



An experimental study on risk effects in a dwarf antelope, *Madoqua guentheri*

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Risk of predation shapes the physiology, behavior, and demography of prey. Among the many studies that have examined effects of risk in ungulates, most have focused on large (> 40 kg) and gregarious species. Much less is known about the effect of risk on smaller or territorial ungulates, which is a diverse group of species that can have pronounced effects on plant communities in tropical ecosystems. Using GPS telemetry, we examined spatial responses of Guenther's dik-dik (*Madoqua guentheri*) to scent marks from a common predator (African wild dogs, *Lycaon pictus*) or cattle. In response to predator scent marks, dik-diks increased fidelity within territories, avoided scent marks, and decreased use of overstory cover. Similar behaviors occurred in response to cattle scent marks, with the exception that use of overstory cover relative to controls did not change. Total amount (length) of movement did not change in response to either type of scent mark. Thus, an increase in perceived risk of predation changed the pattern and distribution of dik-dik movement but did not change total amount of movement. Our results suggest that territoriality may constrain the options available for prey to avoid predation risk.

Key words: African wild dog, behavior, movement, predation, risk, savanna, scent, territory

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Risk of predation affects neurobiology (Daskalakis et al. 2013), physiology (Sheriff et al. 2009), and behavior (Lima and Dill 1990) of prey, with consequences for vital rates of populations and allocation of biomass through food chains (Schmitz et al. 1997). A key conceptual breakthrough in our understanding of how risk affects ecosystems derives from the “landscape of fear” (LOF), which quantifies spatial avoidance of risk (Laundre et al. 2001) and has been used widely to understand animal behavior in terrestrial (Brown et al. 1999; Kotler et al. 2002; Brown and Kotler 2004) and marine (Wirsing et al. 2008) systems.

Whereas a LOF has been quantified for a number of taxa, it was originally developed to explain spatial variation in behavior for large mammals (i.e., elk, *Cervus elaphus*, and bison, *Bos bison*—Laundre et al. 2001) and continues to provide an informative lens through which to understand the ecology of ungulates. For example, spatial variation in risk avoidance behavior has been described for deer (*Odocoileus* spp.—Altendorf et al. 2001; Lingle 2002), caribou (*Rangifer tarandus*—Whittington et al. 2011), guanaco (*Lama guanicoe*—Marino and Baldi 2008), antelope (Jarman 1974; Underwood 1982; Sinclair and

Arcese 1995; Valeix et al. 2009; Ford et al. 2014), elk (Fortin et al. 2005; Kuijper et al. 2013; Middleton et al. 2013), and moose (*Alces alce*—Berger 2007; Gervasi et al. 2013). From this body of work, a clear picture is emerging that the LOF is species specific. For example, sympatric species of prey may respond to risk in different ways, even when hunted by the same carnivore (Lingle 2002; Periquet et al. 2012; Gervasi et al. 2013). If the LOF is species specific, then the functional traits of prey species (e.g., body size, sociality, feeding style) should influence how spatial variation in risk emerges. Indeed, development of a predictive theory for the role of prey traits in mediating risk effects is still in its infancy (Creel 2011), and filling this knowledge gap requires field studies covering a broad range of prey traits and species.

Studies quantifying the LOF in ungulates have focused almost exclusively on large (> 40 kg) and gregarious species that typically alter group size in response to risk (Dehn 1990; Fortin and Fortin 2009; Taraborelli et al. 2014), avoid risky areas (Kuijper et al. 2013), and often increase use of open habitats to facilitate detection of predators (Anderson et al. 2010; Ford et al. 2014). This emphasis on large species does not represent

the diversity of life-history traits among ungulates, of which about 30% have an adult body size < 30 kg (Smith et al. 2003). Gaps in our knowledge regarding the LOF in smaller ungulates are important to address, particularly in light of their abilities to sustain population growth of large carnivores (Hayward et al. 2006; Woodroffe et al. 2007) and to change plant communities dramatically (Augustine and McNaughton 2004; Goheen et al. 2013).

Because small ungulates tend to be solitary, territorial, and utilize crypsis to avoid predation (Brashares et al. 2000; Caro et al. 2004), they may react to a LOF that contrasts with that of larger ungulates. For example, under heightened risk, monogamous species are unlikely to aggregate in groups larger than parents and offspring (Komers 1996a), territorial defense may pre-empt spatial shifts away from risky areas (Brotherton and Rhodes 1996), and crypsis is typically associated with use of dense cover rather than open habitats (Jarman 1974; Ydenberg and Dill 1986). In addition, smaller-sized ungulates are more likely to die of predation than larger animals (Sinclair et al. 2003; Collins and Kays 2011; Fritz et al. 2011), and this vulnerability may increase the strength of antipredator responses (Creel 2011). In spite of the key role that many small ungulates play in ecosystem dynamics, their LOF is largely undocumented.

We report on spatial responses to risk by a 5-kg, monogamous, browsing, and territorial antelope, the Guenther’s dik-dik (*Madoqua guentheri*). We combined GPS telemetry with a simulated cue from African wild dogs (*Lycaon pictus*), which is a common predator of dik-dik (Woodroffe et al. 2007), or a cue of human activity (cattle) in a pastoralist-occupied landscape. To simulate cues, we applied scents derived from the dung of African wild dogs or cattle to dik-dik territories in an ecologically meaningful concentration (sensu Kuijper et al. 2014). Because cattle are always accompanied by people (i.e., herders) in this landscape, dik-dik may associate cattle odor with human activity. We used these data to test 2 hypotheses that explain how dik-dik movements might change in response to perceived risk (Table 1). The displacement hypothesis argues that prey disperse away from areas with heightened risk. For example, elk (Fortin et al. 2005), deer (Altendorf et al. 2001), moose (White and Berger 2001), and several African ungulates (Thaker et al. 2011; Ford et al. 2014) avoid areas where their predators hunt. Such risk avoidance may supersede constraints of territorial defense on movement, similar to some territorial ectothermic (Jones and Paszkowski 1997; Blanchet et al. 2007; Ozel and Stynoski 2011) and avian prey (Dunn et al. 2004). Thus, the displacement hypothesis predicts that dik-dik should increase their dispersion and total distance travelled when they

perceive heightened risk. Conversely, the fidelity hypothesis argues that territoriality reinforces spatial memory of areas where crypsis is most effective. For instance, risk avoidance, and not resource defense, explained why migratory robins were territorial (*Erithacus rubecula*—Cuadrado 1997). In addition, many cryptic (but not necessarily territorial) prey reduce their dispersion and amount of movement under heightened risk (Preisser et al. 2005). Accordingly, the fidelity hypothesis predicts that when risk increases, dik-diks should be less dispersive, travel shorter distances overall, and increase use of overstorey cover (i.e., both tree and shrub cover) to maximize crypsis. We further evaluated whether dik-dik movements are affected by type of scent mark (i.e., predator or cattle) and diel period (i.e., day versus night), 2 mediating factors that can change risk responses in other species of ungulates. For example, olfactory cues associated with natural predators and people may shape prey behavior differentially (Kats and Dill 1998; Berger et al. 2001). Additionally, risk avoidance behavior in ungulates may change with heightened activity level or reduced detection of carnivores, both of which often occur at night in African savannas (Cozzi et al. 2012; Burkepille et al. 2013). Consequently, we included these variables in our analysis to further understand contextual drivers that shape the LOF for dik-dik.

MATERIALS AND METHODS

Study area and focal species.—We conducted our study at the Mpala Research Centre (MRC) in Laikipia County, Kenya (0°17’N, 37°52’E), a semi-arid savanna with mean annual rainfall of approximately 500 mm (CV = 0.35—Augustine 2010). Soils are nutrient-poor, red sandy loams developed from metamorphic basement rock (Goheen et al. 2013). Vegetation consists of discontinuous herbaceous cover and an overstorey of *Acacia* spp. trees and shrubs. The site includes 22 species of wild ungulates along with cattle, goat, and camel ranching (Augustine 2010; Goheen et al. 2013). Dik-diks are the most abundant ungulates (approximately 140 individuals/km²) in our study area—more numerous than all other ungulate species combined—and exhibit the 3rd-highest biomass of all species of wild ungulates at MRC (Augustine 2010). Large (> 10 kg) carnivores include lions (*Panthera leo*), leopards (*P. pardus*), caracals (*Felis caracal*), cheetahs (*Acinonyx jubatus*), black-backed jackals (*Canis mesomelas*), spotted hyenas (*Crocuta crocuta*), striped hyenas (*Hyaena hyaena*), and wild dogs. Hunting is prohibited in the study area, but infrequent poaching is known to occur. Cattle herding is the predominant human activity in this area, and herds are always accompanied

Table 1.—Prediction matrix for the response of Guenther’s dik-dik (*Madoqua guentheri*) to a perceived increase in risk of predation from olfactory cues. [+] indicates the response variable increases with risk, [–] indicates the response variable decreases with risk, and [0] indicates that the hypothesis does not predict a change for that response variable with heightened risk.

	Response variable			
	Dispersion	Scent-mark avoidance	Use of overstorey	Total distance travelled
Displacement hypothesis	+	+	0	+
Fidelity hypothesis	–	0	+	–

by people. Thus, from a dik-dik's perspective, the scent of humans and cows would almost always co-occur in time and space.

Animal capture.—We captured adult female dik-diks during moonless nights between July–August 2010 and August–September 2011 using portable spotlights and long-handled nets, following methods described in Komers (1996b). We fitted each animal with a 200-g GPS collar (Savannah Tracking Ltd., Nairobi, Kenya), programed to record the location of dik-diks every 10 min. During handling, animals' eyes were covered, and verbal communication was prohibited among researchers to reduce stress on the animals. Handling lasted up to 5 min before we released the animal back into its territory. Individuals were collared for approximately 2 months (Table 2). Upon completion of the experiment, we recaptured individuals and removed collars. Handling procedures were approved by the University of Wyoming's Institutional Animal Care Committee, the Kenyan Wildlife Service, and the University of British Columbia, and they are in accord with the American Society of Mammalogists guidelines for handling wildlife (Sikes et al. 2011).

Prior to analysis, we screened GPS relocations likely to be inaccurate using an algorithm presented in Bjørneraas et al. (2010). This algorithm identifies and removes inaccurate GPS relocations when they have an unusually fast step length paired with large turning angles that form "spikes" in the movement pathway. Through this screening process, we excluded 172–778 GPS relocations per individual, which is equivalent to $15\% \pm 23\%$ (SE) of the original data, because they were identified as inaccurate.

Design of field experiment.—We focused on short-term changes in dik-dik behavior to minimize the potential influence of uncontrolled environmental variation in this field experiment. For each individual, we first quantified a baseline range of behaviors from measurements taken over a 24-h period, hereafter referred to as the "before-treatment" period (Table 2). We then measured deviations from this baseline behavior over the following 24-h period (the "after-treatment" period;

Table 2), for a total of 48 h of monitoring for each treatment. There were 3 types of treatments during which we measured behavior and movement of dik-diks: sham controls and 2 types of scent marks (predator and cattle: see below). A sham control treatment preceded each scent-mark treatment, such that each dik-dik was exposed to a total of 2 sham controls. To minimize overall duration of this experiment, the after-treatment period of each sham control overlapped with the before-treatment period for its respective scent-mark treatment (Table 2), such that each trial lasted 72 h.

For sham controls, we did not apply scent marks between the before-treatment and after-treatment periods. By themselves, predator and cattle treatments comparatively test dik-dik response to 2 different olfactory cues, both of which require researchers to work within dik-dik territories and potentially disturb dik-dik movements. Therefore, in the absence of sham controls, it is not clear how much dik-dik behavior varies between 2 sequential 24-h periods under natural, unmanipulated conditions.

For predator and cattle treatments, we applied scent marks to the territories of dik-diks between the before-treatment and after-treatment periods. For the predator treatment, we established a grid of scent marks at the center of each home range using gauze strips (1.3 g each) covered in wild dog feces and predator odor. Wild dogs have occupied the study area since 2003, and about 54% of their diet is comprised of dik-dik (Woodroffe et al. 2007; Woodroffe 2011). We collected scat from areas where wild dogs rested during daylight hours. We mixed scats in a solution of 4 parts water and 1 part scat. Due to a shortage of wild dog scats, we supplemented wild dog scent marks with a commercial predator odor (Triple Dig-it, Kishel's Quality Animal Scents & Lures, Inc., East Aurora, New York). During the predator treatment, we combined both wild dog and commercial odor scent marks within the territories of individual dik-dik. For the cattle treatment, we applied an equal part mixture of soil (to darken the gauze strips), cattle manure, and water to gauze strips, which we then applied in the same locations as predator scent marks.

Table 2.—Schedule of research activity and experimental measurements, 2010 and 2011. Dark gray shading indicates 48-h blocks of the treatment periods when monitoring occurred. Order of cattle or predator scent marks was randomized among individuals for each trial (light gray), during which time we compared the response of dik-dik (*Madoqua guentheri*) during the before- and after-treatment periods (dark gray).

Duration of research activity	Start	After 6 weeks	Trial 1						Trial 2				
			24 h	24 h	0 h	24 h	After 6 days	After 2 weeks	24 h	24 h	0 h	24 h	After 6 days
Research activity in dik-dik territory	Capture	None ^a	None	None	Apply scent-mark grid ^b	None	Remove 1st scent-mark grid	None	None	Apply scent-mark grid ^b	None	Remove 2nd scent-mark grid	
Treatment period: sham control			Before	After					Before	After			
Treatment period: scent mark				Before		After				Before		After	
Timeline ^c	0	42	43	44	44	45	51	65	66	67	67	68	74

^a This period allowed dik-dik to acclimatize to wearing GPS collars.

^b Cattle or predator scent mark.

^c Approximate days elapsed since capture.

All scent marks were hung from bushes and grass ~ 0.75 cm off the ground in a 5 × 5 grid spaced at 10-m intervals on the orthogonal (hereafter “scent-mark grids”). The area encompassed by scent-mark grids is equivalent to 8% ± 1% of the average dik-dik home range in our study area based on a minimum convex polygon of 9.2 ± 1.3 ha from GPS-collared individuals. We placed scent-mark grids within the central feature of each home range using at least 3 days (> 340 locations) of GPS telemetry data per individual. The central feature can be interpreted as the spatial equivalent of a median, and it is calculated by identifying the observation that is most central to the distribution of a series of locations using Geographic Information System (GIS) software (ArcMap v.10.1—ESRI 2012). We did not visit dik-dik home ranges for 6 days prior to or following establishment of scent-mark grids (Table 2). We removed scent marks after 6 days and did not return to dik-dik home ranges until > 2 weeks had elapsed. At this point, we switched the treatment for the 2nd trial of this experiment. Individuals were randomly assigned to either the predator or cattle treatments for the 1st trial of this experiment, and then switched to the other scent-mark treatment for the 2nd trial. Because odors were applied to removable markers and hung on vegetation, residual contamination of scent marks from the 1st trial on the 2nd trial was unlikely. To our best knowledge, rainfall and human activity within each home range remained constant over the duration of this experiment and among the home ranges of collared dik-diks.

A few animals were not exposed to the cattle ($n = 2$) or predator ($n = 1$) treatments because of battery failure in the GPS collars or mortality. Thus, we tracked 7 individuals during July 2010 and 8 different individuals during August 2011, which coincided with the dry season for both years. We captured and fit GPS collars to 15 individuals throughout the course of our study, yielding 61 ± 3 GPS relocations per individual for each combination of treatment period (before, after), treatment (cattle, predator, and sham controls) and diel period (day, night).

Response variables.—We evaluated dik-dik response to sham controls, predator, and cattle treatments (Table 2), focusing specifically on changes in dispersion, avoidance of scent marks, use of overstory cover, and total distance travelled. To measure dispersion, we first quantified utilization distributions (UD) using a Brownian-bridge algorithm (Horne et al. 2007) for each individual and combination of treatment period (i.e., before treatment, after treatment), diel period (i.e., day, night), and treatment type (i.e., cattle, predator, or sham controls). We then used a UD-overlap algorithm (Fieberg and Kochanny 2005) to calculate volume of the UD from the before-treatment period that intersected with UD from the after-treatment period. UD-overlap is largest when individuals used the same areas and with the same intensity during before- and after-treatment periods. Thus, dispersion is defined as 1 – UD-overlap and ranges from 0 (low dispersion) to 1 (high dispersion). To measure avoidance of scent-mark grids, we classified each GPS relocation from the before- and after-treatment periods with a binary variable indicating that the relocation was outside (1) or inside (0) of the scent-mark grid. To measure use of overstory cover

(i.e., trees and shrubs), we first developed a cover map derived from a high-resolution (0.36 m² pixels) Quickbird satellite image (Satellite Imaging Corporation, Houston, Texas) taken in November 2009. Overstory cover was defined as a binary variable, and we determined whether each GPS relocation did (1) or did not (0) overlap with overstory pixels using GIS software. Finally, we calculated total distance travelled as the sum of all step lengths (i.e., sum of the distance between sequential GPS relocations) for each treatment period.

Statistical analysis.—To analyze avoidance of scent-mark grids, use of overstory cover, and total distance travelled, we used treatment period (i.e., before treatment versus after treatment) as the predictor variable. For avoidance of scent-mark grids and use of overstory, we used generalized linear mixed effects models, with a random effect for individual dik-dik and an autoregressive correlation term to account for nonindependence of residuals over sequential observations made on the same individual (Zuur et al. 2009). We compared total distance traveled during the before- and after-treatment periods using a paired *t*-test. We subdivided data by diel period because dik-diks are less active (Manser and Brotherton 1995), while carnivores are typically more active (Cozzi et al. 2012) during the night. These shifting contexts can amplify or attenuate perceived risk (Orrock et al. 2004; Luttbeg and Trussell 2013). Thus, we created separate models for each diel period and treatment.

Because dispersion measures spatial overlap of dik-dik movements between before- and after-treatment periods, we could not use treatment period as a predictor variable as we had done with other responses. Instead, we used a paired Wilcoxon-signed ranks test to compare dispersion during cattle and predator treatments with their respective sham control. We used this nonparametric test because dispersion has a non-Gaussian distribution, thus violating an assumption of the more commonly used *t*-test. All statistical analyses were performed using the Base and MGCV packages in R v.3.0 (R Core Team 2013) and significance was determined at the level of $P < 0.05$.

RESULTS

Responses to the predator treatment were generally stronger than responses to either cattle or sham control treatments, but diel period mediated the strength of these responses (Table 3). Compared to sham controls, dispersion decreased by similar magnitudes (7%) during both predator and cattle treatments during the day, but significantly so only for the predator treatment (Wilcoxon-signed rank test, $V = 21$, $n = 14$, $P = 0.049$; Fig. 1). Thus, movements were more concentrated under heightened risk, at least during the day (Fig. 2).

Pooled among treatments, 28% ± 5% and 39% ± 6% of dik-dik GPS relocations were located within the scent-mark grid during day and night, respectively. For the predator treatment, avoidance of scent-mark grids increased during the after-treatment period in the day and at night compared to the before-treatment period (Table 3). Similarly, for the cattle treatment, avoidance of scent-mark grids was significantly greater in the after-treatment period during the day, but not at night (Table 3).

Table 3.—Effects of scent marks and no experimental intervention (sham control) on movement patterns of adult female Guenther's dik-dik (*Madoqua guentheri*) over a 48-h period at Mpala Research Centre, Kenya. Bold font indicates significant effects at $P < 0.05$.

Trial	Scent mark	Diel period	Response variable					
			Avoidance of scent-mark grid		Use of overstory			Total distance travelled
			β (SE) ^a	P	β (SE) ^a	P	t	P
Predator	Treatment ($n = 14$)	Day	0.498 (0.231)	0.031	-0.030 (0.131)	0.821	-0.952	0.359
		Night	0.982 (0.265)	< 0.001	-0.351 (0.139)	0.011	-0.844	0.088
	Sham control ($n = 14$)	Day	0.278 (0.226)	0.220	0.217 (0.132)	0.102	-0.501	0.625
		Night	-0.824 (0.284)	0.004	-0.098 (0.129)	0.445	0.987	0.342
Cattle	Treatment ($n = 13$)	Day	0.689 (0.234)	0.003	-0.026 (0.143)	0.858	-1.076	0.303
		Night	0.545 (0.284)	0.055	0.037 (0.129)	0.775	-0.613	0.551
	Sham control ($n = 13$)	Day	-0.233 (0.232)	0.314	-0.034 (0.144)	0.813	-0.604	0.557
		Night	-0.243 (0.259)	0.349	0.014 (0.131)	0.917	-0.550	0.593

^a Beta estimates, SE, and P values estimated from a mixed-effect logistic regression.

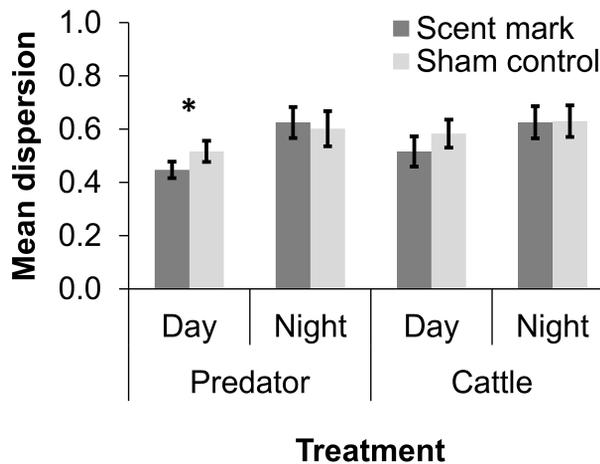


Fig. 1.—Effects of simulated cues of risk on dispersion of Guenther's dik-dik (*Madoqua guentheri*) over a 24-h period at Mpala Research Centre, Kenya, shown for 15 individuals in 2010 ($n = 7$) and 2011 ($n = 8$). Each bar represents mean dispersion over a 24-h period, with increasing dispersion indicating more wide-ranging movements during a 12-h period compared to the preceding 12-h period. We compared dispersion for both predator and cattle treatments, with dispersion over a random 24-h period (sham control) using a Wilcoxon signed rank test. Asterisk indicates a significant difference ($P < 0.05$) in dispersion between treatments and sham controls. Error bars indicate ± 1 SE.

Conversely, use (rather than avoidance) of the scent-mark grid increased significantly more in the after-treatment period for the sham control preceding predator treatment during the day, but grid use did not change significantly ($P > 0.200$) for other sham controls or diel periods (Table 3). Thus, dik-diks tended to avoid olfactory cues from both predators and cattle.

Pooled among treatments, dik-dik use of overstory was similar during the day ($18\% \pm 1\%$) and night ($20\% \pm 1\%$). For the predator treatment, and compared to the before-treatment period, use of overstory in the after-treatment period decreased significantly at night, but did not change across treatment periods for the cattle treatment or sham controls (Table 3). Thus, dik-dik generally did not change habitat use except at night and after exposure to predator cues. Total distance moved was generally higher during the day ($8,035 \pm 566$ m) than night

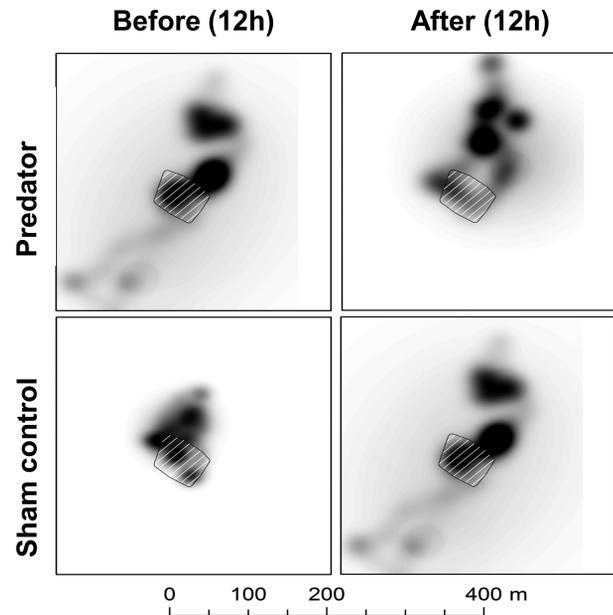


Fig. 2.—An example of how the utilization distribution of a single dik-dik (*Madoqua guentheri*) changes during the day, before (left column) and after (right column) the predator treatment and sham control. Darker areas indicate greater utilization by this individual, and the hashed area shows the location of the scent-mark grid. Dispersion for this individual was 0.42 and 0.68 during the predator treatment and sham control, respectively.

($5,602 \pm 302$ m) but did not change significantly during any treatment or sham control (Table 3). Thus, an increased in perceived risk of predation changed the pattern and location (i.e., dispersion) of dik-dik movement but did not change total amount of movement.

DISCUSSION

In support of the fidelity hypothesis, dik-dik dispersion was reduced following exposure to a simulated cue of risk, though this effect was minor (i.e., change of 7%). However, in support of the displacement hypothesis, dik-diks avoided scent marks from both predators and cattle. Finally, dik-diks increased use of open habitats during the predator treatment, but the total

distance that dik-diks traveled did not change with treatments. Together, our results provide novel insight on how a small, monogamous, and territorial ungulate perceives and responds to a LOF (Laundre et al. 2001).

At least 2 explanations point to why dik-diks avoided scent marks (as predicted by the displacement hypothesis) but did not increase dispersion or distance travelled (as predicted by the fidelity hypothesis) under a simulated increase in risk. First, dik-dik may have attempted to move into a neighboring territory, but defense by neighbors and herding by their mate may have impeded such dispersion. Consequently, dik-dik movements may reflect a tension between avoiding the source of risk (i.e., the scent-mark grid) and being repelled by territoriality. Under this scenario, the displacement hypothesis may be supported more strongly in situations with weaker territorial constraints on movement. For example, extraterritorial movements in dik-diks have been observed when overstory cover (Boshe 1984) or a mate (Komers 1996a) were removed from territories. Thus, as land cover changes or population density of neighboring conspecifics fluctuates, dispersion away from risk may become more likely for dik-diks.

Another possibility is that scent marks triggered a conditioned response of neophobia in dik-diks. Laboratory experiments conducted on fish and amphibians indicate that cues of risk decrease exploratory behavior (Brown et al. 2013), memory (Diamond et al. 1999), and novel object recognition (Zoladz et al. 2008) of prey. Additionally, higher levels of ambient risk, such as those experienced by many small ungulates (Sinclair et al. 2003; Fritz et al. 2011), may invoke a stronger neophobic response than lower levels of background risk (Brown et al. 2014). Indeed, dik-diks in the study area co-exist with one of the most abundant and diverse assemblages of terrestrial carnivores faced by any ungulate, i.e., over 30 individuals of large (> 20 kg) carnivores from > 8 species per 100 km² (Georgiadis et al. 2007; O'Brien and Kinnaird 2011; Woodroffe 2011), and this estimate does not include jackals, baboons, and raptors that also prey upon dik-diks in the study area. Thus, rather than a strategy to avoid risk per se, heightened fidelity and avoidance of scent marks following exposure to predator cues could be a conditioned response to chronic fear, reducing exploration of both novel objects (i.e., scent marks) and space (i.e., areas outside the home range).

Whether dispersion under heightened risk was constrained by neighbors, mates, or fear itself, dispersion decreased significantly only during the day and for the predator treatment. This diel change in dispersion coincides with an overall 30% decrease in distance moved during the night. Because dik-diks generally moved less at night than during the day (even under sham controls), metrics of risk avoidance behavior based on patterns of movement are likely to be less sensitive at night. In studies comparing activity level among ungulates of different sizes, smaller species were less sensitive to fluxes in temperature than larger species were (du Toit and Yetman 2005), likely because smaller species spend a greater proportion of time resting than foraging (Underwood 1982). For dik-diks, a habitual reduction in movement at night, when many predators

are active and difficult to detect, may facilitate vigilance and crypsis without sacrificing time allocated to foraging. As such, the “foraging versus risk avoidance” trade-off that characterizes much of foraging theory (Brown and Kotler 2007) may not explain the antipredator behavior of small ungulates like dik-diks at night.

Although dik-diks and other small antelope are thought to use crypsis as a strategy to reduce exposure to risk (Jarman 1974; Brashares et al. 2000; Caro et al. 2004), defining how such a strategy affects movement patterns is not clear. Crypsis is enhanced by reduced movement and increased use of cover to minimize detection by actively hunting predators (Sih 1992; Luttbeg and Trussell 2013). However, we detected no reduction in total distance moved or increased use of habitats that facilitate crypsis (i.e., overstory cover) during the predator or cattle treatment. Instead, dik-diks actually decreased use of overstory cover during the predator treatment, especially at night. This pattern may be explained by dik-diks attempting to increase visual detection of predators. Though often described as “hidiers” (Jarman 1974; Brashares et al. 2000), dik-diks and other small ungulates increase levels of vigilance in response to heightened risk (Dunbar and Dunbar 1980; Coleman et al. 2008; Lea et al. 2008). Using open habitats to facilitate predator detection is not typically associated with cryptic species and may indicate that vigilance and crypsis are not mutually exclusive. Indeed, the canonical “flee” versus “hide” dichotomy of antipredator behavior in African antelope (Jarman 1974) may be viewed more accurately as a tactical response to avoid capture by an attacking predator rather than a longer-term strategy to reduce the probability of a predator encounter.

The LOF has been used to conceptualize the way organisms respond to spatial variation in risk in 2 nonexclusive ways (Brown et al. 1999; Laundre et al. 2001). First, prey modify their behavior, such as increasing levels of vigilance, while travelling through risky areas (Fortin et al. 2005). Second, prey reduce time in risky areas by travelling faster (Lima and Dill 1990) or altogether avoiding risky areas (Ford et al. 2014). Whether and how these 2 responses emerge may depend on traits such as body size and social organization of both predator and prey (Creel 2011; Preisser and Orrock 2012). Our results highlight the broad and largely unexplored implications of traits like body size, monogamy, and territoriality for spatial responses to risk among ungulates.

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