concentration of photosynthetic pigments has long been used to quantify the ‘greenness’ of forage for herbivores and thus their quality (McNaughton 1979). This approach has expanded to include landscape-scale indices of primary production derived from satellite-imagery (Forchhammer & Post 2004; Pettorelli *et al.* 2005; Christianson *et al.* 2013), which are affected by both the quality and quantity of green vegetation. As a measure of local landscape-scale availability of green forage, we obtained Enhanced Vegetation Index (EVI) values from the MODIS instrument on the Aqua and Terra satellites (Didan 2015). EVI improves upon the Normalized Difference Vegetation Index (NDVI) by using spectral bands that allow correction to remove soil-brightness induced variations, decoupling atmospheric influences from the vegetation signal and avoiding

saturation of the signal at high productivity levels. Each of the two satellites records an image including the study site each day, but the MOD13DQ1 and MYD13Q1 data product provides the best image taken within a 16-day window, with a pixel size of 250m. The 16-day image compositing period of the two satellites are offset by 8 days, providing a unique EVI measurement every 8 days on average, or within 4 days of each wildebeest location. In practice, with cloud- or smoke cover the average time-gap between the date of a wildebeest location, and an EVI value for the pixel including the wildebeest location was 4.8 days, with a standard deviation of 31.0 days and ranging from -112 days (before the wildebeest location was taken) to 124 days (after the wildebeest location was taken) indicating long periods with extensive cloud cover during the rainy season that prevented satellite measurement of EVI.

Although the mean time gap between wildebeest locations and EVI measurements was  $<5$  days, we used a preliminary analysis to test if inferences were affected by the inclusion of points with longer time gaps. We fit a full model of the speed of movement (see *Model Construction* below) to all of the data, and then fit the same model to a data set restricted to locations with EVI values within 10 days. The estimated effect of EVI (and associated  $P$  value) differed little between these models, and the estimated effect of risk on movements (the effect of primary interest) also changed little. The only inference about movement that was altered by restriction of the data was that an effect of proximity to water was detected with the full data set but not with the restricted data. On the basis of this preliminary test, we present results using the full data set.

### Day of Year

As the wildebeest in the Greater Liuwa ecosystem are migratory, the speed and patterns of movement are expected to vary throughout the year. Because migration in Liuwa is partly driven by inundation of the low lying areas, seasonal changes in movement may not be fully described by seasonal changes in forage quantity and quality. We accounted for this effect by including distance to water, and to control any seasonal variation not captured by reproductive status and these environmental variables, we also included the Julian date of each location. We incorporated the Julian date in our model by fitting two parameters that account for the cyclic nature of this variable. These parameters were  $\sin(2\pi * \text{day of year} / 365)$  and  $\cosine(2\pi * \text{day of year} / 365)$ .

### Time of Day

As for most African ungulates, wildebeest activity in LPNP varies throughout the day with obvious peaks around dusk and dawn. We calculated the average speed of movement per hour (Fig. 2), and categorized the 24-hour day into two classes, namely 'High Activity Periods' (from 02:30 to 07:29 and 16:30 to 18:29) and 'Low Activity Periods' (18:30 to 02:29 and 07:30 to 16:29).

### Statistical Models of Effects on Movement

For each dependent variable (speed and turning angle), we tested whether movement responded to LT risk using a linear model that accounted for autocorrelation between consecutive movements and controlled for other potential effects on movement (proximity to water, diet quality and forage quantity, day of year, time of day, and

reproductive status). The details of model form differed for each dependent variable (see *Model form* just below).

### Model Form and Data Transformation

Turning angles were constrained to a bounded interval between 0 and 180, so they were rescaled to the interval [0,1] and modeled as beta distributed using the *betareg* package (Ferrari & Cribari-Neto 2004, Cribari-Neto & Zeileis 2010).

The frequency distribution of speed was leptokurtic and positively skewed, and all common GLMs had clear problems with goodness of fit, so we applied a Box-Cox transformation to speed. With the *MASS* package (Venables & Ripley 2002) in R (R Core Team 2016), the power-term for the Box-Cox transformation,  $\lambda$ , was determined to be 0.222, and with this transformation, quartile-quartile and residual-predicted plots for an ordinary linear model showed no evidence of non-normality or heteroscedasticity.

All models included a lag one autocorrelation term to avoid pseudoreplication. We considered whether movements varied between individuals in a manner that would suggest inclusion of a random effect of individual identity, but boxplots showed there was much more variation within wildebeest than between wildebeest (Fig. 3), so this term was not included. To compare magnitudes of coefficients from the models, we centered and scaled all continuous variables (subtracting the mean and dividing by the standard deviation, so that units for the coefficients are standard deviations).

### Alternative Measures of Long Term Risk

To assess which measure of LT risk best explained effects on wildebeest movement we began with a full model in which LT risk was described by the UD for all predators, in addition to all other variables described above. We then used AIC scores to compare this model with otherwise identical models in which LT risk was replaced by the UD of each species of predator or by UD of each type of predator (coursers or stalkers). We also tested a model containing all variables but not LT risk. The set thus included eight models (risk from all predators, stalkers, coursers, lions, hyenas, cheetahs, wild dogs and no risk).

Several of the variables in the model are seasonal and therefore correlated. When a pair of predictors is correlated, one of them is often discarded because each affects the estimated coefficient for the other. Here, however, the primary purpose of including these variables is diligence in accounting for non-predator effects when testing for an effect of predation risk on movements, so we retained them. We checked if exclusion of correlated variables appreciably altered the magnitudes of estimated coefficients or test statistics for other effects, particularly predation risk. They did not, so we left all variables potentially influencing wildebeest movement, in the model.

## Results

### Speed of Movement

After accounting for autocorrelation between consecutive steps, the speed of wildebeest movement was detectably affected by all covariates in the model except for

reproductive status, diet quality and forage quantity (Table 4.1). Wildebeest moved more slowly in areas of high LT risk (Fig. 4.4), and the estimated effect of risk was larger than all other effects in the model other than diurnal variation, which (unlike the other predictors) was categorized directly on the basis of movements (Fig. 2). With other effects held constant, the predicted speed of wildebeest in the areas of lowest risk was 0.14 km/h, while in areas of highest risk it was 0.06 km/h: wildebeest moved 2.3 times more slowly in areas with high LT risk.

Using AIC scores to identify the best measure of LT risk within the full model, we found that the UD of all predators combined was best supported by the data, with  $\Delta\text{AIC} = 3.43$  relative to the second-best model, which described risk as the UD of hyenas, the most abundant predator in this ecosystem. The AIC score for coursers (hyenas and wild dogs) was third-best supported, with  $\Delta\text{AIC} = 6.72$ , and other alternatives had considerably weaker support. A model excluding LT risk had an AIC score 377 units worse than an otherwise identical model including LT risk (from all predators combined). Overall, these results strongly suggest that wildebeest are sensitive to an integrated measure of LT risk from all of the predators in this ecosystem. Given that wildebeest are the most common (for hyenas, lions, and wild dogs) or second most common (for cheetahs) prey for all of these carnivores in LPNP, this result is not surprising. Thus, for all further inferences (including analysis of turning angles), the model with LT risk described by the UD of all predators combined was used, but as Figure 4.4 shows, the estimated effect of risk on speed of movement was similar for all measures of LT risk,

and the inference that wildebeest move more cautiously in areas of high risk was supported by all measures of risk.

### Deflection and Displacement Angles

The change in bearing between consecutive steps of wildebeest movement paths increased substantially in areas of high LT risk (Table 4.3, Figure 4.5). As with speed of movement, displacement angles were affected by the time of day, day of year and forage quantity, but there was no evidence for a relationship to forage quality, distance to water and reproductive status (Table 4.3).

While factors other than risk had smaller effects, increased LT risk was associated with a substantial increase in deflection bearing changes ( $b = 0.185$ ,  $SE = 0.041$ ,  $z = 4.46$ ,  $P < 0.0001$ ). Back-transforming this effect to the original scale of 0 to 180 degrees, deflection angles in areas with the highest LT risk were 33.3° larger than in areas with the lowest LT risk, and turns greater than 90° were much more common (Fig. 4.5). Inferences about the effect of risk (and other variables) on changes in bearing were not affected by the choice of deflection angle or displacement angle as the dependent variable.

### Combined Effects of Long Term Risk on Speed and Deflection

Estimated average step length (over 4 hours) in areas with no risk was predicted to be 563 meters, while in areas with the highest LT risk step length was predicted to be 241 meters (holding all other effects constant). Estimated average deflection angles were predicted to be 88° for areas with no LT risk and 121° in areas with the highest LT risk (again holding other effects constant). We used these predicted speeds and deflections to

illustrate movement over 20 time steps with a random pattern of deflection to the left or right, and show two representative paths across grid cells of one km<sup>2</sup> in Figure 4.6. The combined effect of a reduction in speed and an increase in deflection is movement that allows much more prolonged assessment of each new cell that a wildebeest enters when in an area of high LT risk.

#### Responses to Direct Encounters with Predators

Behavioral observations of wildebeest encountering predators during radio-collared carnivore follows showed that coursing predators were 7 times more likely to cause a flight response (Fig. 4.7) than stalking predators (proportion = 0.22, 95% CI 0.19-0.26,  $N = 487$  versus 0.03, CI 0.02-0.06,  $N = 270$  respectively). These patterns were consistent for both coursers, with flight in response to 0.219 (95% CI 0.18-0.27,  $N = 343$ ) of encounters with African wild dog and 0.236 (95% CI 0.17-0.32,  $N = 144$ ) of encounters with hyenas, and for both stalkers, with flight in response to 0.0222 (95% CI 0.0012-0.13,  $N = 45$ ) of encounters with lions and 0.036 (95% CI 0.017-0.072,  $N = 225$ ) of encounters with cheetahs (Fig. 4.7).

Not surprisingly, the distance that wildebeest were pursued was greater for coursers than for stalkers ( $t = 3.37$ ,  $df = 82$ ,  $P = 0.0012$ ). Because relatively few chase distances could be recorded accurately, small sample sizes lead to wide confidence intervals for individual species, but the difference in response to stalkers and coursers was clear (Figure 4.8 and Table 4.4).

## Discussion

The effect of immediate, short term exposure to predators is to increase the speed of movement. This increase in movement is relatively minor for responses to stalkers, because only a small fraction of these encounters provoke flight (wildebeest respond primarily with increased vigilance: Creel *et al.* in review) with flight distance averaging only slightly over 100 meters. On the other hand, encounters with coursers more often provoke flight, and flight distances are considerably greater than the linear distance expected for a typical 4-hour step. Because encounters are more likely in areas of high use by carnivores, it is notable that wildebeests decreased their mean rate of movement in areas of high LT risk, even though one would expect that these wildebeest were more likely to engage in short term flight responses. That is, the reduction in speed in response to LT risk was apparent despite being offset by increased short-term movements in response to immediate risk, particularly from coursers.

Overall there is considerable evidence that movements of wildebeests responded to the intensity of use of their location by predators, after controlling for diurnal and seasonally varying bottom-up effects on movement. Step lengths decreased and turning angles increased. The only parameter with comparable estimated effects on movement is the time of day, a result that is expected because most African ungulates, including wildebeests, show strong diurnal differences in activity levels, and we categorized time periods directly on the basis of movement data (see figure 4.2). These results indicate that wildebeest are capable of assessing the LT risk associated with an area, perhaps by the immediate use of smell or perhaps by memory of past patterns of predator detection using

sight, hearing and smell, all of which are acute for wildebeest. Because wildebeest are social, information might also be obtained from other wildebeest using sight, hearing or smell. Even though immediate encounters with predators typically provoked fast, linear flight, the effect of LT risk was to cause wildebeest to move more slowly and less linearly, i.e. to slow down and turn more. The combined effect of slowing down and turning more is to allow wildebeest more time to assess immediate ST risk when moving within an area of high LT risk (Fig. 8). Even without improved assessment of ST risk, moving more slowly could reduce the probability of encountering a predator (Gerritsen & Strickler 1977) or being detected (Cleveland *et al.* 2012; Little *et al.* 2016), particularly if animals confine themselves to structural refuges. Because wildebeest in this study were moving almost entirely in open grassland, it is unlikely that moving less was associated with 'hiding', but reduced movement would nonetheless be expected to reduce encounter rates with randomly located predators (Viswanathan *et al.* 1999). There is a trade-off, however, because predators were not randomly located – by slowing down and turning more in areas of high LT risk, wildebeest spend more time in these dangerous areas (Fig. 8). This response should also make their location more predictable on a time scale of several days, and this predictability could be exploited by predators to increase encounter rates. These patterns suggest that in a homogeneous, open environment without refuges, behavior that promotes wildebeests' ability to assess and detect ST risk is an important aspect of response to cues of high LT risk. Other studies in this ecosystem (Creel *et al.* in review, Dröge *et al.* accepted) have shown that vigilance increased when predators were nearby, and that this response was stronger in locations with high LT risk (and

concomitant reduction in grazing); This result aligns well with the inference that reduced speed and linearity of movement are part of a suite of responses to more cautiously assess ST risk in locations with high LT risk. More broadly, this inference aligns with the earlier suggestions that prey sometimes tolerate (or even select) predator-rich areas if there are advantages to doing so (for example, better opportunities to hide or escape) (Wirsing, Cameron & Heithaus 2010).

Prior studies have examined how ungulate movements respond to direct encounters with predators (Fischhoff *et al.* 2007), to ‘probable encounters’ inferred from GPS collars on both predators and prey (Creel, Winnie & Christianson 2013; Courbin *et al.* 2015; Martin & Owen-smith 2016), or to the immediate presence of predators within a distance of 2-5 kilometers (Creel *et al.* 2005; Proffitt *et al.* 2009; Latombe, Fortin & Parrott 2014). In general, it seems clear that an increase in speed (flight) is common if prey animals are encountered at close range or hunted, but the effect of elevated ST risk that does not necessarily involve close, direct interaction is not well understood (*e.g.*, compare (Creel *et al.* 2005; Proffitt *et al.* 2009; Latombe *et al.* 2014). Because flight often causes prey to speed up after close encounters, one could reasonably hypothesize that altered movement in areas of high LT risk is not a direct response to LT risk itself, but simply a by-product of more frequent ST responses to direct encounters (the ‘summation of ST responses’ hypothesis). Our data do not support this hypothesis. As in other studies, wildebeest often responded to being hunted, particularly by coursers, with high-speed flight over long distances, greatly exceeding the mean step length for a 4-hour period in just a few minutes. Because such responses are inevitably more frequent in

areas that are heavily used by carnivores, the ‘summation ST responses’ hypothesis would predict an increase in mean speed in areas of high LT risk, rather than the decrease that we observed. Thus the effect of LT risk on movement patterns occurs despite reactive movements induced by ST risk.

Several studies have examined how the movements of elk and white tailed deer change during human hunting seasons lasting several days to several weeks (Root *et al.* 1988; Cleveland *et al.* 2012; Rhoads *et al.* 2013; Little *et al.* 2016). The risk in such studies shares some attributes of ST risk in natural systems (abrupt onset, limited duration), but also shares some attributes of LT risk (elevation of risk for days or weeks, rather than minutes or hours). While it is not clear if human hunters are perceived differently than other types of human disturbance. These studies have found considerable variation in responses, with increased movement in some cases, (Root *et al.* 1988; Peckarsky *et al.* 1993; Cleveland *et al.* 2012), no detectable effect in other cases (Neumann, Ericsson & Dettki 2009) and in still other cases increased movement in areas exposed to hunters, but not in refuges closed to hunting (Rhoads *et al.* 2013). The risk period in those studies was restricted to hunting season of several days to several weeks, with relatively widespread and intense risk and frequent disturbance within areas containing refuges and species known to hide from perceived threats. Such a study design may not allow prey to accurately assess spatial and temporal variation in risk patterns, when compared to the responses of prey to LT patterns of risk in intact ecosystems like LPNP. In human hunting studies (Root *et al.* 1988; Rhoads *et al.* 2013; Little *et al.* 2016), there is also an abrupt change in the intensity of risk in an area, with risk increasing over

relatively large areas for a period of intermediate length. Because these attributes are quite dissimilar to the patterns of variation in ST and LT risk typical of undisturbed predator-prey systems, it is difficult to relate inferences about effects of risk on movement from the two types of studies.

The spatial and temporal scale of exposure to risk, and the heterogeneity of risk within these spatial and temporal scales, all play roles in determining the optimal response of prey to risk (Lima & Bednekoff 1999). Proactive adjustments of behavior in response to LT risks depend on the ability of prey to assess this risk (and to pay any costs of assessment), and on their ability to assess and respond to superimposed ST risks. Temporally, the activity peaks of predators in LPNP are predictable, although risk is appreciable throughout much of the 24 h day. African wild dogs concentrate hunting in the crepuscular periods, cheetahs during the day and lions and hyenas during the crepuscular periods through the night (Dröge *et al.* 2017). Spatially, the intensity of use of various areas by predators in our study area was stable, especially for spotted hyenas (the most abundant predator), adding to the predictability of LT variation in risk over space and time. The relative structural homogeneity of our study area causes there to be little influence of vegetation structure on risk when compared to most ecosystems, (though it also eliminates the possibility for wildebeest to retreat to natural refuges). Collectively, these properties perhaps allow better assessment and response to variation in LT risk by wildebeest in LPNP than may prove to be typical, but we need more tests of the response of movements to natural variation in risk before general patterns can be identified.

The effect of risk on movement patterns was considerable for both speed and turning angles, in comparison to the effects of bottom-up variables expected to influence wildebeest movements. We found no evidence for effects due to distance to water or diet quality on speed or turning angles, while there was a relationship between forage quantity and turning angles and some evidence for a relationship between forage quantity and speed. Time of day and time of year also had considerable effects on movements.

While the data suggest that movements are sensitive to risk after accounting for bottom-up effects, some caveats should be noted. First, not all pans hold water year round, and pans dry up at different times of the year depending on their size. Some pans persist through the dry season in wet years but not in dry years. This variation is not captured by the way we measured distance to water (as the distance to the nearest known pan). Consequently, the weak relationship between wildebeest movements and water might be due to the widespread distribution of pans across the study area, but this result might also have arisen because we could not model temporal variation in pan persistence. Second, we used chlorophyll measurements from fecal samples to model forage quality as a factor that varied seasonally. This allowed us to account for seasonal variation in diet quality, but did not allow us to model spatial variation in diet quality. Third, forage quantity was approximated from EVI values, which were linked to wildebeest locations both spatially and temporally. While EVI is a good candidate to measure forage quantity, there is a chance that inundation, which can occur in LPNP to varying extents between December and May, influences EVI measures. Inundation might obscure the relationship between EVI and green biomass.

Finally, the use of an area by wildebeest and predators is correlated, *i.e.*, the UD of wildebeests is highest in the areas with highest predator UD. Thus, our results show that the areas with the highest predator UD have the lowest wildebeest speed and highest turning angles, these responses occur in the areas that are most heavily used by wildebeest in the long term, and it is likely that the relationships between predation risk, wildebeest density and wildebeest movements are all related. Aggregation is a common response to risk in ungulates, and the relationships of wildebeest movements and density to risk are probably not independent.

It is also possible that wildebeest movements are affected by anthropogenic variables not considered here, such as the distance to the park boundary or distance to settlements. We did not include these variables (even though they can affect wildebeest density: M'soka *et al.* in press), because we hypothesized that at the spatiotemporal scale of several hours and several hundred meters, the effects of factors that typically operate at large spatiotemporal scales are likely to be weak, relative to local variation in predation risk, food and water.

Overall we detected considerable pro-active movement responses of wildebeest in LPNP to LT risk after controlling for a range of bottom-up effects, but remain cautious about the causal relationships between risk, density and movements. There is widespread evidence that behavioral changes induced by risk, whether this risk is long term or short term, are often favored by natural selection by reducing the mortal impact of that risk, for many taxa. Lima & Bednekoff (1999) theorized long ago that optimal antipredator responses depend on both the immediate (short term) and background (long term) level of

predation risk. Because we detected behavioral responses to variation in LT risk, the logic of Lima & Bednekoff (1999) suggests that this variation should influence their reactive responses to short term variation in risk. While our data on movement were not sufficient to test this idea, Droge *et al.* (accepted) examined data on vigilance in this same system and found that prey (including wildebeest) reactively responded to acute ST risk more strongly in areas of high LT risk. These results have broad implications for studies that focus on ST risk without measuring or considering variation in LT risk (or vice versa). Studies examining the non-lethal effects of predators on their prey should consider both LT and ST risk, and carefully consider the spatial and temporal scales at which they examine both.

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Conflicts of Interest: None declared

Parameter	Effect on Speed	SE	Test Statistic	<i>P</i>
Intercept	-1.211	0.044	-27.58	<0.0001
LT risk (all predators)	-0.161	0.008	-19.65	<0.0001
Autocorrelation	0.132	0.007	18.52	<0.0001
Daily Activity: Low <sup>1</sup>	-0.483	0.017	-28.84	<0.0001
Distance to Water	0.017	0.007	2.33	0.02
Diet Quality: Low <sup>2</sup>	-0.010	0.043	-0.23	0.82
Forage Quantity (EVI)	-0.014	0.008	-1.72	0.09
POST parturition <sup>3</sup>	0.007	0.030	0.25	0.80
PRE parturition <sup>3</sup>	-0.020	0.058	-0.34	0.73
Day of Year (sin)	0.077	0.010	-7.80	<0.0001
Day of Year (cosine)	-0.025	0.008	-3.28	0.002

Table 4.1 Scaled effects on speed of movement by wildebeest. Here, LT risk was described by the utilization distribution for all predators. 1: reference level is high activity periods. 2: reference level is high diet quality periods. 3: reference level is 'not affected' by late gestation or a newborn calf.  $R^2 = 0.20$ . 4: not reported, because the quantitative effect of seasonal variation (that was not captured by the other covariates) was conditional on the date considered day 1, see methods for details.

Description of Risk	<i>df</i>	AIC
All predators	9	21,062.75
Hyena	9	21,066.18
Coursers	9	21,069.47
Lion	9	21,081.21
Stalkers	9	21,140.42
Wild Dog	9	21,189.46
Cheetah	9	21,201.53
No Risk	8	21,439.94

Table 4.2 A comparison of alternative measures of LT risk in the full model of effects on wildebeest movements, using AIC scores.

Parameter	Effect on angle	SE	Test statistic	<i>P</i>
(Intercept)	-0.707	0.068	-10.44	<0.0001
LT risk (all predators)	0.042	0.012	3.33	0.0008
Autocorrelation	-0.122	0.011	-11.48	<0.0001
Daily activity Low	-0.570	0.026	-22.20	<0.0001
Distance to water	-0.004	0.011	-0.36	0.72
Diet Quality: Low	-0.014	0.067	-0.21	0.83
Forage Quantity (EVI)	-0.030	0.013	-2.29	0.02
POST parturition	0.036	0.047	-0.77	0.44
PRE parturition	0.007	0.090	0.08	0.94
Day of Year (sin)	0.0526	0.01507	3.49	0.0005
Day of Year (cos)	0.0141	0.01268	1.11	0.27

Table 4.3 Scaled effects on displacement angles for wildebeest movements. 1: reference level is high activity periods. 2: reference level is high diet quality periods. 3: reference level is 'not affected' by late gestation or a newborn calf.  $R^2 = 0.07$ . 4: not reported, because the quantitative effect of seasonal variation (that was not captured by the other covariates) was conditional on the date considered day 1, see methods for details.

Species Compared	Log Difference in Distance	Lower CI	Upper CI	<i>P</i>
Hyena-Cheetah	0.68	-0.47	1.83	0.407
Lion-Cheetah	-0.64	-2.30	1.01	0.738
Wild Dog-Cheetah	1.59	0.31	2.88	0.009
Lion-Hyena	-1.33	-2.72	0.06	0.067
Wild Dog-Hyena	0.91	-0.01	1.83	0.053
Wild Dog-Lion	2.24	0.73	3.74	0.001

Table 4.4 Pair-wise differences in the distances (on a log scale) that wildebeest ran in direct encounters with each predator in Liuwa Plain National Park, Zambia, with 95% confidence intervals. Positive values indicate longer flight in response to the first predator in the dyad.

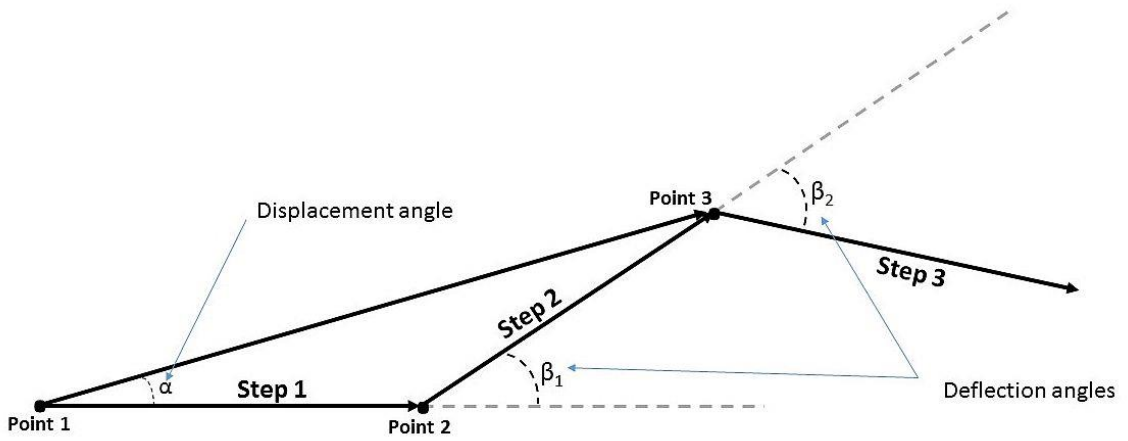


Figure 4.8 Schematic view of step length (speed), displacement angle ( $\alpha$ ) and deflection angle ( $\beta$ ) for wildebeest movement paths. Speed during Step 1 is associated with Point 1. Because they are affected by the change in bearing at Point 2, displacement angle  $\alpha$  and deflection angle  $\beta_1$  are both associated with Point 2.

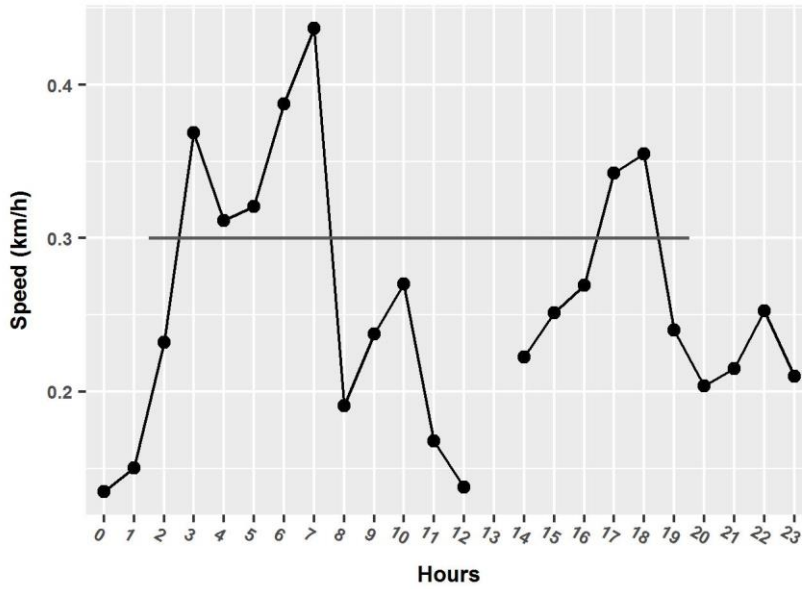


Figure 4.9 Average speed (km/h) of movement for periods centered on each hour of the day. The horizontal bar denotes threshold of 0.3 km/h defining time periods as High or Low Activity.

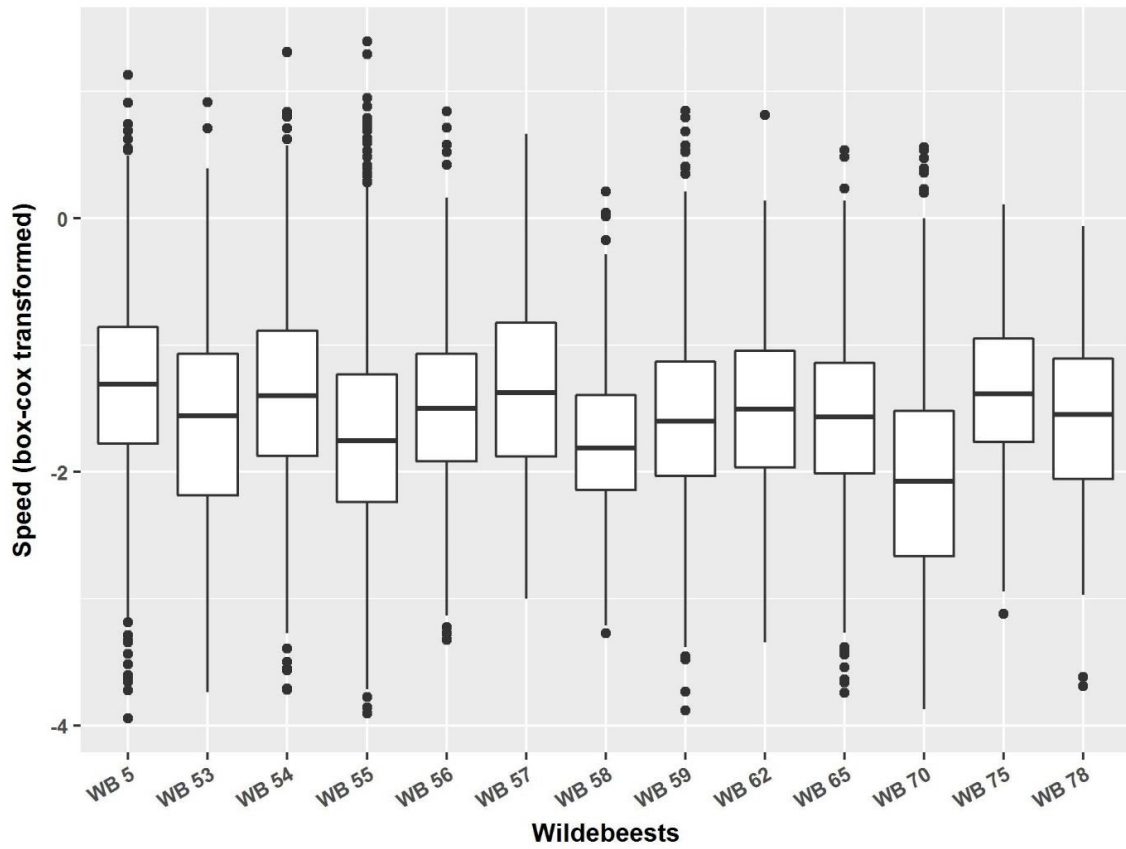


Figure 4.10 Variation within and between individual wildebeest in box-cox transformed speed of movement over 4 hour time steps (median, interquartile range, range, outliers).

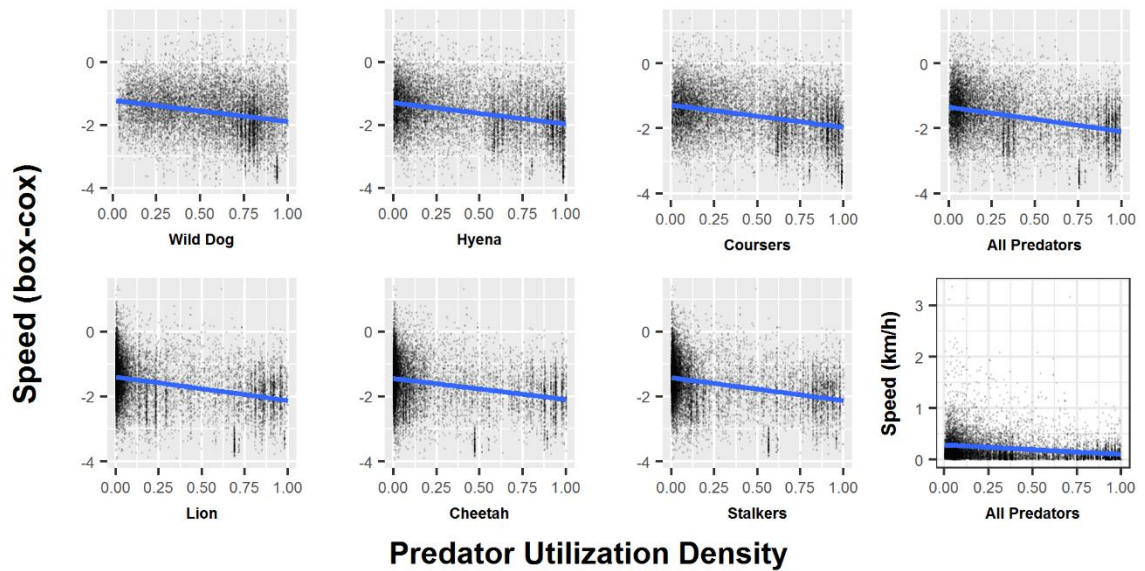


Figure 4.11 The effect of predation risk on speed of wildebeest movements for linear models containing different descriptions of LT risk (by predator species, predator type and for all predators combined). The lower right panel shows the backtransformed response of speed (km/h) to the LT risk from all predators, which was the best-supported model of risk (top right panel, and see Table 2).

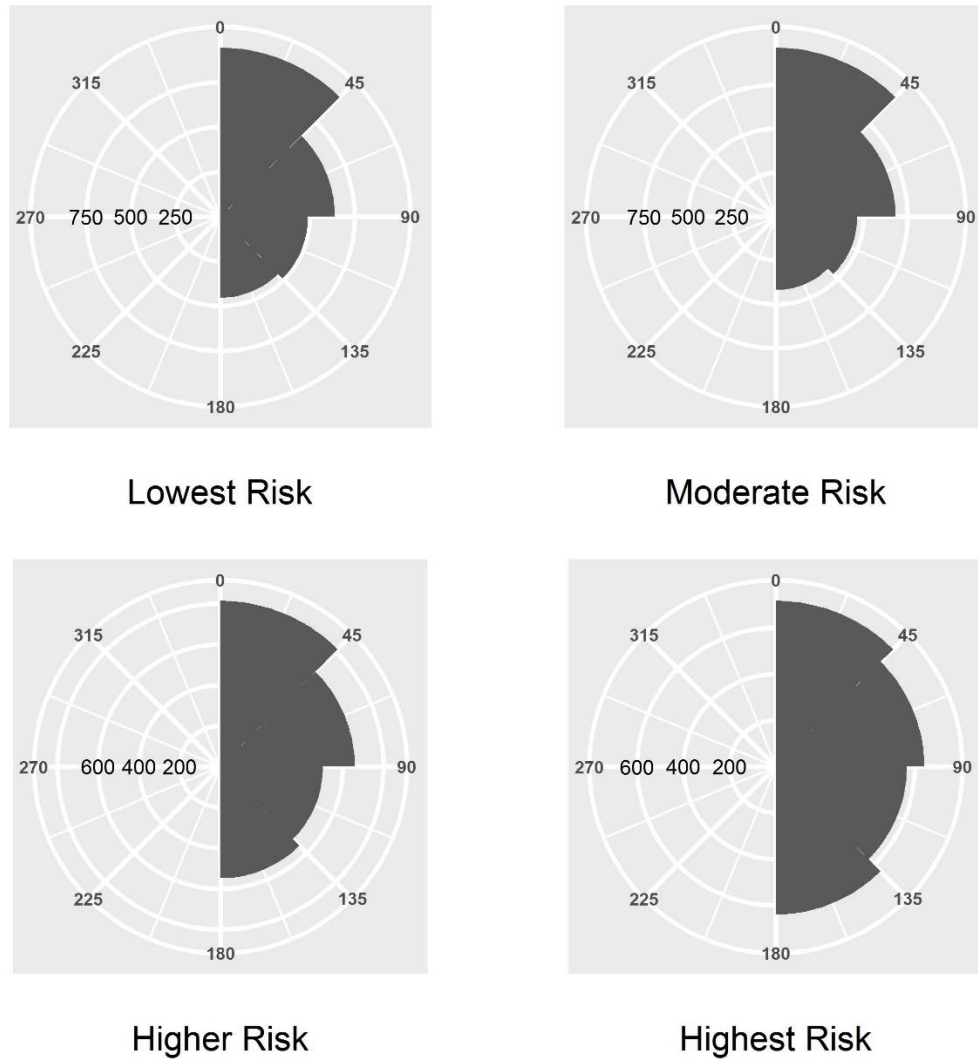


Figure 4.12 The frequency distributions of deflection angles for four categories of LT risk show that large deflections were more common under conditions of high risk. The four categories were defined by the quartiles of the LT risk distribution (as measured by the UD of all predators) and bearing categories reflect categories of turning angles.

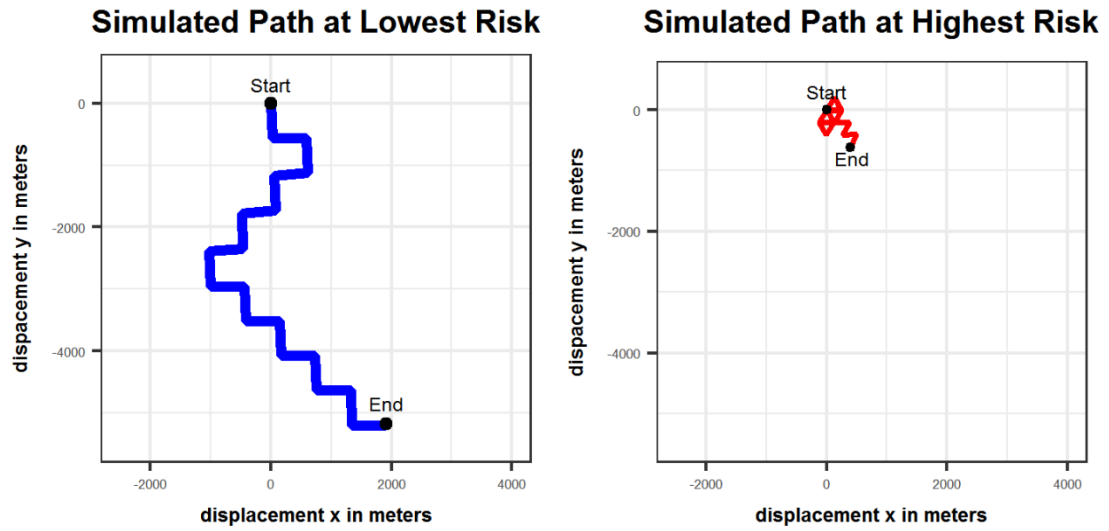


Figure 4.13 Simulation paths for 20 steps of 4 hours with predicted step lengths and deflection angles for areas with the lowest and highest LT risk. Grid cells are 1 km<sup>2</sup>.

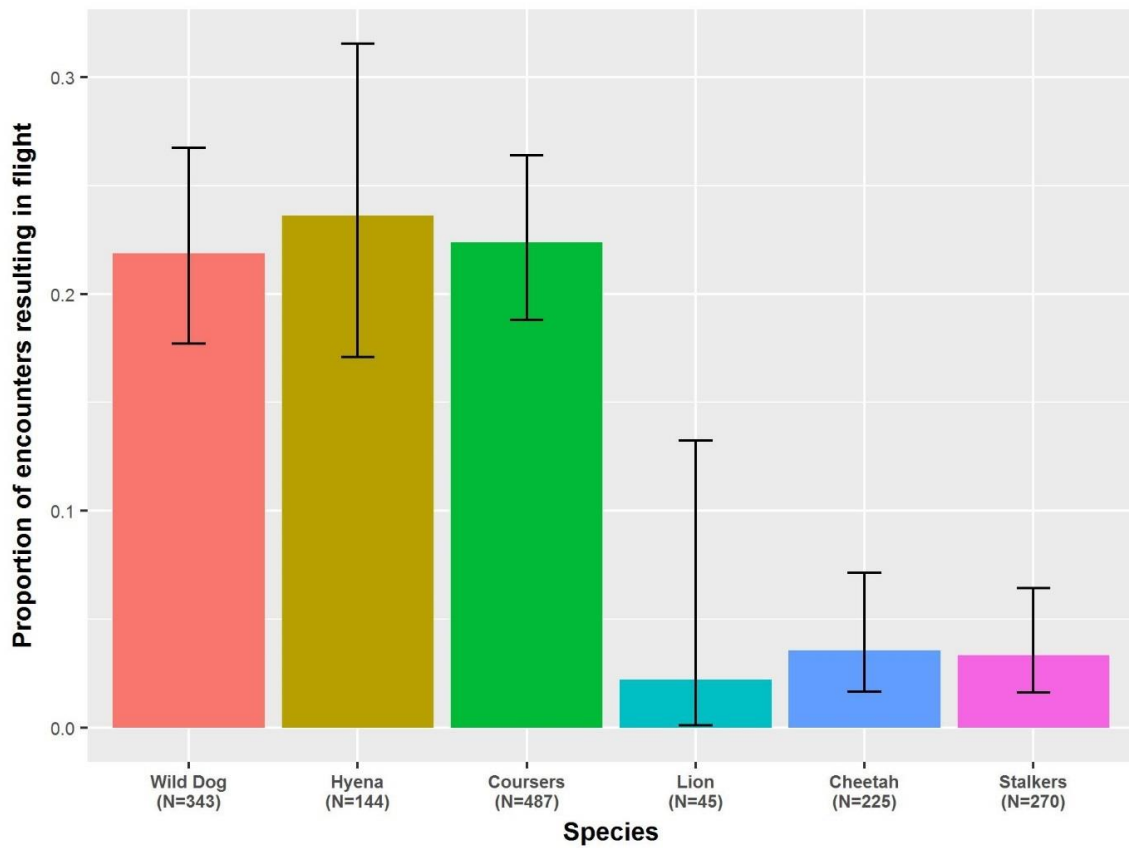


Figure 4.14 The proportion of encounters between predators and wildebeests that resulted in flight by the wildebeest. The whiskers represent the 95% binomial confidence interval.

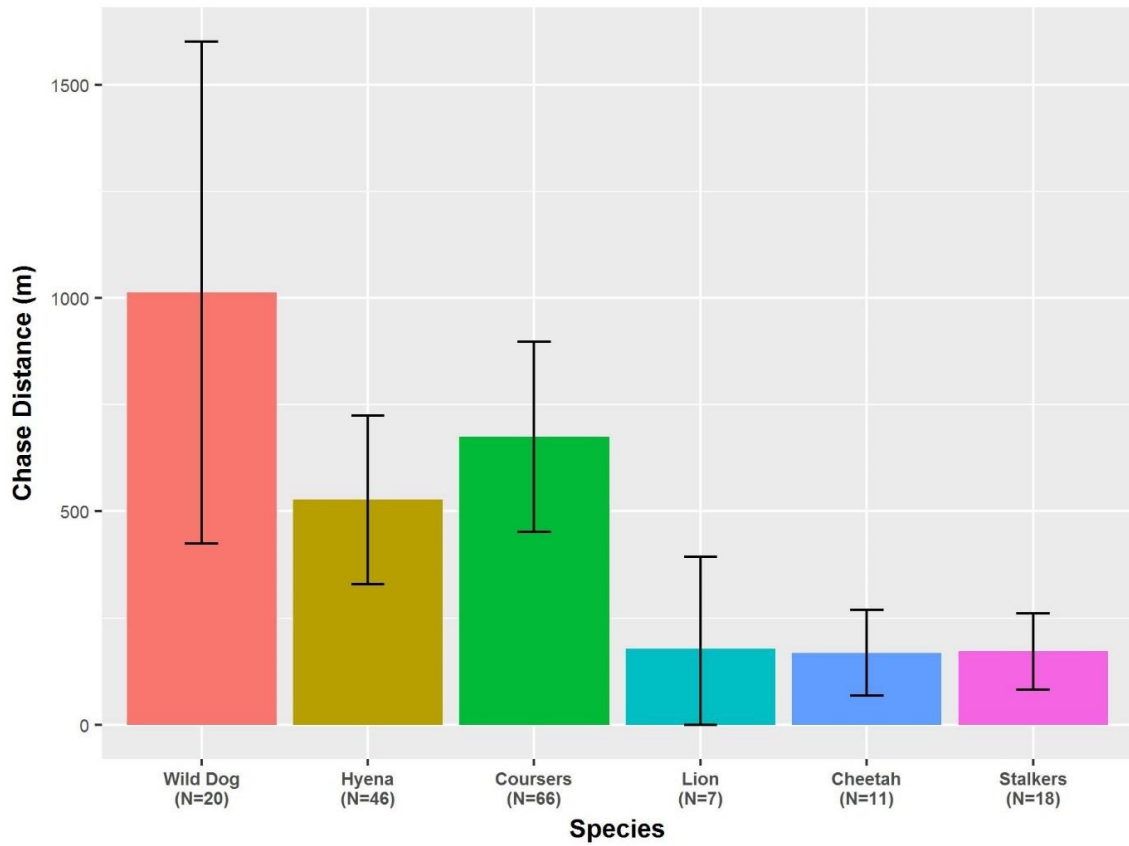


Figure 4.15 Average chase distances of wildebeests by the various predators and their 95% binomial confidence intervals.

Literature Cited

- Basille, M., Fortin, D., Dussault, C., Bastille-Rousseau, G., Ouellet, J.P. & Courtois, R. (2015) Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, **96**, 2622–2631.
- Boonstra, R., Hik, D., Singleton, G.R. & Tinnikov, A. (1998) The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs*, **68**, 371–394.
- Broekhuis, F.C., Cozzi, G., Valeix, M., McNutt, J.W. & Macdonald, D.W. (2013) Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology*, **82**, 1098–1105.
- Brown, G.E., Chivers, D.P., Elvidge, C.K., Jackson, C.D. & Ferrari, M.C.O. (2014) Background level of risk determines the intensity of predator neophobia in juvenile convict cichlids. *Behavioral Ecology and Sociobiology*, **68**, 127–133.
- Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.
- Christianson, D., Klaver, R.W., Middleton, A. & Kauffman, M. (2013) Confounded winter and spring phenoclimatology on large herbivore ranges. *Landscape Ecology*, **28**, 427–437.
- Cleveland, S.M., Hebblewhite, M., Thompson, M., Henderson, R. & Article, O. (2012) Linking elk movement and resource selection to hunting pressure in a heterogeneous landscape. *Wildlife Society Bulletin*, **36**, 658–668.
- Courbin, N., Loveridge, A.J., Macdonald, D.W., Fritz, H., Valeix, M., Makuwe, E.T. & Chamaille-jammes, S. (2015) Reactive responses of zebras to lion encounters shape their predator-prey space game at large scale. *Oikos*, **125**, 829–838.
- Creel, S., Christianson, D., Liley, S. & Winnie, J.A. (2007) Predation risk affects reproductive physiology and demography of elk. *Science*, **315**, 960–960.
- Creel, S., Schuette, P. & Christianson, D. (2014) Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, **25**, 773–784.
- Creel, S. & Winnie, J.A. (2005) Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour*, **69**, 1181–1189.

- Creel, S., Winnie, J.A. & Christianson, D. (2013) Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: An example with wolves and elk. *Ecology and Evolution*, **3**, 5189–5200.
- Creel, S., Winnie Jr, J.A., Maxwell, B., Hamlin, K., Creel, M., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M. (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**, 3387–3397.
- Didan, K. (2015) MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006. NASA EOSDIS Land Processes DAAC.
- Dröge, E.D., Creel, S., Becker, M.S. & M’Soka, J.L.J. (2017) Spatial and temporal avoidance of risk within a large carnivore guild. *Ecology and Evolution*, **7**, 189–199.
- Dröge, E.D., Creel, S., Becker, M.S. & M’Soka, J.L.J. (accepted) Measuring the ‘landscape of fear’: Risky times and risky places interact to affect the response of prey. *Nature: Ecology & Evolution*
- Elgar, M.A. (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biology Reviews*, **64**, 13–33.
- Fischhoff, I.R., Sundaresan, S.R., Cordingley, J. & Rubenstein, D.I. (2007) Habitat use and movements of plains zebra (*Equus burchelli*) in response to predation danger from lions. *Behavioral Ecology*, **18**, 725–729.
- Fitzgibbon, C.D. (1989) A cost to individuals with reduced vigilance in groups of Thomson’s gazelles hunted by cheetahs. *Animal Behaviour*, **37**, 508–510.
- Fitzgibbon, C.D. (1990) Mixed-species grouping in Thomson’s and Grant’s gazelles : the antipredator benefits. *Animal Behaviour*, **39**, 1116–1126.
- Forchhammer, M.C. & Post, E. (2004) Using large-scale climate indices in climate change ecology studies. *Population Ecology*, **46**, 1–12.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**, 1320–1330.
- Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L. & Morales, J.M. (2005) Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology*, **20**, 273–287.

- Gerritsen, J. & Strickler, J.R. (1977) Encounter probabilities and community structure in zooplankton- a mathematical model. *Journal of the Fisheries Research Board Canada*, **34**, 73–82.
- Hebblewhite, M., Pletscher, D.H. & Paquet, P.C. (2002) Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology*, **80**, 789–799.
- Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R. & Boyce, M.S. (2007) Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters*, **10**, 690–700.
- Kuijper, D.P.J., de Kleine, C., Churski, M., van Hooft, P., Bubnicki, J., Jedrzejewska, B., Kleine, C. De, Churski, M., Hooft, P. Van, Bubnicki, J. & Je, B. (2013) Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Bialowieza Primeval Forest, Poland. *Ecography*, **36**, 1263–1275.
- LaManna, J.A., Martin, T.E. & Letters, E. (2016) Costs of fear: Behavioural and life-history responses to risk and their demographic consequences vary across species. *Ecology Letters*, **19**, 403–413.
- Latombe, G., Fortin, D. & Parrott, L. (2014) Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *Journal of Animal Ecology*, **83**, 185–198.
- Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, **79**, 1401–1409.
- Lima, S.L. & Bednekoff, P. a. (1999) Temporal variation in danger drives antipredator behavior : The predation risk allocation hypothesis. *The American Naturalist*, **153**, 649–659.
- Little, A.R., Webb, S.L., Demarais, S., Gee, K.L., Riffell, S.K. & Gaskamp, J.A. (2016) Hunting intensity alters movement behaviour of white-tailed deer. *Basic and Applied Ecology*, **17**, 360–369.
- M’Soka, J.L.J., Creel, S., Becker, M.S., Droge, E.D., Jassiel, M., Creel, S., Becker, M.S. & Droge, E.D. (2016) Spotted hyaena survival and density in a lion depleted ecosystem: the effects of prey availability, humans and competition between large carnivores in African savannahs. *Biological Conservation*, **201**, 348–355.

- M'Soka, J.L.J., Creel, S., Becker, M.S. & Murdoch, J.D. Ecological and anthropogenic effects on the density of migratory and resident ungulates in a human-inhabited protected area (in press). *African Journal of Ecology*, 1–14.
- Martin, J. & Owen-smith, N. (2016) Habitat selectivity influences the reactive responses of African ungulates to encounters with lions. *Animal Behaviour*, **116**, 163–170.
- McNaughton, S.J. (1979) Grazing as an optimization process : Grass-ungulate relationships in the Serengeti. *The American Naturalist*, **113**, 691–703.
- Moll, R.J., Killion, A.K., Montgomery, R.A., Tambling, C.J. & Hayward, M.W. (2016) Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores. *Ecology*, **97**, 1123–1134.
- Murray, M.G. & Illius, A.W. (2000) Vegetation modification and resource competition in grazing ungulates. *Oikos*, **89**, 501–508.
- Neumann, W., Ericsson, G. & Dettki, H. (2009) The non-impact of hunting on moose Alces alces movement, diurnal activity, and activity range. *European Journal of Wildlife Research*, **55**, 255–265.
- Newcombe, R.G. (1998) Two-sided confidence intervals for the single proportion: Comparison of seven methods. *Statistics in Medicine*, **17**, 857–872.
- Pangle, K.L., Peacor, S.D., Johannsson, O.E. & Johannsson, O.E. (2007) Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology*, **88**, 402–412.
- Peckarsky, B.L., Cowan, C.A., Penton, M.A., Cowan, C.A., Penton, M.A. & Anderson, C. (1993) Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology*, **74**, 1836–1846.
- Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., Madzikanda, H., Fritz, H., Macdonald, D.W., Loveridge, A.J. & Lyon, C.B. (2012) Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology*.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N.C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, **20**, 503–510.
- Proffitt, K.M., Grigg, J.L., Hamlin, K.L. & Garrott, R.A. (2009) Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *Journal of Wildlife Management*, **73**, 345–356.

- R Core Team. (2016) R: A language and environment for statistical computing.
- Rhoads, C.L., Bowman, J.L., Eyster, B. & Article, O. (2013) Movements of female exurban white-tailed deer in response to controlled hunts. *Wildlife Society Bulletin*, **37**, 631–638.
- Root, B.G., Fritzell, E.K. & Giessman, N.F. (1988) Effects of intensive hunting on white-tailed deer movement. *Wildlife Society Bulletin*, **16**, 145–151.
- Schmitz, O.J. (2008) Effects of predator hunting mode on grassland ecosystem function. *Science (New York, N.Y.)*, **319**, 952–4.
- Schmitz, O.J. (2012) Direct and indirect effects of predation and predation risk in old-field interaction webs. *The American Naturalist*, **151**, 327–342.
- Seaman, E.D. & Powell, R.A. (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, **77**, 2075–2085.
- Sheriff, M.J., Krebs, C.J. & Boonstra, R. (2009) The sensitive hare: Sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology*, **78**, 1249–1258.
- Shrader, A.M., Owen-Smith, N. & Ogutu, J.O. (2006) How a mega-grazer copes with the dry season: food and nutrient intake rates by white rhinoceros in the wild. *Functional Ecology*, **20**, 376–384.
- Sih, A. & McCarthy, T.M. (2002) Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. *Animal Behaviour*, **63**, 437–443.
- Skelly, D.K., Werner, E.E., Skelly, D.K. & Werner, E.E. (2016) Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology*, **71**, 2313–2322.
- Thaker, M., Vanak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M. & Slotow, R. (2011) Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, **92**, 398–407.
- Turchin, P. (1998) *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates, Sunderland.
- Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. (2009) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, **90**, 23–30.

- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*. Springer, New York.
- Viswanathan, G.M., Buldyrev, S. V, Havlin, S., da Luz, M.G.E., Raposo, E.P. & Stanley, H.E. (1999) Optimizing the success of random searches. *Nature*, **401**, 911–914.
- Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.
- Wilmshurst, J.F., Fryxell, J.M. & Hudson, R.J. (1995) Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioral Ecology*, **6**, 209–217.
- Winnie, J., Creel, S., Winnie Jr, J.A. & Creel, S. (2007) Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Animal Behaviour*, **73**, 215–225.
- Wirsing, A.J., Cameron, K.E. & Heithaus, M.R. (2010) Spatial responses to predators vary with prey escape mode. *Animal Behaviour*, **79**, 531–537.
- Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164–168.

## CHAPTER FIVE

## CONCLUSION TO DISSERTATION

The Liuwa ecosystem has several important ecological properties that affect interactions among large predators and between predator and prey. First, the vegetation structure is highly uniform in relation to the possibility of the studied species for being detected and the lack of possibility to hide within the area we studied, and is typified by open grasslands with good visibility over long distances. Under these conditions, large mammals can detect one another relatively easily and going undetected is not easily accomplished. Second, the ungulate prey community has a simple structure that is highly dominated by wildebeest, with much lower numbers of zebra, oribi and other species. All of the large predator prey heavily on wildebeest, though oribi are also critical prey for wild dogs and especially cheetahs. The relative uniformity of the study area, and the simplicity of the prey community, combined with GPS data on a fine spatial scale, and a large observational dataset on both predators and prey enabled us to focus on several little-studied questions about the effects of predation risk in the wild.

Responses of Carnivores to Within Guild Competition

The dominant competitors, hyenas and lions, specialized almost completely on wildebeest, and African wild dogs, a subordinate competitor, also relied heavily on wildebeest in LPNP, but had a broader dietary niche, particularly due to predation on oribi. This pattern might be explained by differences in the cost/benefit ratio of hunting smaller prey (Creel & Creel 2002), but it also aligns with a basic prediction of

competition theory, that a subordinate competitor can persist by adopting a generalist strategy that reduces overlap with dominant competitors who specialize on the most profitable niche space. Contrary to expectation, space use by African wild dogs was positively related to utilization by lions and hyenas, a result that contrasts sharply with prior comparisons both across ecosystems (Creel & Creel 1996; Swanson *et al.* 2014) and within ecosystems (Mills & Gorman 1997; Creel & Creel 2002; Vanak *et al.* 2013; Steenhuisen *et al.* 2015). In these ecosystems African wild dogs persisted stably over long periods, while they disappeared from LPNP and other open grassland systems dominated by wildebeest (Estes & Goddard 1967; Fanshawe & Fitzgibbon 1993), suggesting that spatial niche partitioning may be critical for competitive coexistence of wild dogs with dominant competitors. Despite the generally positive correlation in space use by wild dogs and dominant competitors, the relationship to relative use by lions was asymptotic while the relationship to relative use by hyenas was linear, even though hyenas outnumbered lions 40-fold. This result does align with prior studies showing that African wild dogs avoid areas with a high probability of encountering lions.

The difference in spatial relationships of wild dogs to lions and hyenas could perhaps be explained by the fact that a small number of lions in a single pride can be avoided more easily and effectively than the much larger number of hyenas in several clans. The difference might also be explained by recognizing that intra-guild predation on wild dogs is more commonly due to lions than to hyenas (Mills & Biggs 1993; Creel & Creel 1998), and that wild dogs can dominate hyenas in competitive interactions if they outnumber them (Estes & Goddard 1967; Fanshawe & Fitzgibbon 1993; Creel & Creel

1996). Nonetheless, our results suggest that on a per-capita basis, the limiting effect of lions on the use of space by wild dogs is strong, and in an open landscape it might be impossible for African wild dogs to establish themselves permanently in the face of unavoidable competitors. In other open, seemingly intact, ecosystems in Africa (Serengeti, Etosha NP, Ngorongoro) African wild dogs are also present only intermittently.

Wild dogs showed appreciable overlap with their dominant competitors in temporal patterns of hunting, but were more active during the crepuscular period and less active in full darkness, as in most other systems (Mills & Gorman 1997; Creel & Creel 2002; Cozzi *et al.* 2012; Rasmussen & Macdonald 2012).

Cheetahs were the only species that did not prey primarily on wildebeest, preferring the much less abundant oribi, and cheetahs had the broadest diets of the four carnivores. As with African wild dogs, these differences can partially be explained by differences in the cost/benefit ratio of hunting small prey, but also align with the hypothesis that cheetahs' dietary niche has evolved to reduce limitation by dominant competitors. Cheetahs focused their activity in areas heavily used by lions in data aggregated over the long term, as has been found elsewhere (Broekhuis *et al.* 2013; Swanson *et al.* 2014), and their space use showed a positive linear relationship with that of hyenas. Broekhuis *et al.* (2013) found that cheetahs avoid lions in space, but in a reactive way (on a short time scale), where they positioned themselves further from lions than predicted by a random distribution within areas of shared use (also see Durant 2000b). For cheetahs, avoidance of both lions and hyenas is typically more clearly related

to temporal patterns rather than spatial patterns (Mills & Biggs 1993). Cheetahs made about 70% of their kills during full daylight, and thereby avoided hunting in the crepuscular and night-time periods in which the other species made approximately three quarters of their kills, and when surprise encounters at close range are more likely.

Contrary to our hypotheses, space use by hyenas was positively correlated to space use by lions, but the relationship was asymptotic, suggesting avoidance of areas most heavily used by lions. Lions and hyenas also showed very similar temporal distributions of hunts. In general, these results align with the inferences from a recent review by Périquet *et al.* (2014) who noted that these species have both negative and positive influences on each other, so that the net effect is complex. Périquet *et al.* (2014) suggested that finer patterns in selection of prey age-sex classes and processes affecting scavenging opportunities facilitate coexistence between hyenas and lions, allowing both species to concentrate their hunting in areas of high prey availability.

It is increasingly clear that within Africa's large carnivore guild, interspecific competition can be a strongly limiting force for cheetahs and especially African wild dogs. Both species use niche partitioning to reduce the risk of dangerous interactions, but in different ways that appear to have ramifications for coexistence. Wild dogs show more dietary and temporal overlap with dominant competitors. Cheetahs combine divergence in diet, temporal avoidance and reactive local spatial avoidance to coexist with lions and hyenas in areas of high prey density, even in open habitats. These results provide new insight into the conditions under which partitioning may not allow for coexistence for one subordinate species, the African wild dog, while it does for cheetah. Because of

differences in mechanisms of response, African wild dogs may be more prone to competitive exclusion (local extirpation), particularly in open, uniform ecosystems with simple (often wildebeest dominated) prey communities, where spatial avoidance is difficult.

The results from chapter 1 suggest that open environments with a simple prey set constrain the options for subordinate species like wild dogs and cheetahs, promoting competitive exclusion. In line with this inference, wild dogs have been competitively excluded from ecologically similar areas in Serengeti National Park (Estes & Goddard 1967; Malcolm & Marten 1982; Creel & Creel 1996), and have not been resident within the LPNP study site examined here for more than a year. Our data also suggest that cheetahs may coexist with dominant competitors under these conditions because of temporal niche partitioning to heavily exploit the safer daylight hours (Swanson et al. 2014). We suggest that wild dogs may be precluded from adopting this tactic by the thermal stress of cursorial hunting, as they often travel many kilometers seeking prey that is pursued at high speeds over long distances (Estes & Goddard 1967; Fanshawe & Fitzgibbon 1993; Creel & Creel 1995).

#### Responses of Prey to Predation Risk

This research advances our understanding of the responses of prey to predation risk in three main ways. (1) First, very few prior studies have examined the responses of complete prey guilds to variation in risk from all of their predators within an ecosystem. (2) Second, most prior studies have measured risk in only one way, rather than considering both long term and short term variation in risk. This situation has persisted

even though theory suggests that responses to short term risk should depend on the pattern of long term risk within which the short term risk is embedded. (3) Finally, we have a very limited understanding of how the strength of antipredator responses relates to the strength of direct predation, and a better understanding of this relationship is critical for a proper understanding of the total limiting effect of predators on prey. In Chapter 2, we found that ungulates were more vigilant in places that were heavily used by predators over the long term. Contrary to expectation, there was little evidence that ungulates were more vigilant if they were closer to the nearest predator at the time of observation. This result came, however, from a model that allowed for interaction between LT and ST risk, and variation in ST risk did affect vigilance in a manner that depended on the LT risk of the location. Vigilance was greatest when high levels of ST risk (a predator immediately nearby) occurred in locations with high LT risk (heavy use by that predator species). It was striking that the best measure of LT risk to describe this interaction was the UD of the predator that was immediately present, indicating a fine-tuned assessment by prey of the relationship between ST and LT risk, rather than a consistently stronger response to specific predator species or functional types. To summarize, prey responded most strongly when they encountered immediate risk in a place where they could have anticipated that very risk.

The results of the study in chapter 4 showed that wildebeest movements responded to the intensity of use of their location by predators, after controlling for other seasonal, diurnal and bottom-up effects on movement. Step lengths were shorter and turning angles were greater, and both of these effects were considerable in comparison to

bottom-up and abiotic effects on movements. These responses reveal that wildebeest are capable of assessing the LT risk associated with an area, perhaps by the immediate use of smell or perhaps by memory of past patterns of predator detection using sight, hearing and smell, all of which are acute for wildebeest. Even though immediate encounters with predators typically provoked fast, linear flight, the effect of LT risk was to cause wildebeest to move more slowly and less linearly, i.e. to slow down and turn around. The combined effect of slowing down and turn more could be to allow wildebeest more time to assess immediate ST risk when moving within an area of high LT risk. Even without improved assessment of ST risk, moving more slowly could reduce the probability of encountering a predator (Gerritsen & Strickler 1977) or being detected (Cleveland *et al.* 2012; Little *et al.* 2016), particularly if animals confine themselves to structural refuges. Because wildebeest in this study were moving almost entirely in open grassland, it is unlikely that moving less was associated with ‘hiding’, but reduced movement would nonetheless be expected to reduce encounter rates with randomly located predators (Viswanathan *et al.* 1999). There is a trade-off, however, because predators were not randomly located – by slowing down and turning more in areas of high LT risk, wildebeest spend more time in these dangerous areas. This response should also make their location more predictable on a time scale of several days, and this predictability could be exploited by predators to increase encounter rates. These patterns suggest that in a relative homogeneous, open environment without refuges, behavior that promotes wildebeests’ ability to assess and detect ST risk is an important aspect of response to cues of high LT risk. However, additional bottom up parameters correlated with movement

patterns can't be fully ruled out. In chapter 2 similar results were found where vigilance increased when predators were nearby, and that this response was stronger in locations with high LT risk. This result aligns well with the inference that reduced speed and linearity of movement are part of a suite of responses to more cautiously assess ST risk in locations with high LT risk. More broadly, this inference aligns with the prior suggestion that prey sometimes tolerate (or even select) predator-rich areas if there are advantages to doing so (for example, better opportunities to hide or escape) (Wirsing, Cameron & Heithaus 2010).

Overall the conclusion can be that the assessment of risk by animals is a very fine-tuned process. Our results confirm that both the *risky places hypothesis* (LT risk) and the *risky times hypothesis* (ST risk) are important, leading to both reactive and proactive responses. Critically, these effects do not act independently in their effects on the strength of antipredator responses. This interaction presents serious challenges for the design of research on risk effects. A real effect of ST risk could easily be masked by unmeasured variation in LT risk (or vice versa), and an apparent effect of ST risk might actually be caused by unmeasured variation in LT risk (or vice versa). Few (if any) prior field studies have employed a design that addresses these complications, so our results have broad implications for the design and interpretation of studies of antipredator behavior, its costs, and its consequences for population and community dynamics.

Literature Cited

- Broekhuis, F.C., Cozzi, G., Valeix, M., McNutt, J.W. & Macdonald, D.W. (2013) Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology*, **82**, 1098–1105.
- Cleveland, S.M., Hebblewhite, M., Thompson, M., Henderson, R. & Article, O. (2012) Linking elk movement and resource selection to hunting pressure in a heterogeneous landscape. *Wildlife Society Bulletin*, **36**, 658–668.
- Cozzi, G., Broekhuis, F.C., McNutt, J.W., Turnbull, L.A. & David, W. (2012) Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, **93**, 2590–2599.
- Creel, S. & Creel, N.M. (1995) Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, **50**, 1325–1339.
- Creel, S. & Creel, N.M. (1996) Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, **10**, 526–538.
- Creel, S. & Creel, N.M. (1998) Six ecological factors that may limit African wild dogs, *Lycaon pictus*. *Animal Conservation*, **1**, 1–9.
- Creel, S. & Creel, N.M. (2002) *The African Wild Dog: Behavior, Ecology and Conservation*. Princeton University Press, Princeton.
- Durant, S.M. (2000) Predator avoidance, breeding experience and reproductive success in endangered cheetahs (*Acinonyx jubatus*). *Animal Behaviour*, **60**, 121–130.
- Estes, R.D. & Goddard, J. (1967) Prey selection and hunting behavior of the African wild dog. *The Journal of Wildlife Management*, **31**, 52–70.
- Fanshawe, J.H. & Fitzgibbon, C.D. (1993) Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour*, **45**, 479–490.
- Gerritsen, J. & Strickler, J.R. (1977) Encounter probabilities and community structure in zooplankton- a mathematical model. *Journal of the Fisheries Research Board Canada*, **34**, 73–82.
- Little, A.R., Webb, S.L., Demarais, S., Gee, K.L., Riffell, S.K. & Gaskamp, J.A. (2016) Hunting intensity alters movement behaviour of white-tailed deer. *Basic and Applied Ecology*, **17**, 360–369.

- Malcolm, J.R. & Marten, K. (1982) Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behavioral Ecology and Sociobiology*, **10**, 1–13.
- Mills, M.G.L. & Biggs, H.C. (1993) Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. *Mammals as Predators* (eds N. Dunstone & M.L. Gorman), pp. 253–268. Zoological Society of London, London.
- Mills, M.G.L. & Gorman, M.L. (1997) Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology*, **11**, 1397–1406.
- Périquet, S., Fritz, H. & Revilla, E. (2014) The lion king and the hyaena queen: large carnivore interactions and coexistence. *Biological Reviews*, **90**, 1197–1214.
- Rasmussen, G.S.A. & Macdonald, D.W. (2012) Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *Journal of Zoology*, **286**, 232–242.
- Steenhuisen, S., Balmer, A., Zoeller, K., Kuhn, N., Midgley, J., Hansen, D., Johnson, S.D., Masenga, E., Jackson, C.R., Mjingo, E.E., Jacobson, A., Riggio, J.S., Lyamuya, R.D., Fyumagwa, R.D., Borner, M. & Roskaft, E. (2015) Insights into long-distance dispersal by African wild dogs in East Africa. *African Journal of Ecology*, **54**, 1–4.
- Swanson, A., Caro, T.M., Davies-Mostert, H., Mills, M.G.L., Macdonald, D.W., Borner, M., Masenga, E., Packer, C., David, W., Borner, M., Masenga, E., Packer, C., Paul, S., Africa, S., Conservation, W. & Centre, R. (2014) Cheetahs and wild dogs show contrasting patterns of suppression by lions. *The Journal of Animal Ecology*, **83**, 1418–1427.
- Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C. & Greatwood, S. (2013) Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology*, **94**, 2619–2631.
- Viswanathan, G.M., Buldyrev, S. V., Havlin, S., da Luz, M.G.E., Raposo, E.P. & Stanley, H.E. (1999) Optimizing the success of random searches. *Nature*, **401**, 911–914.
- Wirsing, A.J., Cameron, K.E. & Heithaus, M.R. (2010) Spatial responses to predators vary with prey escape mode. *Animal Behaviour*, **79**, 531–537.

## REFERENCES CITED

- Basille, M., Fortin, D., Dussault, C., Bastille-rousseau, G., Ouellet, J.P., Courtois, R., Asille, M.A.B., Ortin, D.A.F., Ussault, C.H.D., Ousseu, G.U.B.A. & Ourtois, H.C. (2015) Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, **96**, 2622–2631.
- Baum, J.K. & Worm, B. (2009) Cascading predator and effects of changing oceanic predator abundances. *Journal of Animal Ecology*, **78**, 699–714.
- Blanchard, P. & Fritz, H. (2016) Induced or routine vigilance while foraging. *Oikos*, **116**, 1603–1608.
- Boonstra, R., Hik, D., Singleton, G.R. & Tinnikov, A. (1998) The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs*, **68**, 371–394.
- Broekhuis, F.C., Cozzi, G., Valeix, M., McNutt, J.W. & Macdonald, D.W. (2013) Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology*, **82**, 1098–1105.
- Brook, L.A., Johnson, C.N. & Ritchie, E.G. (2012) Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology*, **49**, 1278–1286.
- Brown, G.E., Chivers, D.P., Elvidge, C.K., Jackson, C.D. & Ferrari, M.C.O. (2014) Background level of risk determines the intensity of predator neophobia in juvenile convict cichlids. *Behavioral Ecology and Sociobiology*, **68**, 127–133.
- Brown, G.E., Ferrari, M.C.O., Elvidge, C.K., Ramnarine, I. & Chivers, D.P. (2013) Phenotypically plastic neophobia: a response to variable predation risk. *Proceedings of the Royal Society B*, **280**, 20122712.
- Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.
- Caro, T.M. & Laurenson, M.K. (1994) Ecological and Genetic Factors in Conservation: A Cautionary Tale. *Science*, **263**, 485–486.
- Caro, T.M. & Stoner, C.J. (2003) The potential for interspecific competition among African carnivores. *Biological Conservation*, **110**, 67–75.

- Cherry, M.J., Morgan, K.E., Rutledge, B.T., Conner, L.M. & Warren, R.J. (2016) Can coyote predation risk induce reproduction suppression in white-tailed deer? *Ecosphere*, **7**, e01481.
- Christianson, D.A. & Creel, S. (2008) Risk effects in elk : sex-specific responses in grazing and browsing due to predation risk from wolves. *Behavioral Ecology*, 1258–1266.
- Christianson, D.A. & Creel, S. (2010) A nutritionally mediated risk effect of wolves on elk. *Ecology*, **91**, 1184–1191.
- Christianson, D. & Creel, S. (2014) Ecosystem scale declines in elk recruitment and population growth with wolf colonization: A before-after-control-impact approach. *PLoS ONE*, **9**, e102330.
- Christianson, D., Klaver, R.W., Middleton, A. & Kauffman, M. (2013) Confounded winter and spring phenoclimatology on large herbivore ranges. *Landscape Ecology*, **28**, 427–437.
- Cleveland, S.M., Hebblewhite, M., Thompson, M., Henderson, R. & Article, O. (2012) Linking elk movement and resource selection to hunting pressure in a heterogeneous landscape. *Wildlife Society Bulletin*, **36**, 658–668.
- Courbin, N., Loveridge, A.J., Macdonald, D.W., Fritz, H., Valeix, M., Makuwe, E.T. & Chamaille-jammes, S. (2015) Reactive responses of zebras to lion encounters shape their predator-prey space game at large scale. *Oikos*, **125**, 829–838.
- Cozzi, G., Broekhuis, F.C., McNutt, J.W. & Schmid, B. (2013) Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation. *Biodiversity and Conservation*, **22**, 2937–2956.
- Cozzi, G., Broekhuis, F.C., McNutt, J.W., Turnbull, L.A. & David, W. (2012) Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, **93**, 2590–2599.
- Creel, S. (2001) Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology*, **15**, 271–274.
- Creel, S. & Christianson, D. (2008) Relationships between direct predation and risk effects. *Trends in Ecology and Evolution*, **23**, 194–201.
- Creel, S., Christianson, D., Liley, S. & Winnie, J.A. (2007) Predation Risk Affects Reproductive Physiology and Demography of Elk. *Science*, **315**, 960–960.

- Creel, S. & Creel, N.M. (1995) Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, **50**, 1325–1339.
- Creel, S. & Creel, N.M. (1996) Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, **10**, 526–538.
- Creel, S. & Creel, N.M. (1998) *Six Ecological Factors That May Limit African Wild Dogs*, *Lycaon Pictus*.
- Creel, S. & Creel, N.M. (2002) *The African Wild Dog: Behavior, Ecology and Conservation*. Princeton University Press, Princeton.
- Creel, S., Dröge, E.D., M'soka, J., Smit, D., Becker, M.S., Christianson, D.A. & Schuette, P.A. The relationship between direct predation and antipredator responses: a test with multiple predators and multiple prey (in review). *Ecology*.
- Creel, S., Schuette, P. & Christianson, D.A. *Direct Predation Rates and the Foraging Costs of Increased Vigilance in Five African Ungulates*.
- Creel, S., Schuette, P. & Christianson, D. (2014) Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, **25**, 773–784.
- Creel, S., Spong, G. & Creel, N.M. (2001) Interspecific competition & population biology of extinction-prone carnivores. *Carnivore Conservation* (eds J.L. Gittleman, S.M. Funk, D.W. MacDonald & R.K. Wayne), pp. 35–61. Cambridge University Press, Cambridge.
- Creel, S. & Winnie, J.A. (2005) Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour*, **69**, 1181–1189.
- Creel, S., Winnie, J.A. & Christianson, D. (2013) Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: An example with wolves and elk. *Ecology and Evolution*, **3**, 5189–5200.
- Creel, S., Winnie, J.A., Christianson, D. & Liley, S. (2008) Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour*, **76**, 1139–1146.
- Creel, S., Winnie Jr, J.A., Maxwell, B., Hamlin, K., Creel, M., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M. (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**, 3387–3397.

- Cresswell, W. & Quinn, J.L. (2010) Attack frequency, attack success and choice of prey group size for two predators with contrasting hunting strategies. *Animal Behaviour*, **80**, 643–648.
- Cresswell, W. & Quinn, J.L. (2013) Contrasting risks from different predators change the overall nonlethal effects of predation risk. *Behavioral Ecology*, **24**, 871–876.
- Crooks, K.R., Vuren, D. Van & Crooks, K.R. (1995) Resource utilization by two insular endemic mammalian carnivores, the island fox and island spotted skunk. *Oecologia*, **104**, 301–307.
- Crowl, T.A. & Covich, A.P. (1990) Predator-induced life-history shifts in a freshwater snail. *Science*, **247**, 949–951.
- Darnell, A.M., Graf, J.A., Somers, M.J., Slotow, R., Szykman Gunther, M. & Gunther, M.S. (2014) Space use of African wild dog in relation to other large carnivores. *Plos One*, **9**, e98846.
- Didan, K. (2015) MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006. NASA EOSDIS Land Processes DAAC.
- Dröge, E.D., Creel, S., Becker, M.S. & M’Soka, J.L.J. (2017) Spatial and temporal avoidance of risk within a large carnivore guild. *Ecology and Evolution*, **7**, 189–199.
- Dröge, E.D., Creel, S., Becker, M.S. & M’Soka, J.L.J. (accepted) Measuring the ‘landscape of fear’: Risky times and risky places interact to affect the response of prey. *Nature: Ecology & Evolution*
- Durant, S.M. (1998) Competition and coexistence : refuges an example from carnivores Serengeti. *Journal of Animal Ecology*, **67**, 370–386.
- Durant, S.M. (2000a) Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, **11**, 624–632.
- Durant, S.M. (2000b) Predator avoidance, breeding experience and reproductive success in endangered cheetahs (*Acinonyx jubatus*). *Animal Behaviour*, **60**, 121–130.
- Elgar, M.A. (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biology Reviews*, **64**, 13–33.
- Estes, R.D. & Goddard, J. (1967) Prey selection and hunting behavior of the African wild dog. *The Journal of Wildlife Management*, **31**, 52–70.

- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pickett, E.K., Ripple, W.J., Sandin, S. a, Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. & Wardle, D. a. (2011) Trophic Downgrading of Planet Earth. *Science*, **333**, 301–306.
- Fanshawe, J.H. & Fitzgibbon, C.D. (1993) Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour*, **45**, 479–490.
- Fischhoff, I.R., Sundaresan, S.R., Cordingley, J. & Rubenstein, D.I. (2007) Habitat use and movements of plains zebra (*Equus burchelli*) in response to predation danger from lions. *Behavioral Ecology*, **18**, 725–729.
- Fitzgibbon, C.D. (1989) A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Animal Behaviour*, **37**, 508–510.
- Fitzgibbon, C.D. (1990) Mixed-species grouping in Thomson's and Grant's gazelles : the antipredator benefits. *Animal Behaviour*, **39**, 1116–1126.
- Forchhammer, M.C. & Post, E. (2004) Using large-scale climate indices in climate change ecology studies. *Population Ecology*, **46**, 1–12.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in Yellowstone National Park. *Ecology*, **86**, 1320–1330.
- Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L. & Morales, J.M. (2005) Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology*, **20**, 273–287.
- Gerritsen, J. & Strickler, J.R. (1977) Ncounter Probabilities and Community Structure in Zooplankton- a Mathematical Model.Pdf. *Journal of the Fisheries Research Board Canada*, **34**, 73–82.
- Ginsberg, J.R., Alexander, K.A., Creel, S., Kat, P.W., McNutt, J.W. & Mills, M.G.L. (1995) Handling and survivorship of African wild dog (*Lycaon pictus*) in five ecosystems. *Conservation Biology*, **9**, 665–674.
- Gorman, M.L., Mills, M.G.M.G.L., Raath, J.P.J.P., Speakman, J.R., Mills, M.G.M.G.L., Raath, J.P.J.P. & Speakman, J.R. (1998) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature*, **852**, 1992–1994.
- Hayward, M.W. & Kerley, G.I.H. (2008) Prey preferences and dietary overlap amongst Africa's large predators. *South African Journal of Wildlife Research*, **38**, 93–108.

- Hayward, M.W., O'Brien, J., Hofmeyr, M. & Kerley, G.I.H. (2006) Prey Preferences of the African Wild Dog *Lycaon Pictus* (Canidae: Carnivora): Ecological Requirements for Conservation. *Journal of Mammalogy*, **87**, 1122–1131.
- Hayward, M.W. & Slotow, R. (2009) Temporal Partitioning of Activity in Large African Carnivores: Tests of Multiple Hypotheses. *South African Journal of Wildlife Research*, **39**, 109–125.
- Hebblewhite, M., Pletscher, D.H. & Paquet, P.C. (2002) Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology*, **80**, 789–799.
- Heithaus, M.R., Wirsing, A.J., Burkholder, D., Thomson, J., Dill, L.M., Heithaus, R. & Wirsing, J. (2009) Towards the tactics a predictive of framework landscape for predator and risk effects: prey escape interaction features. *Journal of Animal Ecology*, **78**, 556–562.
- Hopcraft, J.G.C., Sinclair, A.R.E. & Packer, C. (2005) Planning for success : Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, **74**, 559–566.
- Joyce, B.J., Demers, E.E., Ferrari, M.C.O., Chivers, D.P. & Brown, G.E. (2016) Background Predation Risk and Learned Predator Recognition in Convict Cichlids: Does Risk Allocation Constrain Learning? *Ethology*, **122**, 841–849.
- Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R. & Boyce, M.S. (2007) Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters*, **10**, 690–700.
- Kolowski, J.M., Katan, D., Theis, K.R. & Holekamp, K.E. (2007) Daily patterns of activity in the spotted hyena. *Journal of Mammalogy*, **88**, 1017–1028.
- Kruuk, H. (1972) *The Spotted Hyena: A Study of Predation and Social Behaviour*. University of Chicago Press, Chicago.
- Kuijper, D.P.J., de Kleine, C., Churski, M., van Hooft, P., Bubnicki, J., Jedrzejewska, B., Kleine, C. De, Churski, M., Hooft, P. Van, Bubnicki, J. & Je, B. (2013) Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Bialowieża Primeval Forest, Poland. *Ecography*, **36**, 1263–1275.
- LaManna, J.A., Martin, T.E. & Letters, E. (2016) Costs of fear: Behavioural and life-history responses to risk and their demographic consequences vary across species. *Ecology Letters*, **19**, 403–413.

- Lank, D.B. & Ydenberg, R.C. (2003) Death and danger at migratory stopovers : Problems with 'predation risk'. *Journal of avian biology*, **34**, 225–228.
- Latombe, G., Fortin, D. & Parrott, L. (2014) Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *Journal of Animal Ecology*, **83**, 185–198.
- Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, **79**, 1401–1409.
- Lima, S.L. & Bednekoff, P. a. (1999) Temporal Variation in Danger Drives Antipredator Behavior : The Predation Risk Allocation Hypothesis. *The American Naturalist*, **153**, 649–659.
- Lind, J. & Cresswell, W. (2005) Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, **16**, 945–956.
- Little, A.R., Webb, S.L., Demarais, S., Gee, K.L., Riffell, S.K. & Gaskamp, J.A. (2016) Hunting intensity alters movement behaviour of white-tailed deer. *Basic and Applied Ecology*, **17**, 360–369.
- M'Soka, J.L.J. (2015) *Spotted Hyaena Survival and Density in a Lion Depleted Ecosystem: The Effects of Competition between Large Carnivores African Savannahs*. Montana State University.
- M'Soka, J.L.J., Creel, S., Becker, M.S., Droge, E.D., Jassiel, M., Creel, S., Becker, M.S. & Droge, E.D. (2016) Spotted hyaena survival and density in a lion depleted ecosystem: the effects of prey availability, humans and competition between large carnivores in African savannahs. *Biological Conservation*, **201**, 348–355.
- M'Soka, J.L.J., Creel, S., Becker, M.S. & Murdoch, J.D. Ecological and anthropogenic effects on the density of migratory and resident ungulates in a human-inhabited protected area (in press). *African Journal of Ecology*, 1–14.
- Malcolm, J.R. & Marten, K. (1982) Natural Selection and the Communal Rearing of Pups in African Wild Dogs (*Lycaon pictus*). *Behavioral Ecology and Sociobiology*, **10**, 1–13.
- Mankiw, N.G. (1990) A quick refresher course in macroeconomics. *Journal of Economic Literature*, **28**, 1645–1660.

- Martin, J. & Owen-smith, N. (2016) Habitat selectivity influences the reactive responses of African ungulates to encounters with lions. *Animal Behaviour*, **116**, 163–170.
- Mbizah, M.M., Marino, J. & Groom, R.J. (2012) Diet of four sympatric carnivores in Save Valley Conservancy, Zimbabwe: implications for conservation of the African wild dog (*Lycaon pictus*). *South African Journal of Wildlife Research*, **42**, 94–103.
- McNaughton, S.J. (1979) Grazing as an optimization process : Grass-ungulate relationships in the Serengeti. *The American Naturalist*, **113**, 691–703.
- Mills, M.G.L. & Biggs, H.C. (1993) Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. *Mammals as Predators* (eds N. Dunstone & M.L. Gorman), pp. 253–268. Zoological Society of London, London.
- Mills, M.G.L. & Gorman, M.L. (1997) Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology*, **11**, 1397–1406.
- Moll, R.J., Killion, A.K., Montgomery, R.A., Tambling, C.J. & Hayward, M.W. (2016) Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores. *Ecology*, **97**, 1123–1134.
- Murray, M.G. & Illius, A.W. (2000) Vegetation modification and resource competition in grazing ungulates. *Oikos*, **89**, 501–508.
- Neumann, W., Ericsson, G. & Dettki, H. (2009) The non-impact of hunting on moose *Alces alces* movement, diurnal activity, and activity range. *European Journal of Wildlife Research*, **55**, 255–265.
- Newcombe, R.G. (1998) Two-Sided Confidence Intervals for the Single Proportion: Comparison of Seven Methods. *Statistics in Medicine*, **17**, 857–872.
- Ngoprasert, D., Lynam, A.J., Sukmasuang, R., Tantipisanuh, N., Chutipong, W., Steinmetz, R., Jenks, K.E., Gale, G.A., Grassman, L.I., Kitamura, S., Howard, J., Cutter, P., Cutter, P., Leimgruber, P., Songsasen, N. & Reed, D.H. (2012) Occurrence of three felids across a network of protected areas in Thailand: Prey, intraguild, and habitat associations. *Biotropica*, **44**, 810–817.
- Palomares, F. & Caro, T.M. (1999) Interspecific Killing among Mammalian Carnivores. *The American Naturalist*, **153**, 492–508.
- Pangle, K.L., Peacor, S.D., Johannsson, O.E. & Johannsson, O.E. (2007) Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology*, **88**, 402–412.

- Peckarsky, B.L., Cowan, C.A., Penton, M.A., Cowan, C.A., Penton, M.A. & Anderson, C. (1993) Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology*, **74**, 1836–1846.
- Pereira, L.M., Sciences, E., Owen-Smith, N. & Moleón, M. (2014) Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Review*, **44**, 44–55.
- Périquet, S., Fritz, H. & Revilla, E. (2014) The lion king and the hyaena queen: large carnivore interactions and coexistence. *Biological Reviews*, **90**, 1197–1214.
- Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., Madzikanda, H., Fritz, H., Macdonald, D.W., Loveridge, A.J. & Lyon, C.B. (2012) Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology*.
- Périquet, S., Valeix, M., Claypole, J., Drouet-Hoguet, N., Salnicki, J., Mudimba, S., Revilla, E. & Fritz, H. (2015) Spotted hyaenas switch their foraging strategy as a response to changes in intraguild interactions with lions. *Journal of Zoology*, **297**, 245–254.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N.C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, **20**, 503–510.
- Pianka, E.R. (1981) Competition and niche theory (ed RM May). *Theoretical Ecology*, **8**, 167–196.
- Preisser, E.L., Orrock, J.L. & Schmitz, O.J. (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology*, **88**, 2744–2751.
- Proffitt, K.M., Grigg, J.L., Hamlin, K.L., Garrott, R. a., Proffitt, KM, Grigg, JL, Hamlin, KL, Garrott, RA, Proffitt, K.M., Grigg, J.L., Hamlin, K.L. & Garrott, R. a. (2009) Contrasting Effects of Wolves and Human Hunters on Elk Behavioral Responses to Predation Risk. *Journal of Wildlife Management*, **73**, 345–356.
- QGIS Development Team. (2015) QGIS Geographic Information System.
- R Core Team. (2016) R: A language and environment for statistical computing.
- Rasmussen, G.S.A. & Macdonald, D.W. (2012) Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *Journal of Zoology*, **286**, 232–242.

- Relyea, R.A. (2001a) Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology*, **82**, 523–540.
- Relyea, R.A. (2001b) The Relationship between predation risk and antipredator responses in larval anurans. *Ecology*, **82**, 541–554.
- Rhoads, C.L., Bowman, J.L., Eyler, B. & Article, O. (2013) Movements of female exurban white-tailed deer in response to controlled hunts. *Wildlife Society Bulletin*, **37**, 631–638.
- Ripple, W.J. & Beschta, R.L. (2003) Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management*, **184**, 299–313.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343**, 1241484.
- Ripple, W.J., Larsen, E.J., Renkin, R.A. & Smith, D.W. (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation*, **102**, 227–234.
- Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**, 982–998.
- Root, B.G., Fritzell, E.K. & Giessman, N.F. (1988) Effects of intensive hunting on white-tailed deer movement. *Wildlife Society Bulletin*, **16**, 145–151.
- Rosenblatt, E., Creel, S., Becker, M.S., Merkle, J., Mwape, H., Schuette, P. & Simpamba, T. (2016) Effects of a protection gradient on carnivore density and survival: an example with leopards in the Luangwa valley, Zambia. *Ecology and Evolution*, **6**, 3772–3785.
- Schmitz, O.J. (2008) Effects of predator hunting mode on grassland ecosystem function. *Science (New York, N.Y.)*, **319**, 952–4.
- Schmitz, O.J. (2012) Direct and indirect effects of predation and predation risk in old-field interaction webs. *The American Naturalist*, **151**, 327–342.
- Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, **185**, 27–39.

- Schuette, P., Creel, S., Christianson, D. & Hayward, M. (2016) Ungulate distributions in a rangeland with competitors, predators and pastoralists. *Journal of Applied Ecology*, **53**, 1066–1077.
- Seaman, E.D. & Powell, R.A. (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, **77**, 2075–2085.
- Sheriff, M.J., Krebs, C.J. & Boonstra, R. (2009) The sensitive hare: Sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology*, **78**, 1249–1258.
- Shrader, A.M., Owen-Smith, N. & Ogotu, J.O. (2006) How a mega-grazer copes with the dry season: food and nutrient intake rates by white rhinoceros in the wild. *Functional Ecology*, **20**, 376–384.
- Sih, A. & McCarthy, T.M. (2002) Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. *Animal Behaviour*, **63**, 437–443.
- Silverman, B. (1986) *Density Estimation for Statistics and Data Analysis*. CRC Press, Harvard.
- Sinclair, A.R.E. (1985) Does Interspecific Competition or Predation Shape the African Ungulate Community? *Journal of Animal Ecology*, **54**, 899–918.
- Skelly, D.K., Werner, E.E., Skelly, D.K. & Werner, E.E. (2016) Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology*, **71**, 2313–2322.
- Speakman, J.R., Gorman, M.L., Mills, M.G.L. & Raath, J.P. (2015) Wild dogs and kleptoparasitism: some misunderstandings. *African Journal of Ecology*, **54**, 125–127.
- Steenhuisen, S., Balmer, A., Zoeller, K., Kuhn, N., Midgley, J., Hansen, D., Johnson, S.D., Masenga, E., Jackson, C.R., Mjingo, E.E., Jacobson, A., Riggio, J.S., Lyamuya, R.D., Fyumagwa, R.D., Borner, M. & Roskaft, E. (2015) Insights into long-distance dispersal by African wild dogs in East Africa. *African Journal of Ecology*, **54**, 1–4.
- Steinmetz, R., Seuaturien, N. & Chutipong, W. (2013) Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. *Biological Conservation*, **163**, 68–78.

- Swanson, A., Caro, T.M., Davies-Mostert, H., Mills, M.G.L., Macdonald, D.W., Borner, M., Masenga, E., Packer, C., David, W., Borner, M., Masenga, E., Packer, C., Paul, S., Africa, S., Conservation, W. & Centre, R. (2014) Cheetahs and wild dogs show contrasting patterns of suppression by lions. *The Journal of Animal Ecology*, **83**, 1418–1427.
- Thaker, M., Anak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M., Slotow, R., Vanak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M. & Slotow, R. (2011) Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, **92**, 398–407.
- Trinkel, M. & Kastberger, G. (2005) Competitive interactions between spotted hyenas and lions in the Etosha National Park, Namibia. *African Journal of Ecology*, **43**, 220–224.
- Tumenta, P., Saleh, A., Henschel, P., Masenga, E.H., Jackson, C.R., Ernest, E., Jacobson, A., Riggio, J., Richard, D., Fyumagwa, R.D., Borner, M., Edwards, S., Aschenborn, O., Gange, A.C., Wiesel, I., Hyena, B., Holloway, R., Hill, E., Mcqualter, K.N., Chase, M.J., Julian, T., Mcleod, S.R., Leggett, K.E.A., Masenga, E.H., Jackson, C.R., Ernest, E., Jacobson, A., Riggio, J., Richard, D., Fyumagwa, R.D. & Borner, M. (2015) Note and record. , 103–106.
- Turchin, P. (1998) *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates, Sunderland.
- Valeix, M., Fritz, H., Loveridge, A.J., Davidson, Z., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. (2009a) Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology*, **63**, 1483–1494.
- Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. (2009b) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, **90**, 23–30.
- Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S. & Slotow, R. (2013) Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology*, **94**, 2619–2631.
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*. Springer, New York.

- Viswanathan, G.M., Buldyrev, S. V, Havlin, S., da Luz, M.G.E., Raposo, E.P. & Stanley, H.E. (1999) Optimizing the success of random searches. *Nature*, **401**, 911–914.
- Wand, M.P. & Jones, M.C. (1994) *Kernel Smoothing*. CRC Press, London.
- Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.
- Wilmshurst, J.F., Fryxell, J.M. & Hudson, R.J. (1995) Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioral Ecology*, **6**, 209–217.
- Winnie, J., Creel, S., Winnie Jr, J.A. & Creel, S. (2007) Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Animal Behaviour*, **73**, 215–225.
- Wirsing, A.J., Cameron, K.E. & Heithaus, M.R. (2010) Spatial responses to predators vary with prey escape mode. *Animal Behaviour*, **79**, 531–537.
- Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164–168.
- Ziv, Y., Abramsky, Z., Kotler, B.P. & Subach, A. (1993) Interference competition and temporal habitat partitioning in two gerbil species. *Oikos*, **66**, 237–246.
- Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2009) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology & Evolution*, **1**, 3–14.