

Response of wildebeest (*Connochaetes taurinus*) movements to spatial variation in long term risk from a complete predator guild

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 to reduce the proximity or duration of 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. In Liuwa Plain National Park, we found that wildebeest movements responded to the local intensity of predator use (LT risk), after controlling for other seasonal, diurnal and bottom-up effects. Speed decreased considerably and turning angles increased considerably, combining to markedly decrease linear movements. In contrast, immediate encounters with predators (ST risk) typically provoked fast, linear flight, and this effect was stronger for encounters with coursing predators. 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, which also includes increased vigilance, that promote cautious assessment of ST risks when in locations with high levels of

LT risk. This result has broad implications of understanding the influence of predation risk on foraging patterns of ungulates as this relationship is much more complex than simple avoidance of areas of ‘high risk’.

Keywords: Risk-effects, predator-prey interactions, landscape of fear, anti-predator responses, spatio-temporal scale

Introduction

Many studies have shown that behavioral responses to the predation risk can carry costs for prey by reducing fecundity or survival, with effects on 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). In ungulates, as in most other taxa, 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 at multiple spatial and temporal scales, and studies to date have documented responses to both short term (ST) and long term (LT) variation in risk, but few studies have measured risk at more than one scale or explicitly considered how the scale of risk should affect optimal responses. Ecological studies often test responses of prey to LT variation in risk by quantifying how some measure of risk varies across space (with data aggregated over time) (Hebblewhite et al. 2002; Kauffman et al. 2007). In contrast, behavioral studies often record responses of prey to ST variation in risk, where risk is measured as the distance to the present predator (and modifying factors such as predator species, group size, etc.). With this approach, data are usually aggregated over space, *i.e.*, the attributes of a predator-prey encounter are considered, but not its geographic location (*e.g.*, Creel et al. 2014). These alternative approaches have been termed the ‘risky

places' and the 'risky times' hypotheses respectively (Creel et al. 2008) and much has been learned from each. Considerable evidence now shows that prey can detect and respond to both risky places and risky times (Brown et al. 2014), but research has only begun to consider how antipredator behavior might differ in response to ST and LT risks (Droge et al. 2017).

Here, we hypothesize that prey movement patterns, in particular, should respond differently to LT risk and ST risk. For example, in situations 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 is likely to be a general response in response to LT risk, but that the optimal response to ST risk is likely to vary according to the behavioral specifics of predator-prey interaction. Stalking predators that rely on short, ambush hunts, like lions and cheetahs, 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 cues of the ST presence of a stalker. In contrast, coursing predators that rely on open pursuit, like hyenas and African wild dogs, 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 retreating to safe locations and reducing movement (Sih & McCarthy 2002), but

mayflies responded 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 burrowing 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 moved more slowly on days that wolves were within the same local drainage (with a mean radius of 4.9 km), though this effect was much weaker than simultaneous changes in 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 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 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 our focus here is on the relationship between LT risk and movement patterns, variation in LT risk (or the 'landscape of fear': (Laundré et al. 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 km² 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 to 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 autocorrelation. In ecosystems which hold migratory wildebeest and where they form a considerable part of the ungulate biomass, as is the case in the Greater Liuwa ecosystem, the species has a strong influence on ecosystem functioning and on the composition, size and distribution of the large carnivore guild, thus this study could provide insight into the relationship between wildebeests and large carnivores and aid in the conservation and management of these ecosystems.

Methods

Study Area and Populations

Our data were gathered in a 1200 km² study area in the southern part of the 3660 km² Liuwa Plain National Park (LPNP) in Zambia. The vegetation in the study area is dominated by 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/km² and smaller populations of migratory zebra (1.8 – 8.1 individuals/km²) and non-migratory oribi (1.1— 14.5 individuals/km²) (M'Soka et al. 2017). These densities were estimated by 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. 2017).

Wildebeest Movement Data from GPS Collars

From 2010-06-24 to 2014-10-29, GPS collars from three manufacturers (African Wildlife Tracking, Telemetry Solutions and Telonics) were fitted to 19 adult female

wildebeest. Twelve of the collars reported location errors (seven did not). In preliminary inspection of the data, five collars had large mean location 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 location 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 location 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.

Movement Rates and Turning 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 Appendix I, we determined two measures of the change in direction between consecutive steps. The *deflection angle* (β) for a location was the difference between the bearings of the steps approaching and leaving that point and was calculated using the `ltrai` function of the `AdehabitatLT` package (Calenge 2006). The *displacement angle* (α) 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 Appendix I, the deflection angle β_1 is the autoregressive predictor of β_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.* 2016a), 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 (Droge *et al.* 2017) while a visual representation of resulting utilization distributions (see below) can be found in Dröge *et al.* (2017). In summary, we obtained representative data on the use of space within the 1,200 km² intensive study area by each of the large carnivores, using a combination of GPS and VHF radiocollars. We obtained 1,713 locations for wild dogs, 4,725 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 known 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,
and approved by MSU IACUC.

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; there were frequent relocations for wild dogs during the period they used the site; and cheetah relocations showed no evidence of territorial partitioning of the study area among individuals. Together, these data suggest the sampled individuals provided representative data on space use by each species over the study period (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 & Worton 1989; Seaman et al. 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 UD's 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 set h_{ref} equal to the 90th percentile of the frequency distribution of daily distances moved to eliminate extreme movements (95th for cheetahs, which had sparser data and few extreme movements) as the smoothing parameter. The smoothing parameter has a large influence on the shape and size of the UD with larger bandwidths smoothing more and leading to larger kernels with less change in utilization density between adjacent areas. 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's homerange, then combined and rescaled to result in a total utilization of 1 for the combined UD of the species. 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 of these 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 (ST Risk)

Data on direct encounters between predators and prey were obtained during carnivore 'follows' which are 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 for differences between predator species, while a two-sample t-test was used to test for a difference in mean chase distance between predator functional groups.

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Covariates of Wildebeest Movement Patterns

As described below (see *Model formation and data transformation*), 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) and AIC scores to identify which models would best describe these relationships. 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.

274 *Reproductive Status*: A growing fetus or a calf at heel might restrict the distance a wildebeest
275 moved. We classified reproductive status in three categories: 'Not Affected', 'Pre Parturition'
276 and 'Post Parturition'. For each female, the estimated date of parturition was determined as
277 the midpoint between the last direct observation of the wildebeest without calf, and the first
278 observation with a calf. We assigned "Pre Parturition" to the 30 days prior to parturition and
279 'Post Parturition' to the 30 days immediately after parturition, thus assuming that any effects
280 on movement would be strongest at the end of gestation when the energetic cost of gestation
281 is highest, or immediately after birth when calves are least capable (though quite precocial).
282 The rest of the days of the year were assigned to 'Not Affected'. *Distance to Water*: As
283 wildebeest need regular access to water, the distance from each wildebeest location to the
284 nearest potential water source was calculated. The study area is flat with shallow depressions
285 and is heavily inundated in the wet season, creating hundreds of pans (small ponds with no
286 drainage). During field work we recorded the GPS coordinates of pans with water. These
287 were cross-referenced with images from Google Earth, and unobserved pans were added by
288 inspecting the study area with Google Earth at high resolution. Some pans retain water year
289 round, so water in LPNP is never far in comparison to many ecosystems, but the distance to
290 the nearest pan with water increases in the dry season as some pans dry out. Our analysis
291 treats distance to water as a static variable (distance to the nearest location known to form a
292 pan), because the data were not adequate to state which pans held water on a given date. *Diet*
293 *Quality*: For grazing ungulates, dormant, senescent vegetation provides the least nutritional
294 value while actively photosynthesizing tissue usually provides nutrients above maintenance
295 levels (McNaughton 1979; Wilmshurst et al. 1995; Murray & Illius 2000; Shrader et al.
296 2006). Annual photosynthetic cycles are conspicuous from leaf to landscape levels, and the
297 influence of these cycles on diet quality can be measured by fecal chlorophyll concentration
298 (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 (30 ml each and up to 10 per herd) were collected from individual scats after observing a herd. These samples were frozen in liquid nitrogen until transportation 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 in the strongly seasonal environment of LPNP, 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; Pettoirelli 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 formation and data transformation* 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 (see table in Appendix II). 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 this system 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. 1, 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, λ , 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.

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. 2), 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). For each dependent variable, our full model to assess which parameters were related to movements of wildebeests included the UD of all carnivores as a measure of LT risk, time of day, day of year as a linear combination of sine and cosine with equal periods, our measure of food quality from fecal chlorophyll, food quantity as estimated through EVI values, distance to water and reproduction status. We tested if the final models with a lag one autocorrelation term performed better than without and found that both in the speed model (AIC value 21,063 vs. 21,400) and angle model (-11,610 vs. -11,481) the model with the lag one autocorrelation term performed better.

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 expressed as 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) and the best full model, based on AIC scores was selected. Subsequently we used likelihood ratio-test to test which individual parameters could be dropped from the full model. Several of the variables in the final model are seasonal and therefore potentially 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

Wildebeest moved more slowly in areas of high LT risk (Fig. 3), 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 themselves (Fig. 1). 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. 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 1).

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 (Table 2). 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. As Figure 3 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 3, Fig. 4). 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 3).

Factors other than risk had relatively small effects, but increased LT risk was associated with a substantial increase in deflection bearing changes ($b = 0.185$, $\text{SE} = 0.041$, $z = 4.46$, $P < 0.0001$). 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). 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 the mean predicted speed and deflection 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 km² in Fig. 5 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. 6) 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. 6).

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 (Fig. 7 and Table 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. 2017) 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 in response to LT risk. 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 Fig. 1). 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,

507 information might also be obtained from other wildebeest using sight, hearing or smell. Even
508 though immediate encounters with predators typically provoked fast, linear flight, the effect
509 of LT risk was to cause wildebeest to move more slowly and less linearly, i.e. to slow down
510 and turn more. The combined effect of slowing down and turning more is to allow wildebeest
511 more time to assess immediate ST risk when moving within an area of high LT risk (Fig. 7).
512 Even without improved assessment of ST risk, moving more slowly could reduce the
513 probability of encountering a predator (Gerritsen & Strickler 1977) or being detected
514 (Cleveland et al. 2012; Little et al. 2016), particularly if animals confine themselves to
515 structural refuges. Because wildebeest in this study were moving almost entirely in open
516 grassland, it is unlikely that moving less was associated with ‘hiding’, but reduced movement
517 would nonetheless be expected to reduce encounter rates with randomly located predators
518 (Viswanathan et al. 1999). There is a trade-off, however, because predators were not
519 randomly located – by slowing down and turning more in areas of high LT risk, wildebeest
520 spend more time in these dangerous areas (Fig. 7). This response should also make their
521 location more predictable on a time scale of several days, and this predictability could be
522 exploited by predators to increase encounter rates. These patterns suggest that in a
523 homogeneous, open environment without refuges, behavior that promotes wildebeests’ ability
524 to assess and detect ST risk is an important aspect of response to cues of high LT risk. Other
525 studies in this ecosystem (Creel et al. 2017; Droge et al. 2017) have shown that vigilance
526 increased when predators were nearby, and that this response was stronger in locations with
527 high LT risk (and concomitant reduction in grazing); This result aligns well with the
528 inference that reduced speed and linearity of movement are part of a suite of responses to
529 more cautiously assess ST risk in locations with high LT risk. More broadly, this inference
530 aligns with the earlier suggestions that prey sometimes tolerate (or even select) predator-rich

531 areas if there are advantages to doing so (for example, better opportunities to hide or escape)
532 (Wirsing et al. 2010).

533 Our results are somewhat in line with the results from Hopcraft et al. (2014) who
534 studied movement parameters of wildebeests and zebra (*Equus quagga*). They found that
535 most individual zebra moved more cautiously by slowing their daily movements and
536 changing their course of direction only during the wet season, not the dry season in areas with
537 high risks of predation. However, wildebeests generally did not respond to landscape features
538 related to predation during the wet season, and only weakly during the dry season. They also
539 stated that during the wet season, when the quality of grazing is at its peak, both zebras and
540 wildebeests move the greatest distances and in large groups. They attribute the larger
541 movement distances to bigger groups rapidly depleting localized grazing opportunities and
542 the smaller effects of movement from predation risk to the dilution of the individuals' risk of
543 predation by being in a large group. In LPNP the group sizes of wildebeests are much
544 smaller, rarely reaching thousands, and thus the dilution of predation risk much less. At the
545 same time the food quantity in LPNP is always low, with grass growing very sparsely and
546 thus diminishing the difference between good and bad grazing patches, and thus movements
547 related to this. These smaller differences in group size and forage quantity in LPNP might
548 have given us more power to detect relationships between movement parameters and
549 predation risk.

550 Prior studies have examined how ungulate movements respond to direct encounters
551 with predators (Fischhoff et al. 2007), to 'probable encounters' inferred from GPS data on
552 both predators and prey (Creel et al. 2013; Courbin et al. 2015; Martin & Owen-smith 2016),
553 or to the immediate presence of predators within a distance of 2-5 kilometers (Creel et al.
554 2005; Proffitt et al. 2009; Latombe et al. 2014). In general, it seems clear that an increase in
555 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, KM 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; Article 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, 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 et al. 2009). In other cases increased movement in areas exposed to hunters was detected, 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

581 areas containing refuges and species known to hide from perceived threats. Such a study
582 design may not allow prey to accurately assess spatial and temporal variation in risk patterns,
583 when compared to the responses of prey to LT patterns of risk in intact ecosystems like
584 LPNP. In human hunting studies (Root et al. 1988; Article et al. 2013; Little et al. 2016),
585 there is also an abrupt change in the intensity of risk in an area, with risk increasing over
586 relatively large areas for a period of intermediate length. Because these attributes are quite
587 dissimilar to the patterns of variation in ST and LT risk typical of undisturbed predator-prey
588 systems, it is difficult to relate inferences about effects of risk on movement from the two
589 types of studies.

590 The spatial and temporal scale of exposure to risk, and the heterogeneity of risk
591 within these spatial and temporal scales, all play roles in determining the optimal response of
592 prey to risk (Lima & Bednekoff 1999). Proactive adjustments of behavior in response to LT
593 risks depend on the ability of prey to assess this risk (and to pay any costs of assessment), and
594 on their ability to assess and respond to superimposed ST risks. Temporally, the activity
595 peaks of predators in LPNP are predictable, although risk is appreciable throughout much of
596 the 24 h day. African wild dogs concentrate hunting in the crepuscular periods, cheetahs
597 during the day and lions and hyenas during the crepuscular periods through the night (Dröge
598 et al. 2017). Spatially, the intensity of use of various areas by predators in our study area was
599 stable, especially for spotted hyenas (the most abundant predator), adding to the predictability
600 of LT variation in risk over space and time. The relative structural homogeneity of our study
601 area causes there to be little influence of vegetation structure on risk when compared to most
602 ecosystems, (though it also eliminates the possibility for wildebeest to retreat to natural
603 refuges). Collectively, these properties perhaps allow better assessment and response to
604 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 fine scale temporal, spatial, or individual 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.

Palmer et al. (2017) found that the lunar cycle plays a role in how prey behaves. In particular, they detected more relaxed behavior of wildebeests after moonrise, but wildebeests showed no response to the lunar position and strongly avoided areas of higher lion encounter risk. They found that all species, except gazelles, increased their level of relaxed behaviors during brighter nights and all species altered their distribution within areas with various levels and types of risk. This suggests that animals adjust their behavior and distribution on the risk they perceive. While our study was aimed to determine if prey responded measurably to probabilistic risk in the long run and we weren't able to include lunar luminosity into our models, it is interesting to note that such patterns can also be detected at different time scales. And, like Palmer et al. (2017) note, risk varies through time and space as well.

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 (Stabach et al. 2016) not considered here, such as the distance to the park boundary or distance to settlements. Stabach et al. (2016) noted that wildebeests consistently avoided anthropogenic features and dense woody cover, which were likely associated with predation risk. We did not include these variables (even though anthropogenic features can affect wildebeest density: M'Soka et al. 2016), 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 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. (2017) 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. As noted in the introduction these behavioral responses of prey to predation risk carry a cost to the prey. While we purely focused on movement, it is quite possible that the reduced movement is related to increased vigilance and actually costs more energy than is saved by moving less. These costs of prey can have considerable impacts on fecundity rates, survival and thus on population dynamics (Werner et al. 1983; Peckarsky et al. 1993; Boonstra et al. 1998; Pangle et al. 2007; Sheriff et al. 2009;

678 LaManna et al. 2016) making them important to consider in the management of areas and or
679 species which are exposed to predation risk.

680 In ecosystems that hold migratory wildebeest, this species, which can dominate the ungulate
681 community by a considerable margin, has strong influences on ecosystem function and on the
682 composition, size and distribution of the large carnivore guild. Thus, conservation and
683 management in such systems is strongly guided by consideration of factors that affect the
684 distribution, abundance and movements of wildebeest. Indeed, the boundaries of Serengeti
685 National Park were designed explicitly to encompass the migration of its famous wildebeest
686 population. The Greater Liuwa ecosystem is similarly dominated by wildebeest and they are
687 the most important prey for large carnivores in the ecosystem by an appreciable margin. Our
688 analysis contributes to the understanding of carnivore-ungulate conservation and
689 management in the Greater Liuwa ecosystem by showing that, perhaps contrary to intuition,
690 wildebeest do not speed up and linearize their movements in areas that are heavily used by
691 carnivores. Rather, they slow down and move in a pattern that allows more careful
692 assessment of immediate risks. This result has broad implications for understanding the
693 influence of predation risk on patterns of grazing in the Greater Liuwa ecosystem. More
694 generally, our results show that the influence of predation risk on herbivore movements is
695 much more complex than simple avoidance of areas of 'high risk'. As with other aspects of
696 behaviour, the movements of wildebeests are affected in a complex manner by different
697 responses to long term and short term variation in risk. Interactions between carnivores and
698 their prey are complex and direct and indirect. This study provides insight into the
699 relationship between wildebeests and carnivores in Liuwa Plain National Park and
700 surroundings which contributes to the management and conservation of both in the
701 ecosystem.

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Parameter	Effect on Speed	SE	Test Statistic	P
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 ¹	-0.483	0.017	-28.84	<0.0001
Distance to Water	0.017	0.007	2.33	0.02
Diet Quality: Low ²	-0.010	0.043	-0.23	0.82
Forage Quantity (EVI)	-0.014	0.008	-1.72	0.09
POST parturition ³	0.007	0.030	0.25	0.80
PRE parturition ³	-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 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. Model $R^2 = 0.20$.

Description of Risk	df	AIC	ΔAIC
All predators	9	21,062.75	0
Hyena	9	21,066.18	3.43
Coursers	9	21,069.47	6.72
Lion	9	21,081.21	18.46
Stalkers	9	21,140.42	77.67
Wild Dog	9	21,189.46	126.71
Cheetah	9	21,201.53	138.78
No Risk	8	21,439.94	377.19

Table 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 ¹	-0.570	0.026	-22.20	<0.0001
Distance to water	-0.004	0.011	-0.36	0.72
Diet Quality: Low ²	-0.014	0.067	-0.21	0.83
Forage Quantity (EVI)	-0.030	0.013	-2.29	0.02
POST parturition ³	0.036	0.047	-0.77	0.44
PRE parturition ³	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 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. $R^2 = 0.09$.

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

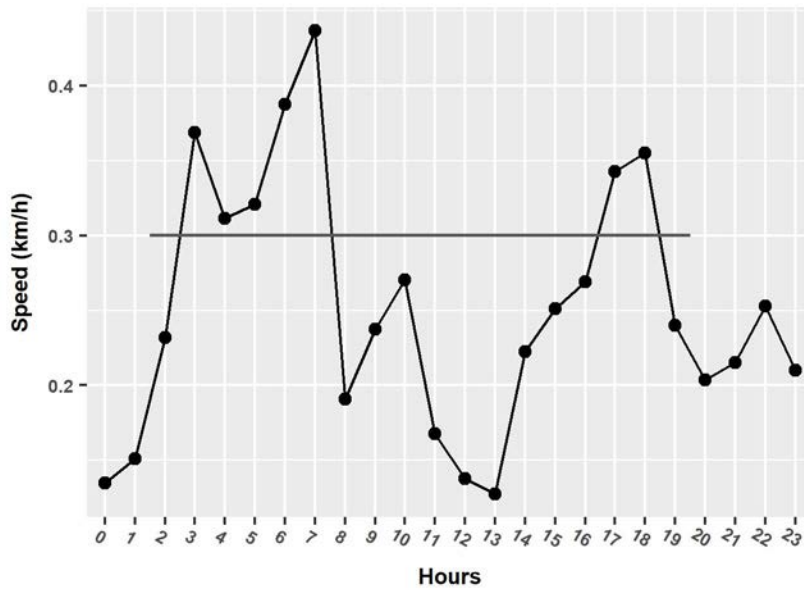


Figure 1: Average speed (km/h) of movement for periods centered on each hour of the day. The horizontal bar denotes threshold of 0.3 km/h defining time periods as High or Low Activity.

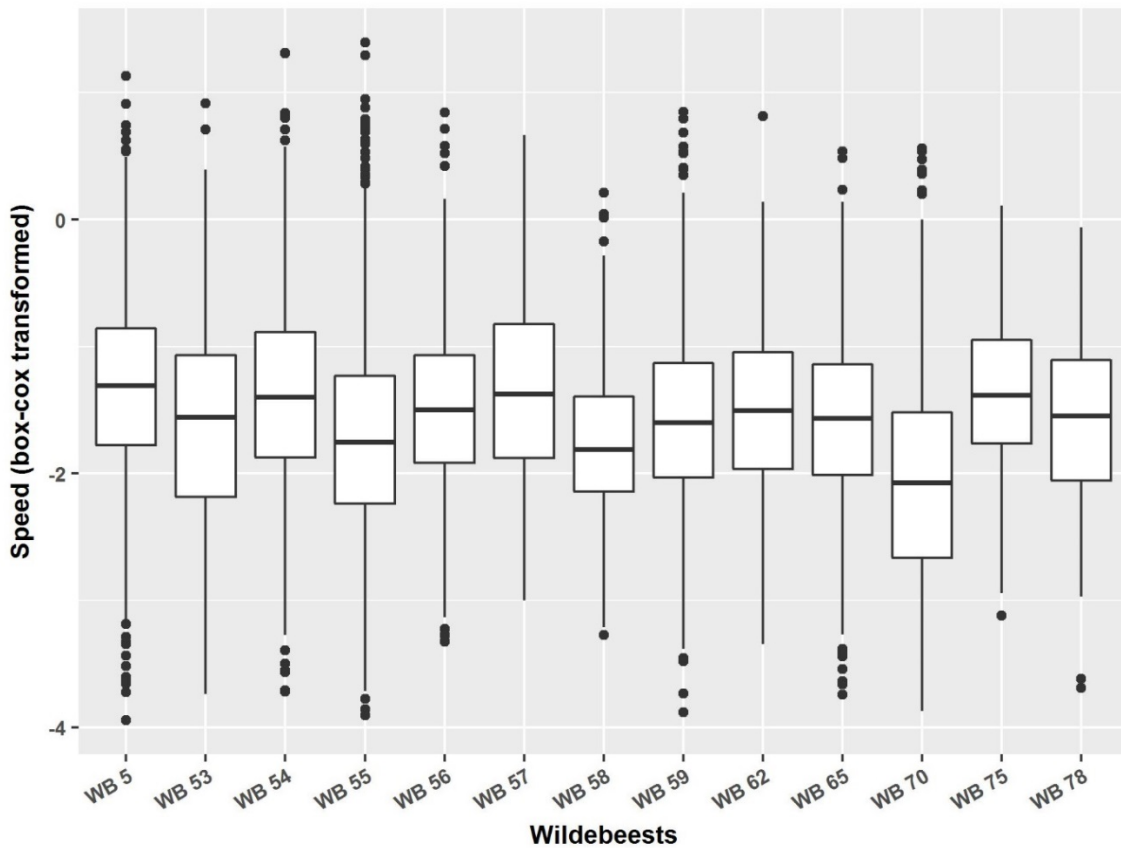
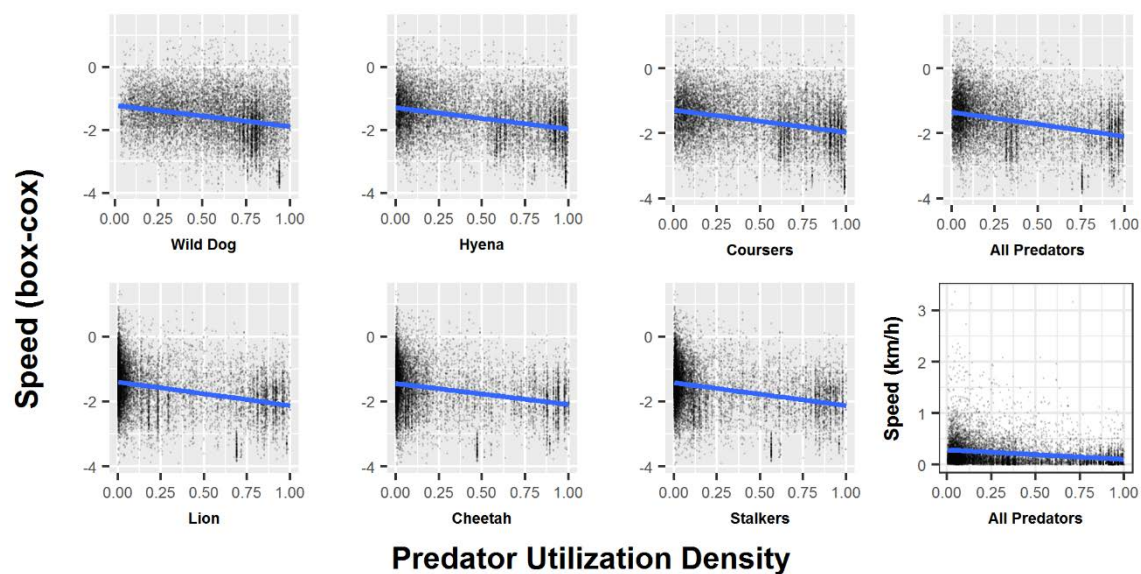


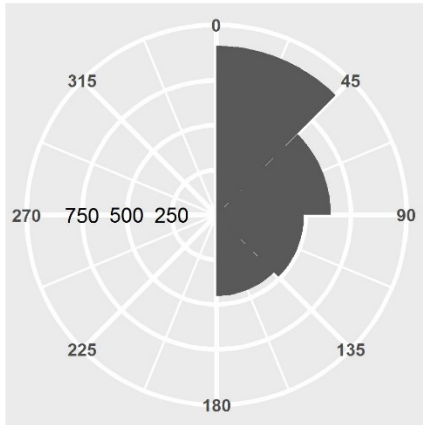
Figure 2: Variation within and between individual wildebeest in box-cox transformed speed of movement over 4 hour time steps (median, interquartile range, range, outliers).



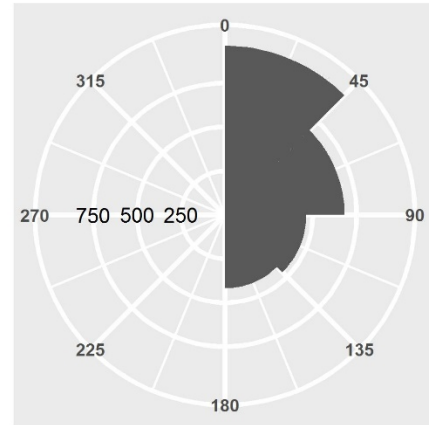
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Predator Utilization Density

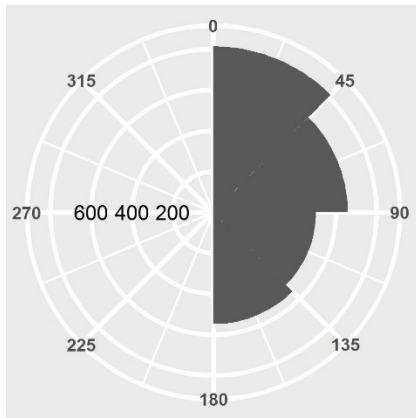
Figure 3: The effect of predation risk on speed of wildebeest movements for linear models containing different descriptions of LT risk (by predator species, predator type and for all predators combined). The lower right panel shows the backtransformed response of speed (km/h) to the LT risk from all predators, which was the best-supported model of risk (top right panel, and see Table 2).



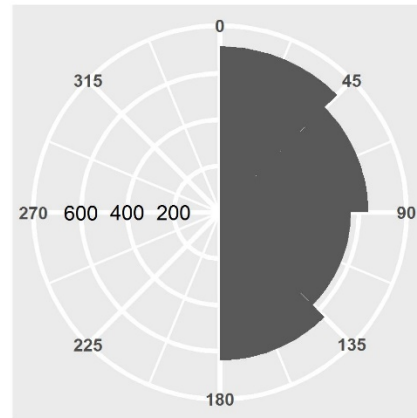
Lowest Risk



Moderate Risk



Higher Risk



Highest Risk

954

955 Figure 4: The frequency distributions of deflection angles for four categories of LT risk show
 956 that large deflections were more common under conditions of high risk. The four categories
 957 were defined by the quartiles of the LT risk distribution (as measured by the UD of all
 958 predators) and bearing categories reflect categories of turning angles.

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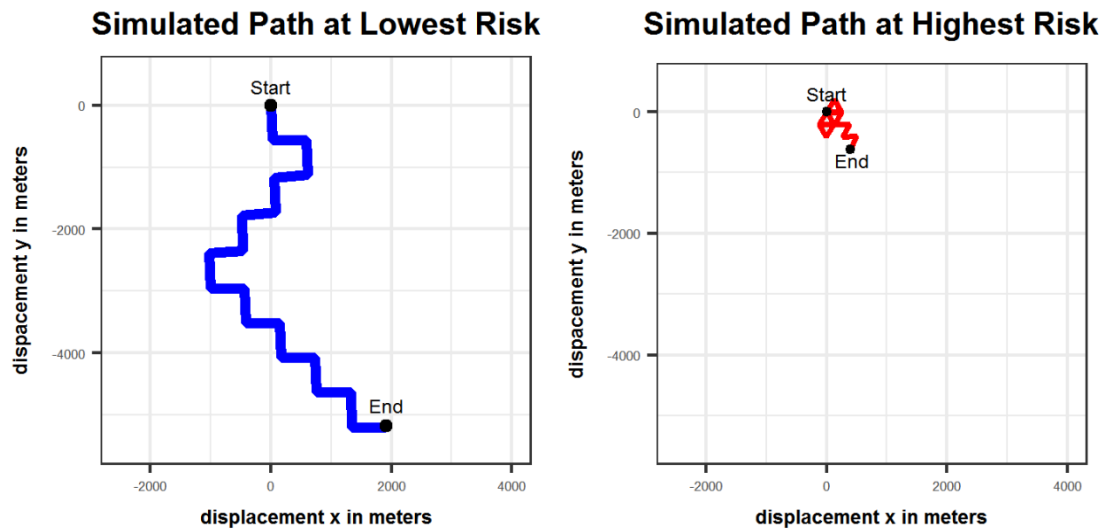


Figure 5: Simulation paths for 20 steps of 4 hours with predicted step lengths and deflection angles for areas with the lowest and highest LT risk. Grid cells are 1 km².

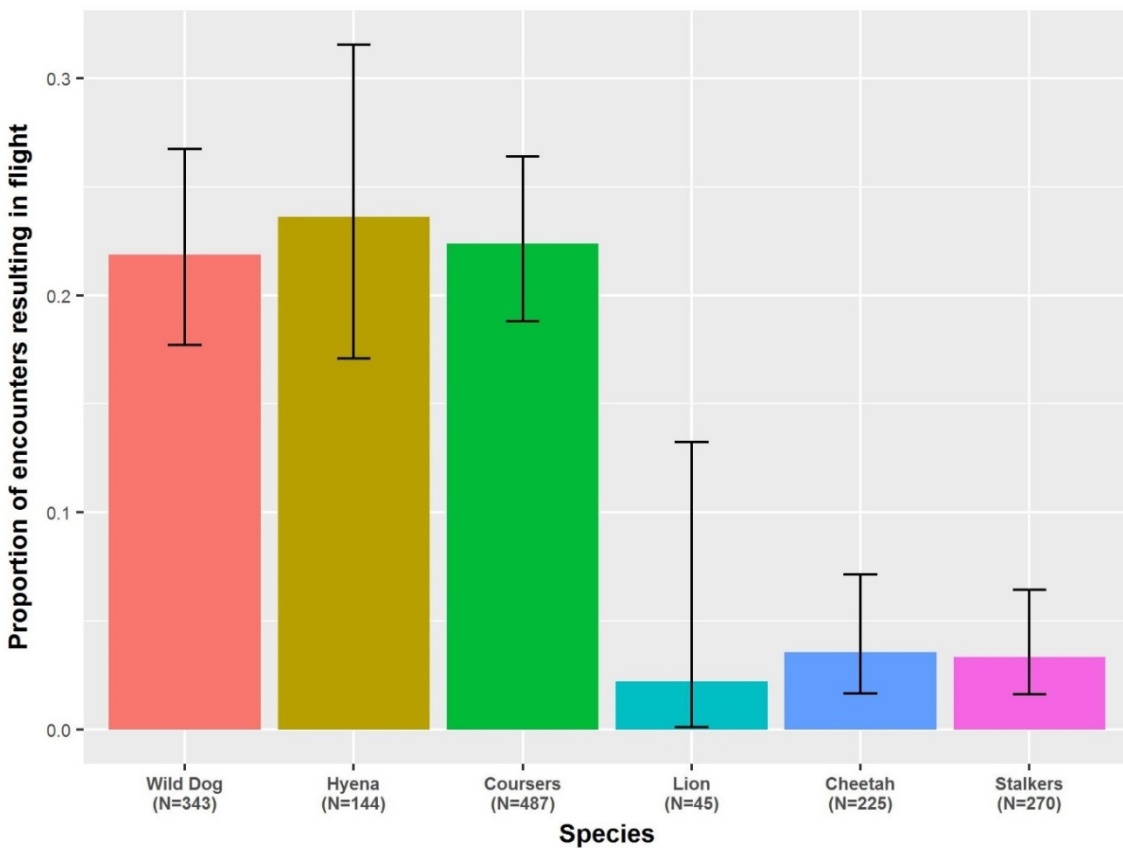


Figure 6: The proportion of encounters between predators and wildebeests that resulted in flight by the wildebeest. The whiskers represent the 95% binomial confidence interval.

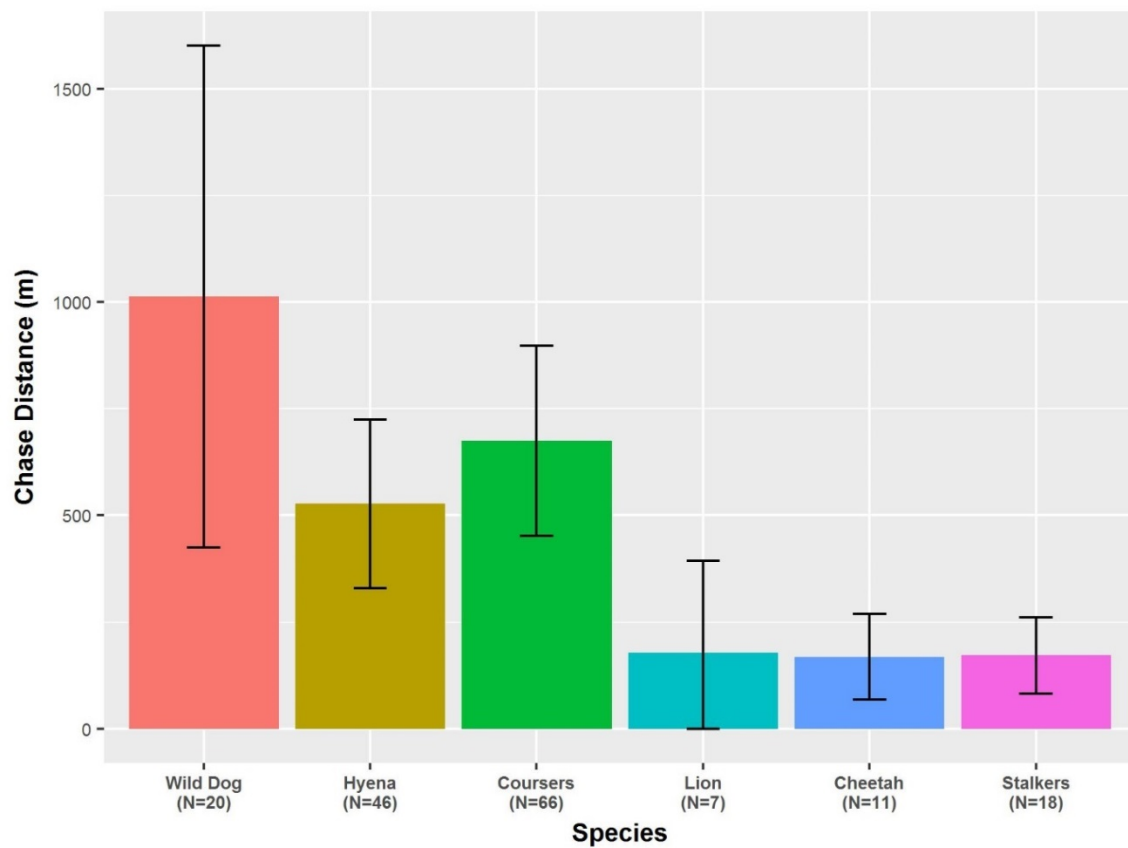
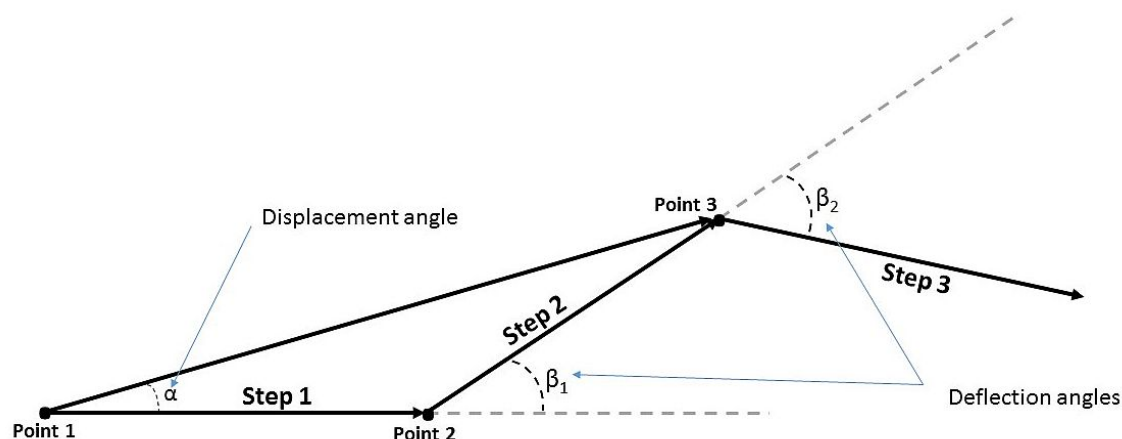


Figure 7: Average chase distances of wildebeests by the various predators and their 95% binomial confidence intervals.



Appendix I: Schematic view of step length (speed), displacement angle (α) and deflection angle (β) 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 α and deflection angle β_1 are both associated with Point 2.

Appendix II

Parameter	Effect on Speed	SE	Test Statistic	P
Intercept	-1.223	0.066	-18.6	<0.0001
LT risk (all predators)	-0.170	0.011	-14.59	<0.0001
Autocorrelation	0.157	0.01	14.95	<0.0001
Daily Activity: Low ¹	-0.582	0.025	-23.04	<0.0001
Distance to Water	-0.003	0.01	-0.32	0.75
Diet Quality: Low ²	-0.0001	0.064	-0.002	0.998
Forage Quantity (EVI)	-0.0279	0.012	-2.29	0.024
POST parturition ³	-0.129	0.077	-1.67	0.095
PRE parturition ³	-0.069	0.231	-0.3	0.76
Day of Year (sin)	-0.056	0.014	-4.12	<0.0001
Day of Year (cosine)	-0.0025	0.011	-0.22	0.825

Appendix II: Scaled effects on speed of movement by wildebeest on the dataset restricted to locations with an EVI value from within 10 days and LT risk described by the utilization distribution for all predators. The only difference is that on this restricted dataset there is no evidence that distance to water is related to differences in speed. 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. Model $R^2 = 0.20$.