




Short-term predation risk and habitat complexity influence cheetah antipredator behaviours

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Animals can reduce predation risk by increasing antipredator behaviours in areas of high long-term risk (risky places hypothesis), escalating antipredator behaviours when exposed to immediate risks (risky times hypothesis), varying responses to short-term risk based on long-term risk (risky times and risky places hypothesis, or predation risk allocation hypothesis) or altering antipredator behaviours based on habitat characteristics (habitat complexity risk mediation hypothesis). Most research on responses to predation risk has come from studies on herbivore prey, whereas little research has focused on mesopredator behavioural responses to risk. We studied antipredator behaviours of mesopredator cheetahs, *Acinonyx jubatus*, exposed to top predator risk from lions, *Panthera leo*, and leopards, *Panthera pardus*, by using a playback experiment to manipulate short-term predation risk in areas of differing long-term risk. We did not find support for the risky places hypothesis; cheetah vigilance was not influenced by long-term risk. On the contrary, we found support for the risky times hypothesis; cheetahs were more vigilant and more likely to flee following lion and leopard playbacks. Additionally, we did not find support for the risky times and risky places hypothesis or the predation risk allocation hypothesis; cheetah antipredator behaviours following a predator playback were not associated with long-term predation risk. Finally, cheetahs had higher baseline vigilance in areas of open vegetation but were more likely to flee from lion sounds in areas of dense vegetation and from leopards in areas of open vegetation. We highlight the importance of understanding spatial and temporal factors that influence mesopredator risk perception and show that antipredator behaviours can differ among trophic levels.

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Predators can influence lower trophic levels through direct predation as well as indirectly through changes in behaviour (Creel & Christianson, 2008). These predator-induced changes in behaviour can scale-up and affect population demography (Creel, Christianson, Liley, & Winnie, 2007; LaManna & Martin, 2016) and structure entire ecosystems (Ford et al., 2014; Suraci, Clinchy, Dill, Roberts, & Zanette, 2016). As predator species worldwide are undergoing population declines and range contractions (Ripple et al., 2014; Wolf & Ripple, 2017), it is important to understand how predators influence the demography and behaviour of lower trophic levels, through either direct predation or nonconsumptive effects (Creel & Christianson, 2008; Creel et al., 2007). In turn,

understanding how top predators influence community level processes can help prioritize conservation actions that address the direct and indirect effects of carnivores on other populations.

Animals under the risk of predation can reduce predation risk through behaviours such as minimizing the amount of time in risky areas (Thaker et al., 2011), increasing vigilance or alarm behaviour (Lima, 1987), or fleeing from risky situations (Cooper, 2003; Stankowich & Coss, 2007). These antipredator behaviours can be beneficial for avoiding predation but can also come at energetic or fitness costs because of trade-offs with foraging or parental care (Lima, 1987). Therefore, animals need to accurately assess predation risk in order to maximize the benefits of antipredator behaviours and minimize their costs.

Perception of predation risk and associated antipredator behaviours can depend on a variety of factors. Animals might exhibit more antipredator behaviours in areas of high long-term predation risk (i.e. the 'risky places' hypothesis; Creel, Winnie, Christianson, &

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Liley, 2008). Alternatively, animals might exhibit more antipredator behaviours when exposed to an immediate risk (i.e. the 'risky times' hypothesis; Creel et al., 2008). Additionally, the long-term risk of predation can affect how animals respond to short-term predation risk, either by exhibiting higher responses to short-term risk in areas of high-long term risk (i.e. the 'risky times and risky places' hypothesis; Dröge, Creel, Becker, & M'soka, 2017), or by exhibiting the highest response to short-term predation risk when long-term predation risk is low ('predation risk allocation' hypothesis; Lima & Bednekoff, 1999).

In addition, environmental characteristics such as habitat complexity can influence the responses of prey to predation risk. Although dense vegetation might serve as a refuge for prey species, it might also reduce visibility, which in turn could increase predation risk (Camp, Rachlow, Woods, Johnson, & Shipley, 2012; McCormick & Lönnstedt, 2013). The costs and benefits of habitat complexity might also differ when considering short-term versus long-term risk. If a predator species and a prey species rely on the same habitat features, the prey species can either increase antipredator behaviours because long-term risk is predictable in certain habitat types (Schmitz, Miller, Trainor, & Abrahms, 2017), or the predator can increase encounter rates with prey in the shared habitat because predators are able to readily predict the locations of prey (Smith et al., 2019). Thus, areas of dense vegetation might serve as a strong proxy for long-term predation risk in systems with ambush predators and induce increased antipredator behaviours to reduce the risk of detection or capture. Finally, responses to predation risk might be affected by sex. Because males and females often differ in their reproductive tactics and parental care, there can be sex-specific differences in responses to predation risk (Lima & Dill, 1990).

Most of our understanding of antipredator behaviours and risk perception comes from studies of herbivore prey species (Dröge et al., 2017). Although recent research has investigated spatial and temporal partitioning of apex predators and mesopredators as a form of risk avoidance (Broekhuis, Cozzi, Valeix, McNutt, & Macdonald, 2013; Cozzi et al., 2012; Swanson, Arnold, Kosmala, Forester, & Packer, 2016), less research has been conducted on reactive antipredator behaviours such as vigilance in mesopredators (but see Chitwood, Lashley, Higdon, DePerno, & Moorman, 2020; Durant, 2000), especially compared to studies on herbivore vigilance. Mesopredators need to avoid the risk of predation by top predators, while still finding and catching prey. However, dissimilar to prey species, carnivorous mesopredators might not often experience trade-offs between antipredator behaviour and foraging, because they hunt relatively infrequently compared to foraging herbivores (Jeschke, 2007). Additionally, because apex predators typically prey on herbivores rather than mesopredators (Palomares & Caro, 1999), the behavioural responses of mesopredators to long-term or short-term predation risk might differ from responses of herbivore prey. Therefore, a greater understanding on how mesopredators perceive and respond to variation in predation risk is needed.

The large carnivore guild of South Africa offers an ideal system to investigate risk perception in mesopredators. Cheetahs, *Acinonyx jubatus*, are subordinate to lions, *Panthera leo*, and leopards, *Panthera pardus*, and the majority of cheetah mortality is from lions and leopards (Gigliotti, Slotow, Hunter, Fattebert, Sholto-Douglas, et al., 2020b; Laurenson, 1994). Previous research has shown that cheetahs respond to short-term risk from apex predators, through behavioural adjustments (Durant, 2000), and respond to long-term risk by altering fine-scale habitat use patterns (Swanson et al., 2014). However, although cheetahs have been found to alter their space use in response to both long- and short-term risk (Broekhuis et al., 2013), less is known about how cheetahs respond to both long-term and short-term risk simultaneously using other forms of antipredator

behaviours such as vigilance. Additionally, recent research has shown that cheetah survival is driven by both long-term and short-term habitat use in relation to vegetation complexity and predation risk (Gigliotti, Slotow, Hunter, Fattebert, Sholto-Douglas, et al., 2020a). Therefore, spatial variation in antipredator behaviours might influence spatial patterns of demography.

Here we use long-term data from an intensively studied cheetah population in a study area with known spatial variation in long-term predation risk and manipulated short-term predation risk to investigate how mesopredators such as cheetahs perceive predation risk. Specifically, we tested the following five main hypotheses, and associated predictions, related to risk perception (Table 1).

- (1) Risky places hypothesis: cheetah antipredator behaviours depend on long-term predator cues.
- (2) Risky times hypothesis: cheetahs antipredator behaviours depend on short-term predator cues.
- (3) Risky times and risky places hypothesis or predation risk allocation hypothesis: cheetah antipredator behaviours depend on a combination of long-term and short-term predator cues.
- (4) Habitat complexity risk mediation hypothesis: cheetah antipredator behaviours depend on vegetation characteristics.
- (5) State-specific risk responses: cheetah antipredator behaviours will differ between females with cubs and males.

By identifying factors that influence antipredator behaviours in cheetahs, we can obtain a greater understanding of how mesopredators perceive predation risk, which in turn can be used to help understand the role of apex carnivores in ecological systems and how community level effects of predation risk could be affected by apex carnivore declines.

METHODS

Study Area

We studied cheetah responses to predation risk in the Mun-Ya-Wana Conservancy (also known as Phinda Private Game Reserve) in KwaZulu-Natal, South Africa. The Conservancy is 285 km² and is surrounded by electrified game fencing. The dominant vegetation type is broad-leaf woodland, with open grasslands and semi-open wooded grasslands interspersed throughout the reserve. The elevation of the Conservancy ranges from 4 to 201 m above sea level. The climate is subtropical with warm, dry winters (April–September) and hot, humid summers (October–March), with the majority of rain falling in the summer. Cheetahs and lions were reintroduced into the reserve in 1992 and have been monitored since (Hunter, 1998; Hunter et al., 2007), and they exist at densities of 0.06–0.18 cheetahs/km² and 0.06–0.17 lions/km². Leopards have historically occurred in the study area and currently exist at a stable population density (Balme, Slotow, & Hunter, 2010). Predation is the main cause of cheetah mortality in the system, with lions (63.3% of cheetah cub predation deaths and 35.7% of adult cheetah predation deaths) and leopards (3.3% of cheetah cub predation deaths and 21.4% of adult cheetah predation deaths) comprising the most predation mortality (Gigliotti et al., 2020b). Although spotted hyaenas, *Crocuta crocuta*, also occur at low densities in the study area and compete with cheetahs for resources, they rarely kill cheetahs in our study population (Gigliotti et al., 2020b), so we did not consider them in our study.

Playback Sounds

We tested hypotheses related to mesopredator perception of predation risk by conducting a playback experiment. We used two

Table 1
Hypotheses and associated predictions, response variables and model covariates related to cheetah responses to short- and long-term risk

Hypothesis	Predictions	Response variable	Model covariates ^a
Risky places	Antipredator behaviours will be stronger in areas of higher long-term risk	(1) Proportion of time vigilant preplayback	(1) Lion risk (2) Leopard risk
Risky times	Antipredator behaviours will be stronger in response to short-term risk (lion and leopard playbacks) compared to control playbacks (hoopoe playbacks)	(1) Change in vigilance (2) Probability of fleeing	(1) Playback type (lion, leopard or hoopoe)
Risky times and risky places	Antipredator behaviours in response to short-term risk (predator playbacks) will be stronger in areas of higher long-term risk	(1) Change in vigilance (2) Probability of fleeing	(1) Playback type*lion risk (2) Playback type*leopard risk
Predation risk allocation hypothesis	Antipredator behaviours in response to short-term risk (predator playbacks) will follow a nonlinear relationship with the strongest responses in areas of lower long-term risk	(1) Change in vigilance (2) Probability of fleeing	(1) Playback type*lion risk ² (2) Playback type*leopard risk ²
Habitat complexity risk mediation hypothesis	Antipredator behaviours will be stronger in areas of dense vegetation	(1) Proportion of time vigilant preplayback (2) Change in vigilance (3) Probability of fleeing	(1) EVI (2) EVI*playback type (3) EVI*lion risk (4) EVI*leopard risk
State-specific risk responses	Female cheetahs with cubs will exhibit stronger antipredator behaviours compared to male cheetahs	(1) Proportion of time vigilant preplayback (2) Change in vigilance (3) Probability of fleeing	(1) Sex*playback type (2) Sex*lion risk (3) Sex*leopard risk

^a All models include cheetah identity (ID) as a random effect.

predator sounds (lion and leopard) as treatment sounds (e.g. stimuli tested to elicit a predicted response) and sounds of African hoopoes, *Upupa africana*, as control sounds (e.g. stimuli that act as comparisons). We selected the hoopoe as our control because they are active throughout the day, are found across the entirety of our study area, are neither potential predators nor prey for cheetahs and have similar sound qualities (e.g. mean frequency, maximum frequency, mean amplitude) to lions and leopards. We acquired sound clips from online audio databases and edited them to 10 s exemplars, which are sound clips representing a specific species (5 exemplars per species for a total of 15 separate exemplars). For lion and leopard exemplars, we used contact call vocalizations of single animals to mimic the presence of a predator, rather than the direct aggression of a predator. We ensured that all exemplars across all treatments (lion and leopard sounds) and controls (hoopoe sounds) were similar with regard to sound frequency and amplitude (Blumstein, Cooley, Winternitz, & Daniel, 2008) and ensured similar volume across exemplars by testing decibel levels at a distance of 15 m using the Decibel X Sound Level Analyzer for iPhones (Sky Paw Co. Ltd, Hanoi, Vietnam). All playbacks were conducted using a portable speaker (Klipsch Groove, Indianapolis, IN, U.S.A.) set-up inside an open-top vehicle, at an average volume of 100 dB, which is within the range of naturally occurring lion and leopard sounds (Grinnell & McComb, 2001; Schel & Zuberbühler, 2009). Cheetahs in this study areas are well habituated to vehicles, so the presence of a vehicle alone was unlikely to affect their behaviour.

Data Collection

We collected data from February 2018 to September 2019. Data collection was approved by the Institutional Animal Care and Use Committee of Clemson University (IACUC no. AUP2017-077). When we encountered a nonsleeping adult cheetah, we calculated the GPS location of the animal based on its bearing and distance from the vehicle, the number of individuals (including cubs) present, the distance of the vehicle to the animal, the time of day, the weather (overcast, sunny, or any type of precipitation), the wind speed (categorized into high, medium and low categories) and identified any other animals or vehicles visible within the area. Playbacks

were conducted an average \pm SE of 15.5 ± 1.1 m from the focal cheetahs and began approximately 5–10 min after encountering an animal.

If multiple adult cheetahs were at the same sighting, we randomly selected one to be the focal animal. In addition, we randomly selected a treatment and exemplar for each playback. Using a handheld video camera (Sony HDRX405 Handycam, Tokyo, Japan) we recorded the baseline behaviour of the focal animal for 5 min. We then played a 10 s exemplar and recorded an additional 5 min of video postplayback. To ensure that cheetahs were not habituated or negatively affected by the playbacks, we only conducted playbacks on individual cheetahs a maximum of twice per week, and we did not conduct playbacks on successive days. The average \pm SE time between playbacks on the same individual cheetah was 49.6 ± 8.2 days. We did not collect data on cheetah cubs, female cheetahs with cubs younger than 6 months or cheetahs that were at kill sites.

Environmental Covariates

For each playback location we created a 50 m buffer and extracted environmental covariates. We selected 50 m as our buffer distance because cheetahs are likely able to perceive conditions within this distance, as evidenced by their ability to locate prey 50 m away (Eaton, 1970). Given that encounter risk and predation risk are positively related (Moll et al., 2017), we used encounter risk of lions and leopards as a proxy for true predation risk. Cheetahs are killed by predators throughout the study area, independent of habitat type (Gigliotti et al., 2020a); therefore, the risk of encountering predators, rather than habitat features, should represent spatial variation in risk. We estimated lion encounter risk by creating seasonal utilization distributions of lion and leopard sightings data (see Gigliotti et al., 2020a for full methods). In short, trained guides collected data on sightings of lions and leopards during October 2017 – September 2019, which we then divided into seasons corresponding to our behavioural data collection. Because visual sightings can lead to spatial biases in location data, we first evaluated potential spatial biases in the data and determined that the data were suitable for estimating course-scale

distributions (Appendix). Using the sightings of lions and leopards separately, we created seasonal utilization distributions (UDs) using a fixed kernel estimator with plug-in bandwidth selection (Gitzen, Millsaugh, & Kernohan, 2006). For both lions and leopards, our risk rasters were at a resolution of 30 m and scaled from 0 to 1, where 0 indicated no risk of encounter and 1 indicated a high risk of encounter. Finally, we used seasonal enhanced vegetation index (EVI) as an index for vegetation complexity because it is correlated with vegetation structure in Africa, with open areas having low EVI values and areas with dense vegetation having high EVI values (Tsalyuk, Kelly, & Getz, 2017). We obtained EVI data at 250 m resolution (https://lpdaac.usgs.gov/data_access/data_pool) and calculated seasonal EVI values on a yearly basis by averaging EVI values across the entirety of a season. We used our 50 m buffer to extract average EVI values corresponding to the season when each data point was collected.

Video Analysis

We analysed videos using the behavioural analysis program JWatcher (Blumstein & Daniel, 2007). Following Caro (1994), we defined cheetah vigilance behaviour as time spent visually scanning the surrounding area. To this end, we considered lying alert, sitting and standing body positions as vigilance (Caro, 1994). For each trial, we calculated the proportion of time vigilant pre- and postplayback, as well as the change in vigilance between pre- and postplaybacks (i.e. the proportion of time vigilant postplayback minus the proportion of time vigilant preplayback). We also recorded whether the focal cheetah fled the playback location, which we defined as moving out of sight, or greater than 100 m. All cheetahs were stationary prior to playbacks; therefore, we did not need to assess changes in locomotion speed.

Data Analysis

To ensure that additional factors were not influencing responses to playback sounds, we first ran analyses to assess the effects of wind, distance to focal animal and time of day on vigilance, both pre- and postplayback. For all analyses, we ran models in program R (R Core Team, 2019) and assessed significance using an α value of 0.05.

Risky Places Hypothesis

To assess how long-term predation risk influences antipredator behaviour (Table 1), we analysed baseline vigilance behaviour prior to playback of sounds. Therefore, any behaviours would have been a result of background or long-term spatial covariates. Although cheetahs could potentially minimize long-term risk by selecting for low-risk habitats, previous research in this study area found that cheetahs use all areas of reserve, irrespective of risk (Gigliotti et al., 2020a; Rostro-García, Kamler, & Hunter, 2015), and thus investigating fine-scale antipredator behaviours might offer more insight into response to long-term risk than habitat selection. For our risky places analyses, we included data from all trials, regardless of the sound that was eventually played. We used beta regression models with a random effect of cheetah identity (ID) using the glmmTMB R package (Brooke et al., 2017) to compare the baseline proportion of time vigilant with the long-term predator encounter risk or EVI within 50 m. Because males and females might have different responses to long-term risk, we included sex as a factor in all models. Because of a low sample size of female cheetahs without cubs, we only included males and females with cubs older than 6 months in our analysis including sex.

Risky Times Hypothesis

To assess how short-term predation risk influenced vigilance (Table 1), we ran linear mixed effects models with the difference between the proportion of time vigilant between post and preplaybacks as our response variable and playback type as our predictor variable, using the lmer function in the lme4 R package (Bates, Maechler, Bolker, & Walker, 2015). To assess how short-term predation risk influenced probability of fleeing, we ran logistic regression models with a binary response variable (flee = 1; did not flee = 0) and playback type as our predictor variable. We included cheetah ID as a random effect in all models. We also tested for differences in short-term perception of predation risk by sex, by including an interaction between sex and playback type for the change in vigilance and the probability of fleeing models separately. Because of a low sample size of female cheetahs without cubs, we only included males and females with cubs older than 6 months in our analysis including sex.

Risky Times and Risky Places Hypothesis or Predation Risk Allocation Hypothesis

We assessed how long-term risk might influence perception of short-term predation risk (Table 1). We used linear mixed effects models with change in proportion of time vigilant between post- and preplaybacks as our response variable, and an interaction between long-term encounter risk and playback type as our predictor variables (Table 1), using the lmer function in the lme4 R package (Bates et al., 2015). By including an interaction between long-term encounter risk and the playback type, we were able to assess changes in vigilance in response to predator playbacks and long-term risk, relative to the changes in vigilance following the control sounds. We also used logistic regression with a binary response variable (flee = 1; did not flee = 0) and an interaction between long-term encounter risk and playback type as our predictor variable (Table 1) to analyse the effects of long-term encounter risk on the probability of fleeing postplayback. In addition to testing for a linear relationship between long-term risk and change in vigilance or probability of fleeing, we assessed quadratic terms of lion risk and leopard risk, which would be consistent with the predictions of the predation risk allocation hypothesis (Table 1). Finally, we tested the hypothesis that vegetation complexity would influence short-term responses to risky situations by analysing the influence of EVI on the change in vigilance or the probability of fleeing, by including interactions between EVI and playback type (Table 1). For all models we included cheetah ID as a random effect.

RESULTS

We collected data on 16 individual cheetahs for a total of 78 trials. The trials consisted of 19 hoopoe playbacks, 21 leopard playbacks, 23 lion playbacks and 15 trials where we only collected preplayback data. The locations where we conducted trials varied in terms of environmental conditions when we considered lion encounter risk (mean = 0.36; range 0–0.91), leopard encounter risk (mean = 0.28; range 0–0.99) and EVI (mean = 0.30; range 0.19–0.39). There was no relationship between preplayback vigilance and wind speed ($P_{\text{low wind-high wind}} = 0.82$; $P_{\text{medium wind-high wind}} = 0.26$; $P_{\text{low wind-medium wind}} = 0.35$), distance from observer to cheetah ($P = 0.98$) or time of day ($P = 0.64$) and no relationship between postplayback vigilance and wind speed ($P_{\text{low wind-high wind}} = 0.82$; $P_{\text{medium wind-high wind}} = 0.28$; $P_{\text{low wind-medium wind}} = 0.18$), distance from observer to cheetah ($P = 0.76$) or time of day ($P = 0.77$); therefore, we were able to include data from all trials in our subsequent analyses.

Risky Places Hypothesis

The long-term encounter risk of lions and leopards did not influence baseline levels of cheetah vigilance regardless of whether we considered only the risk of lions ($P = 0.94$) or only the risk of leopards ($P = 0.93$). Additionally, baseline vigilance was not influenced by an interaction between long-term encounter risk and sex, regardless of whether we considered only the risk of lions ($P = 0.91$) or only the risk of leopards ($P = 0.68$).

Habitat complexity and encounter risk were not strongly correlated ($|r| = 0.41$). Habitat complexity was related to baseline levels of cheetah vigilance for female cheetahs with cubs ($P = 0.04$), with female cheetahs exhibiting higher proportions of time vigilant in open areas (Fig. 1), although this same relationship was not significant for males ($P = 0.08$). In the most open areas (e.g. areas with the lowest EVI), female cheetahs with cubs spent a mean \pm SE of $62.3 \pm 15.1\%$ of time vigilant, whereas in the most closed areas female cheetahs with cubs spent $16.8 \pm 6.8\%$ of time vigilant.

Risky Times Hypothesis

Across all individuals, cheetahs changed vigilance following lion ($P < 0.01$) and leopard ($P < 0.01$) playbacks, compared to hoopoe playbacks (Fig. 2a), but change in vigilance behaviour did not differ among lion and leopard trials ($P = 0.45$). Specifically, cheetah increased vigilance by $61.0 \pm 8.2\%$ following leopard playbacks and increased vigilance $52.6 \pm 8.8\%$ following lion playbacks. Cheetahs were more likely to flee following leopard playbacks ($P = 0.05$) compared to hoopoe playbacks (Fig. 2b), but the probability of fleeing did not differ between lion and hoopoe trials ($P = 0.21$).

When comparing change in vigilance behaviour by sex, female cheetahs with cubs increased vigilance more following leopard playbacks than male cheetahs ($P = 0.05$), with females with cubs increasing vigilance $82.8 \pm 8.0\%$ following a leopard playback and males increasing vigilance by $49.4 \pm 11.5\%$ following a leopard playback (Fig. 3). There was no difference in change in vigilance between males and females following lion playbacks ($P = 0.97$) or hoopoe playbacks ($P = 0.52$). There was no difference in the probability of fleeing between males and females following lion ($P = 0.99$), leopard ($P = 0.97$) or hoopoe ($P = 0.98$) playbacks.

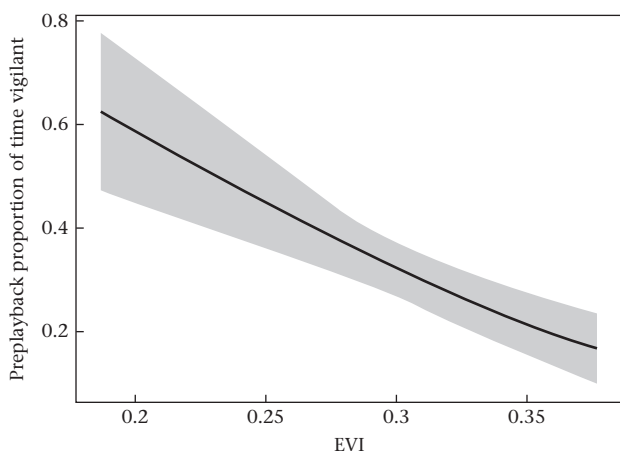


Figure 1. Relationship between average enhanced vegetation index (EVI) within 50 m of playback location and baseline vigilance for female cheetahs with cubs, Mun-Ya-Wana Conservancy, KwaZulu-Natal, South Africa, 2018–2019. Shaded regions indicate 95% confidence intervals.

Risky Times and Places Hypothesis or Predation Risk Allocation Hypothesis

There was not a linear relationship (as predicted by the risky times and places hypothesis) between long-term lion encounter risk and change in cheetah vigilance ($P = 0.98$) or probability of fleeing ($P = 0.91$) following lion playbacks, relative to the change in vigilance following hoopoe playbacks. Similarly, there was not a linear relationship (as predicted by the risky times and places hypothesis) between long-term leopard encounter risk and change in cheetah vigilance ($P = 0.82$) or probability of fleeing ($P = 0.49$) following leopard playbacks, relative to the change in vigilance following hoopoe playbacks.

There was not a quadratic relationship (i.e. lion or leopard risk squared; as predicted by the predation risk allocation hypothesis) between long-term lion encounter risk and change in cheetah vigilance ($P = 0.67$), or probability of fleeing ($P = 0.82$) following lion playbacks relative to the change in vigilance following hoopoe playbacks. Similarly, there was not a quadratic relationship (as predicted by the predation risk allocation hypothesis) between long-term leopard encounter risk and change in cheetah vigilance ($P = 0.29$) or probability of fleeing ($P = 0.87$) following leopard playbacks relative to the change in vigilance following hoopoe playbacks.

There was no relationship between habitat complexity and change in cheetah vigilance following either lion ($P = 0.58$) or leopard ($P = 0.27$) playbacks relative to hoopoe playbacks. However, cheetahs (both male and female) were more likely to flee following a lion sound in areas of higher EVI ($P < 0.01$) and following a leopard sound in areas of lower EVI ($P < 0.01$; Fig. 4) relative to hoopoe playbacks.

DISCUSSION

We found that cheetah antipredator behaviour varied based on spatial and temporal factors. Our results build on previous research on cheetah antipredator behaviours and habitat use (Broekhuis et al., 2013; Dröge, Creel, Becker, & M'soka, 2016; Durant, 2000; Swanson et al., 2016) to reveal that cheetah antipredator behaviours are reactive rather than predictive. Not only do our results offer insight into drivers of cheetah antipredator behaviours, but they also indicate that antipredator behaviours may differ across trophic levels. In particular, differences between our results and studies of risk perception in herbivore prey highlight the need to consider how top-down effects on behaviour might vary among multiple trophic levels within a system.

We found that long-term encounter risk did not influence cheetah vigilance, indicating that the risky places hypothesis does not always adequately describe antipredator behaviours. There are three possible explanations as to why we did not find support for the risky places hypothesis. First, differences in the ecology of herbivore prey and mesopredators could explain our observed lack of support for this hypothesis. Several studies of prey behaviour in relation to long-term predator risk in a variety of systems have found higher antipredator behaviours in areas of high long-term predation risk (Donadio & Buskirk, 2016; Lung & Childress, 2007; Thaker, Vanak, Owen, Ogden, & Slotow, 2010; Valeix, Fritz, et al., 2009), although there are trade-offs for prey between antipredator behaviour and foraging (Lima, 1987). Additionally, prey species often exhibit predictive responses to long-term risk by avoiding areas with the highest risk of predation (Thaker et al., 2011; Valeix, Loveridge, et al., 2009). Unlike for prey, there likely is not a strong vigilance–foraging trade-off for mesopredators that do not forage continuously, so they can exhibit some level of antipredator behaviour regardless of the background level of risk without

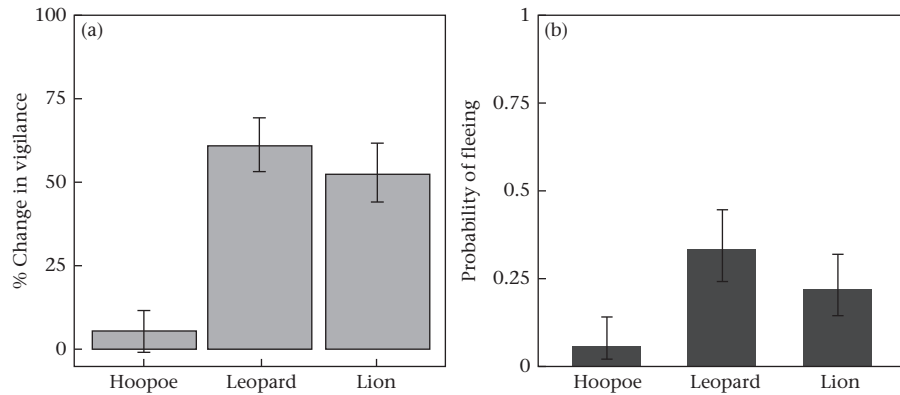


Figure 2. Relationship between playback type and cheetahs' (a) percentage of change in vigilance or (b) probability of fleeing, Mun-Ya-Wana Conservancy, KwaZulu-Natal, South Africa, 2018–2019. Means and error bars are based on raw data; error bars represent SE.

incurring negative energetic consequences. Indeed, we found that most cheetahs exhibited some baseline vigilance behaviour regardless of background levels of risk.

Second, differences between prey and mesopredators ecology in relation to lethal encounters with apex predators might lead to our results showing that long-term predation risk does not influence cheetah antipredator behaviours. Even in areas of high long-term predation risk, encounters between apex predators and mesopredators do not always result in mortality (Linnell & Strand, 2000). For example, wolves (*Canis lupus*) often encounter coyotes, *Canis latrans*, at kill sites, but the majority of these encounter do not end in coyote mortality (Merkle, Stahler, & Smith, 2009). In our system, there is typically a large amount of spatial overlap between cheetahs, lions and leopards (Swanson et al., 2014), and cheetahs are adept at fleeing from apex predators (Hunter et al., 2007b). Additionally, cheetahs often exhibit course-scale spatial overlap with lions and leopards but use fine-scale spatial and temporal adjustments to avoid encounters (Broekhuis et al., 2013; Hayward & Slotow, 2009; Vanak et al., 2013) indicating that cheetah responses to predation risk are reactive rather than predictive, and thus, increased antipredator behaviour in areas of high risk does not provide a large benefit.

Third, the perception of long-term risk requires the ability to assess predation risk (Weissburg, Smee, & Ferner, 2014), which necessitates reliable cues of risk as well as the cognitive ability of

the prey or mesopredator to associate these cues with risk (Gaynor, Brown, Middleton, Power, & Brashares, 2019). We used robust data sets of lion and leopard locations, but our measurement of risk ultimately might not have been able to capture the absolute risk for cheetahs in this system. Rather than evaluating lion and leopard space use, other proxies for risk such as predator kill sites or predator scat and markings might have been stronger cues for cheetahs to assess long-term risk (Cornhill & Kerley, 2020). Similarly, lions usually vocalize daily as a means of long-distance communication (Grinnell & McComb, 2001), and, therefore, cheetahs may have been using actual audio cues to assess where lions actually were on any given day. Additionally, lions and leopards are typically most active at night (Hayward & Slotow, 2009), and, therefore, cheetahs might have perceived risk to be lower during the daytime hours when we were able to collect data. Instead, cheetahs might have only altered behaviour based on long-term risk during the nighttime to best respond to the actual risk of predation. We also did not consider spotted hyaenas as a potential source of risk for cheetahs. Although spotted hyaenas rarely kill cheetahs in our study area (Gigliotti et al., 2020b), they still compete with cheetahs for resources and kleptoparasitize cheetah kills (Hunter, Durant, & Caro, 2007a). Therefore, the space use of spotted hyaenas, along with that of lions and leopards, might contribute to the overall risk landscape for cheetahs.

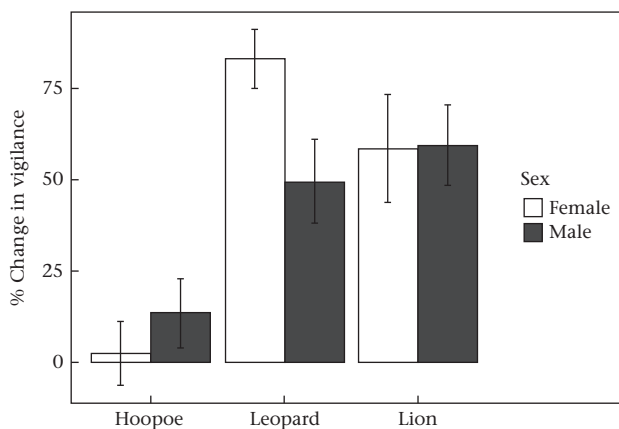


Figure 3. Differences in vigilance behaviour between female cheetahs with cubs and male cheetahs following predator (lion and leopard) and control (hoopoe) playbacks, Mun-Ya-Wana Conservancy, KwaZulu-Natal, South Africa, 2018–2019. Means and error bars are based on raw data; error bars represent SE.

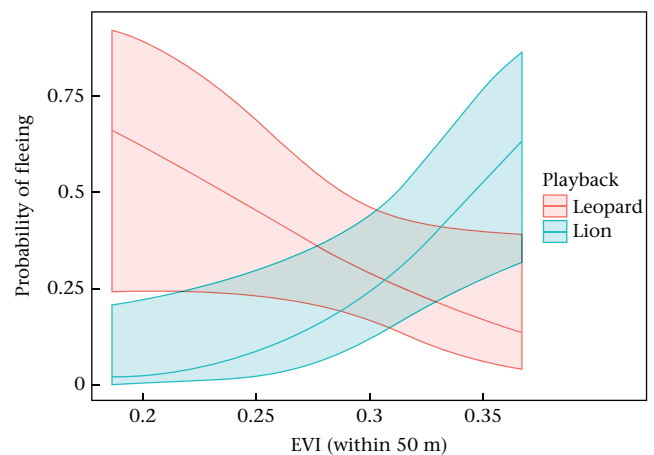


Figure 4. Probability of cheetahs fleeing following lion and leopard playbacks based on average enhanced vegetation index (EVI) within 50 m of playback location, Mun-Ya-Wana Conservancy, KwaZulu-Natal, South Africa, 2018–2019. Shaded regions represent 95% CI.

Similar to previous research in the Serengeti (Durant, 2000), we found that cheetahs exhibited strong antipredator behaviours to short-term risk, as expected by the risky times hypothesis. Our result indicating strong responses to short-term risk also corroborate previous research on cheetah spatial responses to risk, which indicated that cheetahs only respond to risk of top predators at close distances (Vanak et al., 2013). When faced with an immediate threat, the benefits of antipredator behaviour likely outweigh any potential costs (Lima & Dill, 1990). The majority of cheetah mortality, especially for cubs, is a result of predation by lions and leopards (Laurenson, 1994); thus, it makes sense that female cheetahs with cubs exhibited higher vigilance than males in response to short-term risk. Additionally, cubs might not be able to flee from predators as efficiently as adult cheetahs (Caro, 1987); therefore, increased vigilance by females with cubs likely serves as a means of enhanced detection of predators to allow cubs the maximum amount of time to flee from a risky situation. Similar to our results, previous research on cheetah behaviour at kill sites in the Serengeti found that female cheetahs with cubs spent more time vigilant than feeding (Hilborn et al., 2018). Increased antipredator behaviour by females with offspring has been observed in a variety of herbivore prey (Burger & Gochfeld, 1994; Toïgo, 1999), likely as a means of prioritizing offspring safety to maximize lifetime reproductive success. Thus, the effects of parental status on antipredator behaviours seems to hold for both herbivore prey and mesopredators.

As opposed to research on herbivore prey, we did not find support to suggest that long-term predation risk affects cheetah behavioural responses to short-term risk. Herbivores such as elk, *Cervus elaphus*, have been found to alter vigilance based on exposure to predators consistent with the predation risk allocation hypothesis; elk were more vigilant in areas with intermittent exposure to wolves, compared to areas with high wolf exposure (Creel et al., 2008). Recent work in Liuwa Plain National Park, Zambia found that ungulates exhibit the highest level of antipredator behaviours when they are exposed to short-term risk in areas of high long-term risk (Dröge et al., 2017). Regardless of the relationship between long-term and short-term risk, herbivore prey seem to modify behaviours based on a combination of long-term and short-term risk, whereas we did not find this relationship for cheetahs. Similar to our results related to the risky places hypothesis, our failure to find support for either the risky times and places hypothesis or the predation risk allocation hypothesis could be related to the inability of cheetahs to assess background risk, or it could be related to ecological differences between herbivore prey and mesopredators, particularly the lack of a vigilance–foraging trade-off for cheetahs. Overestimation of risk is more beneficial than underestimating risk (Bouskila & Blumstein, 1992); therefore, responding to playbacks regardless of background risk level would have likely been the most profitable for cheetahs, given that there likely was not a large energy trade-off for these antipredator behaviours.

Habitat complexity has been found to influence habitat use and demography of mesopredators (Gigliotti et al., 2020a; Janssen, Sabelis, Magalhães, Montserrat, & van der Hammen, 2007), and our results indicate that habitat complexity can also affect mesopredator antipredator behaviours. Instead of responding to long-term risk, we found that cheetahs modified baseline vigilance behaviour based on habitat characteristics: females spent the highest proportion of time vigilant in open areas. Other species such as warthogs, *Phacochoerus africanus*, and wildebeest, *Connochaetes taurinus*, exhibit higher vigilance in open areas, likely because of the risk of being spotted by nearby predators and the higher probability of detecting nearby predators (Scheel, 1993). Female cheetahs also likely follow this pattern because they are

potentially more vulnerable in open habitats. Because lions and leopards do not typically target cheetahs as a source of food (Laurenson, 1994), the probability of an attack on a cheetah likely only depends on a lion or leopard spotting a cheetah and having the time or energy to attack them. Therefore, in areas where apex predators can see cheetahs from a further distance, cheetahs benefit from increased vigilance, allowing them to detect a predator before they are detected.

Additionally, we found that habitat complexity affected how cheetahs differentially expressed flee responses to leopards compared to lions. Compared to vigilance, fleeing represents a greater cost because of higher energetic demands and leaving a potentially profitable area (Ydenberd & Dill, 1986). Thus, animals should only flee when they experience the highest cost to their fitness. Lions are ambush predators that benefit from concealment in dense vegetation (Davies, Tambling, Kerley, & Asner, 2016). Therefore, our results suggest it is likely that when cheetahs hear lion sounds, but cannot see them, the risk of staying is greater than the costs of leaving. Although leopards are also ambush predators (Balme, Hunter, & Slotow, 2007), we found the opposite relationship between vegetation complexity and fleeing. However, as opposed to lions, leopards typically avoid open habitats (Balme et al., 2007). Therefore, cheetahs' higher probability of fleeing from leopard sounds in open habitats could be a response to a novel predatory threat, given that they associate leopard sounds with predation risk, but they are hearing the sound in an area that they do not usually associate with leopards. Additionally, leopards are often less conspicuous than lions because of their reliance on stealth to capture prey, compared to group-hunting tactics of lions (Hayward et al., 2006). This stealthy behaviour might increase cheetahs' perceived risk in areas where they are visible to leopards, and therefore influence their antipredator behaviour. Several recent studies have demonstrated the need to consider the effects of multiple predators on prey behaviour because of variation in responses to different predators, which do not always follow predicted relationships (Creel et al., 2017; Thaker et al., 2011). Because we found variation in mesopredator responses to different predators, our results suggest the importance of also considering multipredator effects on mesopredator species as well, rather than attempting to simplify the complexity of multiple predator effects (Montgomery, Moll, Say-Sallaz, Valeix, & Prugh, 2019). When considering cheetah responses to habitat complexity both in relation to long-term risk and short-term risk, our results suggest that detection or escape probabilities (as mediated through habitat complexity) might be more indicative of risk for cheetahs than the probability of encountering a predator. Therefore, assessing habitat characteristics, rather than the space use of dominant predators, can offer insight into the landscape of fear for cheetahs and other mesopredators (Gaynor et al., 2019).

Collectively, our results offer insight into how mesopredators might perceive predation risk and how risk and antipredator behaviours are related to spatial and temporal factors. Many studies use vigilance or other antipredator behaviours as a proxy for predation risk (Moll et al., 2017), but our research adds to the growing body of literature to suggest that risk and risk effects need to be considered across multiple spatial and temporal scales because behavioural responses do not always match the underlying risk of predation and because habitat complexity can influence these responses (Gaynor et al., 2019; Moll et al., 2017). Our results also suggest that habitat complexity might serve as a better proxy for long-term risk than encounter probability.

Additionally, our study is one of the most comprehensive studies of behavioural response to risk in mesopredators. We show that the behavioural responses of mesopredators to short-term and long-term predation risk sometimes differ from what is observed in

prey species, potentially because of differences in trade-offs between energy and antipredator behaviours, or because individual species are equipped with different ways of detecting and evading risk. With increased recognition of the importance of nonconsumptive effects of predators in structuring communities, it is important to understand differences in responses to risk among trophic levels, as well as how spatial and temporal factors can influence responses to risk.

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Appendix

Investigating Potential Spatial Biases in Lion and Leopard Sighting Locations

Although sightings data has been successfully used to evaluate the course-scale habitat use of wildlife populations (Palma, Beja, & Rodrigues, 1999; Sequeira, Roetman, Daniels, Baker, & Bradshaw, 2014), spatial biases can emerge as a result of spatial variation in detection and effort. We evaluated several forms of potential spatial bias within our lion and leopard sightings data to ensure that the available data was suitable to assessing course-scale habitat use. We first investigated potential bias in our sightings data because of nonhomogeneous variation in sightings, which would result from variation in data collection effort across our study area.

To assess nonhomogeneous sampling biases, we ran Cox point-process models with a Thomas clustering distribution using the R package spatstat (Baddeley, Rubak, & Turner, 2015). Cox point-process models test for complete spatial randomness (CSR) across varying spatial scales within a focal area; thus, spatial biases in data collection would be indicated by a lack of CSR at any spatial scale. We ran Cox point-process models for lions and used Ripley's *K* function with a 95% simulation envelope based on 500 simulations using the spatstat R package. Based on this simulation, observed Ripley's *K* estimates falling outside of the 95% simulation envelope would indicate potential sampling biases within the study area.

For both lions (Fig. A1a) and leopards (Fig. A1b), the observed Ripley's *K* estimate fell within the 95% simulation envelope across all distances, indicating that the locations were not clustered or dispersed at any distance. Therefore, we are confident that there were no effort-related biases within our lion and leopard data.

Next, we investigated potential bias in our sightings data because of differing detection rates based on vegetation density (EVI). Because we first sighted animals while driving on roads, we predicted that it would be easier to see animals further away from roads in areas of low EVI (i.e. more open areas). For each recorded lion and leopard sighting, we calculated the distance to the nearest road and extracted point-specific EVI values from the corresponding seasonal EVI raster. We investigated whether there was a relationship between sighting location EVI and distance to the nearest road using a Pearson's product-moment correlation test using the cor.test function in R (R Core Team, 2019). Based on this analysis, there was no correlation between EVI and detection distance for lions ($r = 0.01$, $P = 0.75$) or leopards ($r = 0.02$, $P = 0.71$), which shows that we were not more likely to detect lions or leopards at longer distances in areas of open vegetation. Therefore, we did not find any evidence to suggest that we needed to account for differences in sighting detections in relation to EVI.

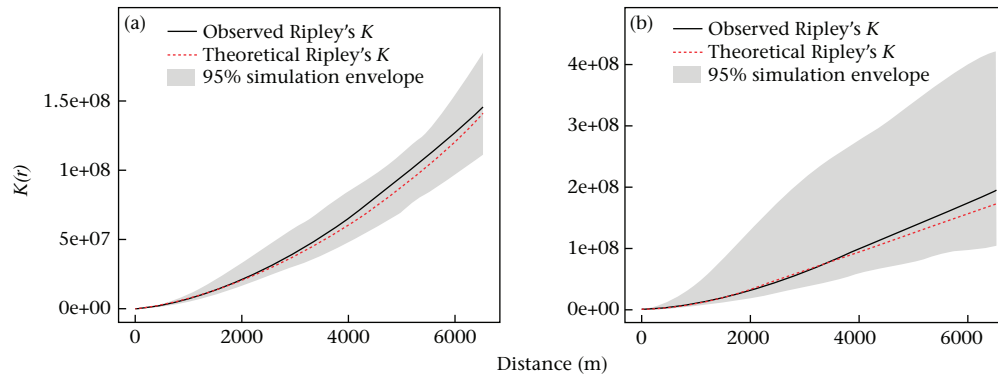


Figure A1. Results of Cox point-process models using Ripley's K function with a 95% simulation envelope based on 500 simulations using the spatstat R package to test for complete spatial randomness of (a) lion and (b) leopard locations.