

Changes in feeding behavior and patch use by herbivores in response to the introduction of a new predator

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Abstract

Top-order carnivores are naturally returning, or are being reintroduced, in a number of places where they have previously been extirpated. To explore how prey species adjust their antipredator behavior in response to these predators, we measured giving-up densities (GUDs) in experimental feeding patches and time spent vigilant for greater kudu (*Tragelaphus strepsiceros*), sable antelope (*Hippotragus niger*), and warthogs (*Phacochoerus africanus*) before and after an introduction of wild dogs (*Lycan pictus*). Before the introduction, the only predators in the system were cheetahs (*Acinonyx jubatus*). After the release, none of the prey species changed their microhabitat preference, in that they all preferred open grasslands to mixed tree and bush-clumps and bush-clumps. However, kudu and sable fed more intensively (i.e., achieved lower GUDs) and had lower vigilance in open grasslands, while reducing their feeding effort (i.e., higher GUDs) and increasing their vigilance near denser vegetation. When the wild dogs denned in the study site, potentially increasing contact with the prey species, the time kudu spent vigilant and their GUDs increased significantly across all patches, and continued to increase over time. In contrast, sable and warthogs stopped feeding from the experimental patches altogether during this period. The change in feeding intensity and vigilance levels by kudu likely reflected an additive antipredator response to both cheetahs and wild dogs, whereas sable and warthogs only responded to the increased risk from the wild dogs. Our results indicate that the addition of wild dogs influenced the foraging-safety trade-off for the 3 prey species, but that the antipredator behaviors utilized by these species to mitigate predation risk varied within the newly established 2-predator system.

Key words: feeding effort, GUDs, patch use, predation risk, predator-prey interactions, vigilance

Large mammalian predators are returning to ecosystems in many areas (Linnell et al. 2005; Ripple and Beschta 2006; Hayward and Somers 2009; Chapron et al. 2014; Ford et al. 2015). Recent studies have investigated responses of prey species to these predators (Creel and Winnie 2005; Sand et al. 2006; Laundre et al. 2010). However, the majority of these studies have focused on single-predator systems where ungulates experienced virtually no predation pressure prior to the return of the predator (Ripple and Beschta 2003; Laundre et al. 2010; Nicholson et al. 2014). Although these studies have documented many ecological effects of large predator reintroductions, single-predator systems are generally rare and the explanatory power of these studies for multi-predator systems is limited (Ale and Brown 2009; Hayward and Somers 2009; Fritz et al. 2011; Thaker et al. 2011). A few studies have examined effects of predator reintroductions in multi-predator environments (e.g., Tambling et al. 2015), but have not directly addressed the question of how prey responded to the addition of a second predator.

To minimize risk within multi-predator systems, prey species need to discriminate among different predators, and employ a range of predator-specific antipredator strategies (Caro 2005; Creel et al. 2014; Moll et al. 2016; Makin et al. 2017). Prey will likely recognize the cues of a returning predator if closely related predators have remained on the landscape (the multipredator hypothesis—Blumstein 2006). How prey respond to a returning predator will vary depending on the extent to which the hunting tactics, such as cursorial versus ambush predation, differ among the different predators. If hunting tactics differ between 2 predators, prey may adjust their behavior to a compromise that minimizes overall risk (McIntosh and Peckarsky 1999). Alternatively, when risk from 1 predator is much greater than that from another, prey may try to avoid the most dangerous predator (hierarchical response; e.g., Chamaille-Jammes et al. 2014). In doing so, prey may inadvertently improve the hunting success of 1 predator by trying to avoid the other (predator facilitation—Kotler et al. 1992). Conversely, if the different predators use similar hunting tactics, prey are likely to maintain similar antipredator responses to both predators (McIntosh and Peckarsky 1999). The extent to which antipredator responses such as landscape use change after a predator addition should therefore depend on the contrast between the initial and the novel risk.

Changes in perceived predation risk should be reflected in how prey species utilize patches within habitats. Specifically, prey should select patches that allow them to meet daily energetic demands, while minimizing predation risk (Lima and Dill 1990; Owen-Smith 2014). For example, utilizing food patches in open grasslands may reduce perceived predation risk in response to stalking predators such as African lions (*Panthera leo*—Thaker et al. 2011). Valeix et al. (2009) found that plains zebra (*Equus burchelli*), African buffalo (*Syncerus caffer*), wart-hogs (*Phacochoerus africanus*), and wildebeest (*Connochaetes taurinus*) spent more time utilizing grasslands when lions were close (seen within 24 h in the area) as a means to improve predator detection. In contrast, utilizing patches near denser vegetation may be advantageous when avoiding cursorial predators such as wild dogs (*Lycaon pictus*) that rely on high encounter rates and prefer prey to flee when detected (Mills 1984; Creel and Creel 2002). In Yellowstone National Park, elk (*Cervus elaphus*) responded to increased predation risk from wolves (*Canis lupus*) by moving away from open grassland into the cover of woodlands to avoid detection (Creel et al. 2005).

Monitoring the amount of time animals dedicate to activities such as vigilance and foraging provides a means of measuring perceived predation risk (Sinclair 1985; Fitzgibbon 1990). Increased vigilance can result in a trade-off of lower foraging effort within patches (e.g., Fortin et al. 2004). Therefore, increases in costly antipredator behaviors should only be exhibited when the perceived predation risk by an individual is high enough to warrant lower foraging efficiency.

Due to the foraging costs imposed by antipredator behaviors, prey species that were initially at low risk, and likely displayed lower levels of antipredator behavior, have more potential to respond to increased predation risk than those initially at higher risk and that already display stronger antipredator behaviors (Droge et al. 2017; Moll et al. 2017). Thus, we predict that, when an introduced or returning predator has the same hunting tactics as the predators already present, prey that were initially at low risk should respond more than those that were at high risk.

To address this, we explored how the addition of a predator into a single-predator, multi-prey system of

large mammals shaped the perceived predation risk of 3 prey species. At the start of our study, the only predators in the system were cheetahs (*Acinonyx jubatus*). A pack of 12 wild dogs was then introduced to the study area. To determine how sable antelope (*Hippotragus niger*), greater kudu (*Tragelaphus strepsiceros*), and warthogs, prey species of varying levels of preference by cheetahs and wild dogs (Hayward et al. 2006b; Clements et al. 2014), adjusted their antipredator strategies, we recorded foraging intensity by measuring giving-up densities (GUDs) in experimental feeding patches (Brown and Kotler 2004), vigilance, and microhabitat use both before and after the wild dog introduction. GUDs provide a measure of feeding effort at a patch level in response to differences in perceived predation risk.

We hypothesized that the addition of wild dogs would result in species-specific changes in antipredator strategies. We predicted that: 1) If perceived predation risk did not increase following the introduction of the wild dogs, then feeding effort of the prey species would increase (lower GUDs) and vigilance levels would decrease over time as forage availability on the landscape declined as the dry season progressed during the period of our study (see Shrader et al. 2012). 2) The decrease in feeding effort would be greater (higher GUDs and higher relative increase in vigilance levels) for sable compared to the other herbivores because sable had lower levels of predation risk before the wild dog introduction, as they are rarely targeted by cheetahs. 3) Feeding effort would decrease (GUDs and vigilance levels would be higher) in open grasslands compared to areas near bush-clumps and mixed trees and bush-clumps. This would most likely be due to the prey species shifting away from more open areas where they could potentially be seen by the wild dogs, to areas where the ability of the wild dogs to detect them would be reduced. Alternatively, perceived predation risk maybe lower in open grasslands due to improved predator detection. This would then result in greater feeding effort (lower GUDs) and lower vigilance levels.

Materials and methods

Study site.—We conducted our study in Tswalu Kalahari Reserve (Tswalu hereafter), Northern Cape, South Africa (27°13'30"S and 022°28'40"E). The fenced reserve encompasses 100,000 ha of restored farmland (Cromhout 2007) located in the southern Kalahari (Roxburgh 2008). The landscape comprises open grasslands containing many small (5-15 m diameter) bush-clump and mixed tree and bush-clump patches. These patches are dense, blocking sightlines and preventing large herbivores from moving through them. Large mammalian herbivores found on the reserve include greater kudu, springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), roan (*Hippotragus equinus*), and sable antelope. However, prior to our study only adult and subadult male sable had been released in the study sites; thus, we did not record juveniles or calves. Surface water is pumped in artificial waterholes throughout the year and thus water availability for animals in Tswalu is relatively constant. In May 2014, Tswalu managers introduced a pack of 14 wild dogs into the fenced 80,000-ha, western section of the reserve, where cheetahs were the only large predators present. The total number of cheetahs in the reserve is not known. However, during our study, we identified 10 individual cheetahs within our 12-km² study area. This indicates a local density of 0.83 cheetahs/km², which potentially makes it one of the highest cheetah densities found in small, fenced, protected areas in South Africa (Lindsey et al. 2011). Despite both these predators being considered cursorial, the fact that cheetah only chase prey for ~300 m, whereas wild dogs will chase prey for up to 3 km, puts them on extreme ends of the cursorial predator spectrum. Finally, brown hyenas (*Hyena brunnea*) also occur in the reserve, but do not hunt large mammals as they are primarily scavengers (Skinner and Chimimba 2005).

Wild dogs are social predators that, owing to their cooperative hunting strategy, are able to kill a large variety of prey, ranging in weight from 10 to 250 kg (Woodroffe et al. 2007; Clements et al. 2014). Prior to their introduction, the herbivores within the western section of Tswalu had not encountered wild dogs. In contrast, cheetahs, which tend to hunt alone or in pairs, prey on species with a weight range of 14-135 kg (Clements et al. 2014), and had been in the reserve for 20 years. A comparison of prey preferences for cheetahs and wild dogs at other study sites indicates that greater kudu (120-270 kg) are preferred by wild

dogs and taken relative to their availability by cheetahs, sable (220-235 kg) are avoided by cheetahs and taken relative to their availability by wild dogs, and wart- hogs (45-150 kg) are avoided by cheetahs and taken relative to their availability by wild dogs (Hayward et al. 2006a, 2006b). During our study, we only observed 7 kudu and 2 sable being killed by wild dogs and no kills by cheetahs; thus, we could not accurately determine predation rates of the 2 predators at our study site. Due to the differences in their hunting styles, ranges of prey weight, and reported prey preferences elsewhere, however, the degree of perceived risk from these 2 predators likely differed by prey species.

Experimental design.—Seasons in the Kalahari are defined by a very long dry season (April-May to November-December) with less than 10 mm of rain falling during this period (Roxburgh 2008), followed by a short wet season (January to March). We collected data from May to November 2014, during the extended dry season. During the dry season, natural forage quality and availability declines due to plant senescence and utilization by large herbivores, respectively (Le Houerou 1980; Katjiua and Ward 2006; Shrader et al. 2012). We divided our study into 4 periods related to the presence of potential predators on the landscape: 1) 1 month before wild dog introduction (only cheetahs present), 2) 1 month after the introduction (both cheetahs and wild dogs present), 3) 2 months after the introduction (when the wild dogs denned within our study area), and 4) 6 months after the introduction (when wild dogs had finished denning). Wild dogs generally move and hunt extensively across their home ranges throughout the year (Fuller and Kat 1990; Davies-Mostert et al. 2009). However, once they den, they make hunting trips out from the den site, thus acting like central place foragers. Fuller and Kat (1990) found that in the Serengeti, wild dogs foraged between 4 and 9 km out from the den, whereas Ford et al. (2015) found that wild dogs foraged within 3 km of the den site. As the wild dogs denned between 1 and 4 km from our 3 sites, this likely increased the encounter rates (Fischhoff et al. 2007; Thaker et al. 2011) and harassment (Creel and Creel 2002) experienced by prey species in our study. By first collecting data when only cheetahs were on the landscape, we could determine the foraging intensity and microhabitat use of the kudu, sable, and warthogs prior to the release of the wild dogs.

To tease apart the separate impacts that cheetahs and wild dogs had on the foraging and microhabitat use of the prey species, we collected GUDs (amount of food left in a patch once a forager has quit feeding from the patch—Brown 1988) in experimental feeding patches (see below). Predation risk plays an important part in determining the feeding effort of prey species (Lima 1998; Brown 1999). Specifically, an individual should cease feeding in a patch once the harvest rate (H) is equal to the metabolic (C), predation (P), and missed opportunity costs (MOC) of foraging in that patch ($H = C + P + MOC$ —Brown 1988). As harvest rate is a direct function of food quantity, GUDs can be used as an index of an animal's quitting harvest rate (Schmidt et al. 1998). Thus, GUDs provide insight into the trade-offs individuals make when seeking to maximize feeding effort while simultaneously reducing predation risk (Brown and Kotler 2004). When metabolic and missed opportunity costs are constant across patches, greater feeding intensity (lower GUDs) reflects lower perceived predation risk within an area, whereas lower feeding intensity (higher GUDs) reflects greater perceived predation risk (Brown and Kotler 2004).

For this study, we habituated kudu, sable, and warthogs to the experimental feeding patches prior to the release of the wild dogs. We designed species-specific experimental feeding patches for each of the prey species using plastic packing crates (60 x 40 x 28.5 cm; Fig. 1). To provide diminishing returns (Hochman and Kotler 2007), we filled the patch with a matrix of 10 liters of inedible substrate (10-cm-long cut PVC tubing). The inclusion of the matrix provides diminishing returns by increasing the feeding effort from the feeding patches as food availability declines and therefore simulates a natural patch whereby food availability and intake rate decline with increased time spent foraging from the patch (Brown 1988). For both kudu and sable, we raised the patches 1 m off the ground to exclude smaller herbivore species. We further adjusted diminishing returns by attaching a wire grid (1 horizontal and 2 vertical strands of wire) over the top of each feeding patch so that the strands were separated by 15 cm on the kudu patches and 20 cm on the sable patches. The wire grid prevented the herbivores from moving their muzzles through the substrate from 1 side of the feeding patch to the other. As a result, herbivores were unable to push the substrate out

and thus reduce the difficulty of feeding in the patch. For warthogs, we placed the patches on the ground, and did not attach a wire grid on these patches as it could have caught on the warthogs' tusks.

To determine changes in feeding intensity in relation to the different predator treatments, we collected data on the 3 prey species at 3 sites in the northern section of the reserve. To reduce the sampling of the same individuals from the different prey species, we selected sites that were 1 km apart and separated by a series of hills. However, despite this, it is likely we resampled some individuals.



Fig. 1. a) Greater kudu (*Tragelaphus strepsiceros*), b) warthogs (*Phacochoerus africanus*), and c) sable antelope (*Hippotragus niger*), feeding in the experimental feeding patches, in open grasslands (at night), in a mixed tree and bush-clump patch, and next to a bush-clump patch, respectively. Images below the different herbivores show the top of the respective species-specific feeding patches.

Following 2 weeks of habituation to the experimental feeding patches, we collected GUDs from 24 experimental feeding patches per prey species per site, with 8 of these patches placed in open grassland, 8 within 2 m of isolated 3 x 3 m bush-clumps, and 8 within 2 m of 10 x 10 m mixed tree and bush-clumps (Fig. 1). This resulted in 72 feeding patches per site (24 sable patches, 24 kudu patches, 24 warthog patches). We separated each of the feeding patches by 20-30 m, with the patches for the individual prey species placed in separate locations. The position of these patches in relation to vegetation structure provided varied predation risks (Kotler et al. 2001; Shrader et al. 2008; Stears and Shrader 2015). Specifically, visibility is limited close to dense vegetation, although the denser vegetation also could potentially reduce detection by predators, thus reducing predation risk. Escape opportunities for large herbivores such as greater kudu and sable were limited close to dense vegetation, but these areas may have offered a potential refuge for warthogs. In contrast, herbivores feeding in open grasslands would have greater sightlines with which to detect approaching predators (but also would be likely to be seen more easily by predators), and no obstacles that might reduce escape opportunities.

Due to the time required to collect and restock the experimental feeding patches, we were only able to collect data from sites concurrently. To ensure that the data collected from all sites were comparable, we collected data from the sites in a rotating manner, moving the patches from 1 of the sampled sites to the site

that did not have patches every 14 days. We did this over the full duration of the study.

To ensure that the data reflected the feeding of the target species, we placed Bushnell Trophy Video Cameras (Bushnell, Overland Park, Kansas) with motion and infrared triggers across all sites. Each video camera was positioned to record from more than 1 experimental feeding patch (recording distance of 1-40 m with the field scan feature), thereby allowing us to monitor which herbivore species utilized the patches at each site. We only included data in the analysis where we could clearly view which of the herbivore species had utilized the patches. Where nontarget species were observed feeding from the patches (e.g., baboons—*Papio ursinus*), those GUD values were excluded from the data set. We also excluded GUDs where more than 1 of the target species ate from a single feeding patch. However, these events were infrequent. During the study, all 72 patches were utilized by the 3 herbivore species with varying feeding intensity, and therefore GUD values included in the analysis reflected the use of all feeding patches over time.

Early each morning (0600 h), we poured 200 g of food (Lucerne-based sheep pellets) over the matrix in each feeding patch. We then left the feeding patches out all day and sifted out the remaining food at dusk (1800 h). We then replenished the feeding patches and left them out overnight, collecting the remaining pellets the following morning at 0600 h. We put out the experimental feeding patches for the 3 herbivore species during all 4 time periods (1 month before the wild dog release, and 1, 2, and 6 months after the release). Not all the species fed from the patches in all the periods. GUDs were collected only from sites where there had been clear feeding activity; no GUDs were collected from sites that the herbivores had not visited on a particular day, as these values would not reflect the perceived predation risk experienced while feeding from a particular patch, but rather that they were not active in the area.

We monitored vigilance behavior of the herbivores using the same Bushnell video camera traps deployed across the feeding sites. Camera traps were placed at a height of approximately 2.5 m with a clear unobstructed view of the artificial patches, with a horizontal and vertical range of approximately 25 and m, respectively. This provided a large field of view by which to observe individual behavior at patches. From the videos, we used a scan sampling technique whereby we recorded the amount of time each individual within a group allocated to vigilance (Forbes-Watson 1967; Altmann 1974). For each individual, we recorded their behavior for between 1 and 20 min. Only individuals whose behavior was clearly discernible were included in the analysis. To avoid pseudoreplication through recording the same individuals or groups of individuals over a continuous basis, we stopped recording their behavior once an individual had left the field of view of the video camera trap and ceased recording any groups of a similar size for a period of 30 min (Tambling et al. 2015). This period reflects a trade-off between recording the same individuals on a continual basis, and missing new individuals utilizing the artificial foraging patches (Tambling et al. 2015). Vigilant individuals had their head up, erect posture, and ears alert, scanning the surrounding area for potential threats (Sundararaj et al. 2012).

Data analysis.—The GUD and vigilance data were not normally distributed and differed for the 3 herbivore species. Rather than using generalized linear models with different species-specific distributions for errors, we maintained the same approach for all prey species by using quantile regression models comparing medians, which are better measures of central tendencies for skewed distributions (Koenker 2005; Davino et al. 2013). With these models, we determined variation in GUDs and the time spent vigilant of the herbivore species between microhabitats (mixed tree and bush-clumps, bush-clumps, open grassland) and patch use over time (4 time periods). We initially included the interaction between these 2 variables in the models, but found this interaction to always be nonsignificant. We therefore present here the simpler additive models. To determine where significant differences existed for each species across habitats over time, we ran post hoc pairwise comparison tests of medians. All data were analyzed in R (R Core Team 2014) using the *quantreg* package (Koenker et al. 2015). We did not make comparisons between the herbivore species as the artificial species-specific patches were set up differently, and the amount of food the different species eat is affected by their body size and the attractiveness of the feeding patches.

Results

Kudu and sable showed lower GUDs at patches located in open grasslands and higher GUDs at patches located near bush-clumps and mixed tree and bush-clumps (Table 1; Fig. 2). These 2 species maintained higher vigilance levels near bush-clumps and mixed tree and bush-clumps than when they fed in open

grasslands (Fig. 2; Table 1). In contrast, warthogs did not show a relationship between GUDs and specific microhabitats during the study (Table 1). However, they were more vigilant in open grasslands compared to when they were near mixed tree and bush-clumps (Fig. 2; Table 1).

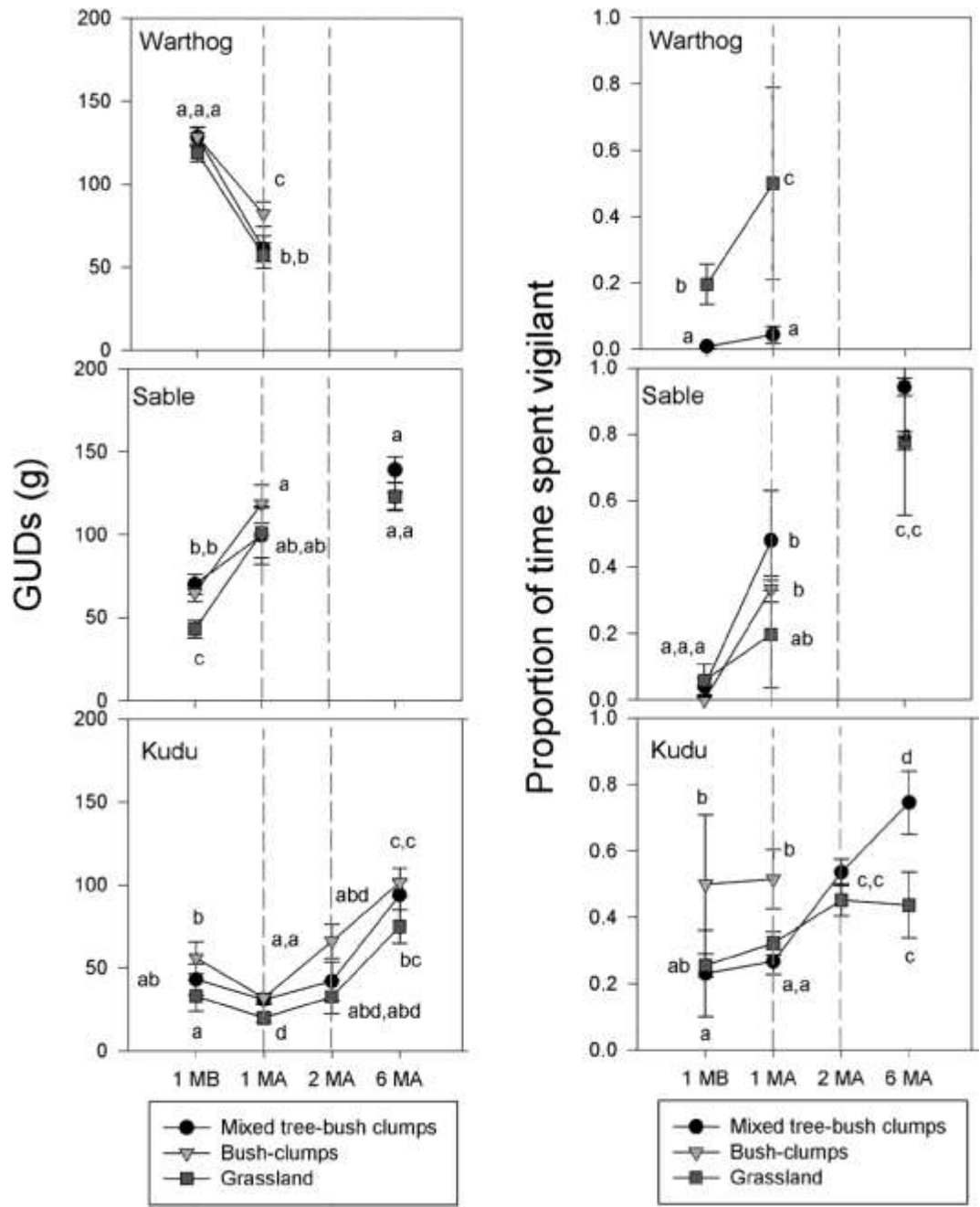


Fig. 2. Giving-up densities (GUDs) and proportion time spent vigilant recorded for greater kudu (*Tragelaphus strepsiceros*), sable (*Hippotragus niger*), and warthogs (*Phacochoerus africanus*) before and after the introduction of wild dogs (*Lycaon pictus*). Time periods: 1 MB = 1 month before, 1 MA = 1 month after, 2 MA = 2 months after, and 6 MA = 6 months after introduction of wild dogs. Dashed lines represent period when the wild dogs denned in the study area. Symbols show the medians and bars represent median SEs. Values sharing letters are not significantly different, as assessed by the post hoc pairwise comparison tests.

Table 1.—Quantile regression model comparing the median giving-up densities (GUDs) and proportion of time spent vigilant by greater kudu (*Tragelaphus strepsiceros*), sable (*Hippotragus niger*), and warthogs (*Phacochoerus africanus*) in response to landscape features (open grassland, bush-clumps, and tree and bush-clumps) and period before and after the introduction of wild dogs (1 month prior—cheetahs [*Acinonyx jubatus*] only predator present, and 1, 2, and 6 months after).

Type	Species	Variable	Residual <i>df.</i>	<i>df</i>	<i>F</i>	<i>P</i>
GUDs	Sable	Landscape feature	308	2	6.49	0.001
		Period	308	2	57.42	< 0.001
	Kudu	Landscape feature	685	2	10.56	< 0.001
		Period	685	3	24.33	< 0.001
	Warthog	Landscape feature	483	2	0.47	0.625
		Period	483	1	37.43	< 0.001
Vigilance	Sable	Landscape feature	61	2	1.56	0.119
		Period	61	2	7.46	0.001
	Kudu	Landscape feature	583	2	3.22	0.041
		Period	583	3	20.45	< 0.001
	Warthog	Landscape feature	105	2	2.80	0.006
		Period	105	1	1.03	0.303

For all 3 herbivore species, GUDs differed before and after the wild dog introduction (Table 1; Fig. 2). GUDs increased from 1 month before release to 6 months after release for both sable and kudu in all patches (Fig. 2). Despite sable falling outside the preferred weight range of wild dogs, their median GUDs increased from 59 to 130 g over the 6-month period, indicating a 36% decrease in feeding effort in the experimental patches (Fig. 2). After the wild dogs were initially released, sable responded by immediately decreasing their feeding effort by 24% across all microhabitats (Fig. 2). Median GUDs for greater kudu increased from 44 g before the release of the wild dogs to 90 g 6 months after the release, a 23% reduction in feeding effort in the experimental patches (Fig. 2). However, only a small, temporary decrease (9%) in GUDs was recorded for kudu after the immediate introduction of the wild dogs (Fig. 2). GUDs for warthogs initially dropped from 127 to 76 g after the wild dogs were released, a 30% increase in feeding effort (Fig. 2). However, when the wild dogs denned in the study area a month after release, warthogs stopped feeding from the artificial patches (Fig. 2).

Immediately after the release of the wild dogs, sable significantly increased their vigilance by 33%, and overall from 5% to 89% of the time they were observed during the 6-month period following the release (Table 1; Fig. 2). Similarly, kudu increased their vigilance from 26% of the time they were observed before the release of the wild dogs to 54% 6 months after the release (Table 1; Fig. 2). Warthogs maintained similar vigilance levels before and after the release of the wild dogs when feeding in the mixed tree and bush-clumps (< 5% of the time they were observed), but significantly increased their vigilance when feeding in grasslands (20% before compared to 50% after wild dogs were released) before they stopped utilizing the patches when the wild dogs denned (Fig. 2; Table 1).

DISCUSSION

In multi-predator systems, prey should develop antipredator strategies that limit their overall risk from all predators (Relyea 2003; Thaker et al. 2011). However, what strategies prey species incorporate (e.g., hierarchical, compromise, additive response) when a system shifts after a new predator moves in, is generally unknown. Here, we show how the addition of wild dogs into a single-predator system altered the foraging of 3 prey species that were previously only exposed to depredation from cheetahs. For all 3 species, the observed changes in response to both predators were not linked to a shift in microhabitat selection. Rather, we observed changes in the amount of food consumed from experimental feeding patches and differences in vigilance levels suggesting that the addition of wild dogs influenced the foraging-safety trade-off for the 3 prey species. As predation risk from cheetahs and wild dogs differed for each prey species, however, the mechanisms driving these changes were likely different.

Sable and kudu both generally reduced their feeding effort and became much more vigilant after the introduction of the wild dogs. This response was stronger for sable than for kudu, despite sable falling outside of the preferred weight range of wild dogs (Hayward and Kerley 2008; Clements et al. 2014). This

matches our prediction that species that were initially less at risk would respond more strongly to the addition of a predator, as their initially low levels of antipredator behavior allowed them to spend more time feeding. Although cheetahs and wild dogs have > 70% dietary overlap (Hayward and Kerley 2008), the pack hunting of wild dogs allows them to take larger prey than cheetahs, which are unlikely to prey on adult sable, based on their preferred weight ranges (Hayward et al. 2006a; Clements et al. 2014). Thus, the introduction of wild dogs into Tswalu has most likely shifted predation risk for sable from safe (virtually no predation, cheetahs only) to risky (wild dogs), as wild dogs kill sable based on their availability on the landscape (Hayward et al. 2006b). As a result, despite 2 predators being on the landscape, the adjustments to the antipredator strategy of sable (i.e., reduced feeding effort) was likely in response to the threat generated by the wild dogs only. This is supported by the fact that the sable moved away from the feeding sites when the wild dogs denned (2 months after their release, $n = 0$ GUDs, compared to $n > 18$ GUDs obtained in other periods; Fig. 2), possibly due to increased contact with the wild dogs during this period.

In contrast to sable, the feeding effort and vigilance levels of kudu changed very little during the first month after the wild dog reintroduction. The small 9% increase in feeding effort in the first month is unlikely to be biologically meaningful, and suggests that kudu perceived a decline in predation risk with the presence of wild dogs on the landscape, which is unlikely. Despite this unexplained small initial increase, kudu reduced their overall feeding effort and increased their vigilance levels as the study progressed and their exposure to the wild dogs increased during the denning period of the wild dogs. As this was not associated with changes in patch selection related to woody features, which could modify visibility and detectability, we conclude that kudu displayed an additive antipredator response to the additional threat from the wild dogs. Cheetah density in Tswalu was relatively high, and kudu thus probably already devoted significant effort to antipredator behaviors. Despite this, they were still able to increase their antipredator response to compensate for the increased risk from the wild dogs. However, what was surprising was that the changes in feeding effort were not as dramatic for kudu, which faced 2 predators, as they were for sable, which were only hunted by wild dogs. The presence of the wild dogs may have suppressed the hunting of cheetahs, and thus reduced the overall pressure on kudu. This, however, requires further investigation.

Compared to sable and kudu, warthogs displayed dramatically different responses to the introduction of the wild dogs. Firstly, they fed more intensively in patches right after the wild dog introduction (30% increased feeding effort). This was unexpected as warthogs are usually taken relative to their availability by wild dogs and warthogs had relatively high local density ($3/\text{km}^2$) in Tswalu. A tentative explanation for this could be the risk-food-availability trade-off, where warthogs increased their feeding effort from experimental feeding patches with the progression of the dry season as availability of natural food declined. However, with the denning of the wild dogs in the study site and their increased proximity, the increased risk of predation likely outweighed the benefit of feeding from the artificial patches and the patches were abandoned.

Warthogs also differed from the other prey species in that they were not observed at the feeding sites after the wild dogs had finished denning. Warthogs may have moved out of the study sites due to increasing contact with the wild dogs and thus greater perceived risk. Alternatively, warthogs may have left the feeding site due to a decline in natural forage with the progression of the dry season. However, if this was the case, the larger herbivores should have left the feeding sites first and not returned, as larger herbivores are more limited in their ability to obtain adequate food intake as food availability declines (Fryxell 1991). Finally, warthogs habituated to the artificial feeding patches may have been killed by the wild dogs. If we are correct, then increased predation risk had a greater effect on the warthogs than on either the kudu or sable. Thus, the introduction of wild dogs likely shifted predation risk from safe (warthogs generally avoided by cheetahs) to risky (warthogs preyed on by wild dogs).

The foraging behavior of the herbivore species could have been influenced by either a decline in the availability of food on the landscape during the dry season, or changes in group size, rather than by perceived predation risk. If foraging behavior responded to declining availability of natural food, feeding effort in the artificial patches should have increased as the dry season progressed. Shrader et al. (2012)

observed this for goats (*Capra hircus*) in the semidesert of Northern Cape, South Africa. Prey species also can respond to increased predation risk by increasing group sizes, which increases feeding pressure such that large groups attain lower GUDs than small groups (Makin et al. 2012; Creel et al. 2014). However, in contrast to both of these possibilities, feeding effort of the sable and kudu in the artificial patches declined (higher GUDs) as the dry season progressed, suggesting that predation risk was the main driver.

At the landscape scale, kudu and sable foraged more in patches located in the open grasslands compared to those located near trees and bush-clumps, whereas warthogs showed no preference for any vegetation type, and this pattern did not change after the introduction of wild dogs. Predicting the effect of vegetation structure on predation risk is complex, as it integrates the hunting mode of the predator as well as the predator-detection ability, avoidance behavior, and escape strategy of the prey (Kauffman et al. 2007; Gorini et al. 2012). However, visibility is generally a major determinant of safety, as it allows for early detection of the predators and subsequent monitoring, which increases escape time (Cresswell et al. 2010; Bell et al. 2012).

Wild dogs may chase prey into thick vegetation to reduce the escape options of the prey, and thus increase kill success (Creel and Creel 2002). In contrast, by foraging close to or within dense vegetation, detection by predators may be reduced (Mech et al. 2001; Creel and Winnie 2005). The fact that kudu and sable preferred to feed in open grasslands where sightlines were greater both before and after the introduction of the wild dogs suggests that the potential for predator detection reduced perceived predation risk more than hiding from predators. Moreover, it seems that the predation risk posed by wild dogs was not sufficiently different from the type of predation risk posed by cheetahs to change how habitat features (e.g., cover) affected overall perceived predation risk. However, if an ambush predator such as African lions had been introduced, this may have elicited a different antipredator response (a hierarchical instead of an additive response) as their style of hunting differs considerably from that of cheetahs (West et al. 2013).

Predicting prey and ecosystem responses to the return of predators is timely and important, but challenging. Until now, most studies have focused on single-predator systems and the response of 1 prey species at a time. This study provides an important step toward extending our knowledge to more complex multi-predator-multi-prey systems. We, however, emphasize that only replication of field studies such as this, grounded in the theory of how prey species adjust their behavioral responses to returning predators within a multi-predator environment, will allow our knowledge to advance at the rapid pace required by the current dynamics of predator returns and reintroductions.

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