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# Human- and risk-mediated browsing pressure by sympatric antelope in an African savanna

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## ARTICLE INFO

### Keywords:

Anti-predator behaviour  
Consumer-resource dynamics  
Foraging  
Plant defense  
Rangeland  
Savanna  
Trophic cascade  
Ungulate

## ABSTRACT

Human activity shapes landscape heterogeneity, which can influence where and how species interact. In African savannas, human-mediated changes to woody cover affect perceptions of risk and foraging decisions by large herbivores. Through cafeteria-style feeding trials, we presented two common, browsing ungulates (Guenther's dik-dik [*Madoqua guentheri*] and impala [*Aepyceros melampus*]) with branches from four tree species that varied in their relative investment in mechanical and chemical defenses. We conducted trials in habitats that were perceived as risky to either dik-dik (i.e., open habitat) or impala (i.e., bushland habitat). We found that dik-dik preferred to eat thorny trees low in tannin content within bushland habitats, while the larger-bodied impala preferred tannin-rich but thorn-less branches within open habitats. Risk-induced habitat use homogenized browsing pressure in the lower canopy, but increased heterogeneity in browsing pressure in the upper canopy. In addition, plant defenses neutralized the effects of risk, and foraging height on browsing pressure. Our results demonstrate how foraging experiments—typically the basis for field studies on species coexistence—can be extended to make inferences about consumer-resource dynamics in human-modified landscapes.

## 1. Introduction

People are causing unprecedented changes in animal abundance (Dirzo et al., 2014), behaviour (Gaynor et al., 2018; Tucker et al., 2018), and evolution (Otto, 2018). Conservation efforts to understand and reverse these changes have focused primarily on the structural components of the ecosystem, i.e., habitat, species diversity, and density. Less appreciated in this focus is the influence of people on species interactions and how human activity shapes the outcome of trophic flows across landscapes (Fraser et al., 2015; Schmitz et al., this issue). As such, the capacity to restore nature is hindered, in part, by a lack of understanding about the mediating influence of people on the critical interactions that make ecosystems function.

In many terrestrial ecosystems, trophic dynamics are shaped by spatially structured variation in consumptive (the direct killing of prey) and non-consumptive (the triggering of anti-predator behaviors or

traits, often with a demographic cost) species interactions (Creel et al., this issue; Owen-Smith, this issue). For example, carnivores select areas to hunt where they are most likely to encounter prey (Murray et al., 1994; Spong, 2002), or most likely to kill prey given an encounter (Hopcraft et al., 2005; Kauffman et al., 2007). Likewise, herbivores target areas on the landscape where plants are most abundant (McNaughton, 1985) or most nutritious (Aikens et al., 2017; Fornara and Du Toit, 2007), or where it is safest to forage (Creel, 2018; Ford et al., 2014; Moll et al., 2017; Owen-Smith, this issue).

The spatial interplay between consumptive and non-consumptive interactions is also influenced by human activity. For example, in Banff National Park, wolf avoidance of a town site created a 'human shield' (sensu Berger, 2007) that attracted elk, intensifying local impacts of browsing on the shrub community (Hebblewhite et al., 2005). This localized browsing pressure altered the distribution of other shrub-dependent species, like songbirds and beavers (Hebblewhite et al., 2005).

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The combination of fear avoidance and browsing had cascading impacts through the ecosystem, prompting wildlife managers to change how they interact with urbanized elk. More broadly, the potential for such consumptive and non-consumptive cascades to emerge in human-modified landscapes have motivated calls to conserve large carnivores (Ripple et al., 2014).

In African savannas, human-caused changes in the pattern of woody cover influence both consumptive and non-consumptive predator-prey dynamics for many large mammals (Augustine, 2004; Ford et al., 2014; Veblen, 2012; Young et al., 1995). Fire, mega-herbivore extirpation, overgrazing, and climate change have contributed towards woody cover encroachment in some areas, and loss of woody cover in other areas (Bond, 2008; Ford et al., 2016). In addition, the distribution of woody cover has implications for the persistence of grassland-associated wildlife and human livelihoods that depend on access to grass (Ali et al., 2018, 2017). For these reasons, there is urgency to develop a more robust understanding how human-mediated landscape structure influences consumer-resource dynamics in African savannas.

We examined the effects of risk-averse foraging behaviour for two sympatric herbivores, Guenther's dik-dik (*Madoqua guentheri*; ca. 5 kg) and impala (*Aepyceros melampus*; ca. 40 kg) in a human-dominated rangeland ecosystem. At our study sites in central Kenya, both herbivores consume *Acacia* sp. (i.e., *Vachellia* sp.) and other trees, and are commonly killed by leopards (*Panthera leo*) and African wild dogs (*Lycaon pictus*) (Ford, 2015). In this system, traditional grazing practices by pastoralists and modern ranching operations create a patchwork of 'glades' (0.5–2 ha open meadows) in a landscape of high woody cover (Goheen et al., 2018). For larger herbivores, risk of predation is associated with woody cover, while woody cover is safer for smaller-bodied species (Ford, 2015).

The contrasting effects of risk, mediated through woody cover, on different-sized herbivores sets up a rich framework of inquiry as to how carnivores, herbivores, and plants interact in human-modified landscapes. First, a 10-fold difference in body size between dik-dik and impala may translate into distinct food preferences via different susceptibilities to plant defense strategies, with dik-dik potentially more averse to chemical defenses and impala potentially more averse to mechanical defenses (thorns and spines; Demment and Van Soest, 1985; Cooper and Owen-Smith, 1986). Second, impala and dik-dik use different strategies to minimize exposure to predators. Dik-dik live in small family groups, defend territories, and hide from predators in woody cover (Ford and Goheen, 2015a). Impala live in harems of 10–50 individuals, and avoid tree cover at night to maximize detection and evasion of predators (Ford et al., 2014). Third, dik-dik feed to a height up to 1 m while impala can feed at heights 0–1.5 m. This height difference potentially affords impala exclusive access to food at upper branch heights. In combination, these species-specific, habitat-mediated perceptions of risk and resource availability may result in spatial heterogeneity in leaf loss: preferred (less thorny) foods of impala should incur more leaf loss in open areas, and on higher branches, whereas preferred (less chemically defended) foods of dik-dik should incur more leaf loss in bushy areas, and on lower branches. Because our study focused only on two species of herbivore, we are unable to attribute differences in perceived risk, food preference, or their interaction to body size or other facets of their biology. Instead, we based predictions of species-specific, habitat-mediated perceptions of risk and resource availability on the aforementioned earlier studies.

From our past experiments, we know that dik-dik and impala differ in associating risk of predation with open areas and with woody cover, respectively (Ford et al., 2014; Ford and Goheen, 2015a). Using these results as a starting point, we conducted cafeteria-style feeding experiments to compare three dimensions of foraging activity (risk-induced habitat use, plant defense, and foraging height) between dik-dik and impala. We quantified leaf consumption and persistence in habitats that varied in perceived risk of predation (open vs. bushland), among common species of trees that varied in defense strategy (mechanical vs.

chemical [see Supplemental information Table S1]), at two heights (0–1 m and 1–2 m). Under a hypothesis of strong resource-use overlap, we expected dik-dik and impala to display indistinguishable preferences in foraging habitat, woody plants, and browsing heights (i.e., in the lower canopy). Under a hypothesis of strong resource partitioning, we expected non-overlapping foraging habitats, woody plants, and browsing heights for dik-dik and impala, leading to spatial homogeneity in browsing pressure.

## 2. Materials and methods

### 2.1. Study area

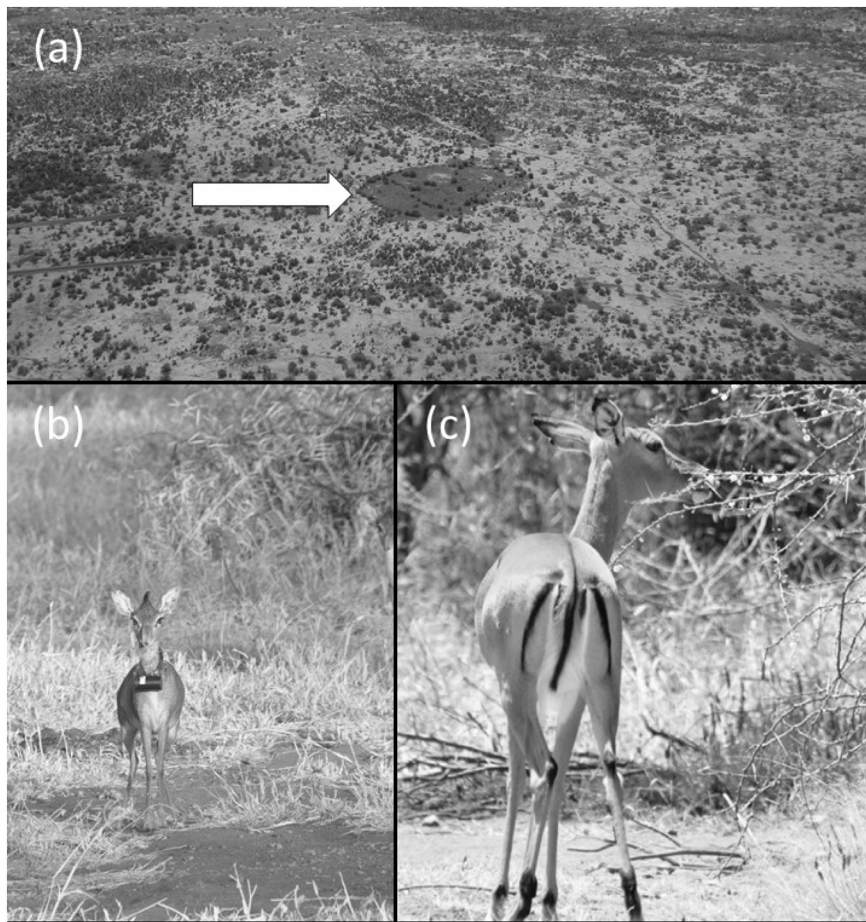
We conducted our study between December 2012 and July 2014 at the Mpala Research Centre (MRC) in Laikipia County, Kenya (0° 17' N, 37° 53' E) at 1600–1800 m above sea level. The MRC and the associated Mpala Ranch comprise ca. 200 km<sup>2</sup> of semi-arid savanna where people, livestock, and wildlife co-occur. Rainfall averages 508 mm annually and is weakly trimodal, with a major peak in April–May, and minor peaks in August and in October–November (Augustine, 2003a).

Maximum biomass density of wild herbivores stands at ca. 5282 kg per km<sup>2</sup>; elephant (*Loxodonta africana*) are most abundant (but migratory) at 2882 kg per km<sup>2</sup>, followed by impala (*Aepyceros melampus*) at 813 kg per km<sup>2</sup>, and dik-dik (*Madoqua guentheri*) at 693 kg per km<sup>2</sup>. Combined, these three species constitute ca. 80% of the total wild herbivore biomass at the study area (Augustine and McNaughton, 2010). Other large (> 5 kg) wild herbivores found include plains zebra (*Equus burchellii*), giraffe (*Giraffa camelopardalis*), waterbuck (*Kobus ellipsiprymnus*), buffalo (*Syncerus caffer*), and eland (*Taurotragus oryx*) (Georgiadis et al., 2007a). Large (> 20 kg) carnivores at MRC and the Mpala Conservancy include African wild dog (*Lycaon pictus*), lion (*Panthera leo*), leopard (*P. pardus*), spotted hyena (*Crocuta crocuta*), and striped hyena (*Hyaena hyaena*).

As the most (numerically) abundant species of wild herbivores, we selected dik-dik and impala as foci for our study (Fig. 1). Dik-dik and impala consume similar foods, although impala differ from dik-dik in eating significant amounts of grass in the wet season (Cerling et al., 2011; Kartzinel et al., 2015). Impala spend most of their time in open areas known as 'glades' which are derived from former cattle corrals and are perceived by impala as safer than the surrounding bushland (Augustine, 2004; Ford et al., 2014; Figure 1). Conversely, dik-dik spend most of their time in bushland (Manser and Brotherton, 1995; Ford and Goheen, 2015a; Figure 1). We focused on how impala and dik-dik forage upon four tree species - *Acacia brevispica*, *A. etbaica*, *Croton dichogamus* and *Grewia bicolor* - which together account for > 80% of woody stems at the study area (Young et al., 1995) and exhibit a range of defensive traits. *Acacia brevispica* is characterized by smaller thorns, larger leaves, and higher levels of condensed tannins compared to *A. etbaica*, although differences in tannin content between *A. etbaica* and *A. brevispica* do not influence diet preferences of impala (Ford et al., 2014). In addition to short, recurved thorns, *A. etbaica* exhibits long, straight thorns, and thus is the best mechanically-defended species of the four trees in our study. *Croton dichogamus* and *G. bicolor* have no spines or thorns, and exhibit leaf sizes comparable to *A. etbaica*. With respect to tannin concentration, *C. dichogamus* is the best chemically defended of the four focal species in our study (Supplemental information Table S1). *Grewia bicolor* exhibits similar chemical composition to that of the two *Acacia*, and thus is likely the least defended tree in our study system (Supplemental information Table S1).

### 2.2. Field methods

We assessed foraging by impala and dik-dik on the four tree species (*A. etbaica*, *A. brevispica*, *G. bicolor*, *C. dichogamus*) in two habitat types (glade and bushland). Each experimental trial lasted two nights, and consisted of three plots ( $n = 1$  in the glade and  $n = 2$  in the bushland);



**Fig. 1.** Oblique aerial photo of (a) a typical glade (arrow) surrounded by a matrix of bushland habitat. Bushland is characterized by visibility of ~25 m and is used by (b) dik-dik. Typically, glades are 1 ha, characterized by visibility of ~50 m and used by (c) impala.

plots within an experimental trial were positioned 50–100 m apart. Plots in glades were > 50 m from the edge of the glade. Plots in bushland habitat were 50 m from the edge of the glade in a pre-determined, random direction from glade plots. At any given site, our experimental plots were within 200 m of one another. Bushland plots were established in areas with sign of impala or dik-dik (e.g., game trails, dung middens) to maximize the probability that a plot would be visited. In pilot studies, we found comparatively few detections of either species of wild herbivore at bushland plots. As such, and to maximize sampling across habitat types, we paired two bushland plots with each glade plot ( $n = 19$  sites;  $n = 19$  glade plots;  $n = 38$  bushland plots).

A plot consisted of a single branch cutting from each of two species anchored in separate pots filled with sand and water to maximize persistence of green foliage. Tops of the two pots were levelled with the ground and covered with local substrate to minimize animals' perceptions of human activity. The two pots were ca. 1-m apart. A single combination of two tree species was selected for each trial, and the same combination was used in all the three plots in a trial. We conducted 10 trials of each of the 6 combinations of two tree species.

We assessed leaf consumption (biomass of leaves removed on each branch cutting after 2 trial nights) and leaf persistence (biomass of leaves remaining on each branch cutting after 2 trial nights) for the four tree species at lower (~0.5 m) and upper (~1.5 m) foraging heights. Leaf consumption measures how herbivores perceive and utilize resources. Leaf persistence measures the impact of herbivory on the plant, with greater persistence suggesting weaker browsing pressure. At the start and completion of each trial, we counted leaves on a 10-cm marked section of each branch cutting within each foraging height. We

estimated leaf consumption from the product of the numbers of removed leaves multiplied by dry matter weight of the average leaf (Supplemental material Table S1). We estimated leaf persistence from the product of the numbers of remaining multiplied by dry matter weight of the average leaf.

At each plot, we placed a single, motion sensitive camera trap (Reconyx RM45 - Reconyx, Inc., Holman, WI, USA) approximately 8-m away from the branch cuttings, allowing us to view all animals foraging on either branch cutting. Camera traps were set to take 5 photos per trigger with no delay between trigger intervals. Our final dataset included 1304 trial-nights distributed among 19 sites.

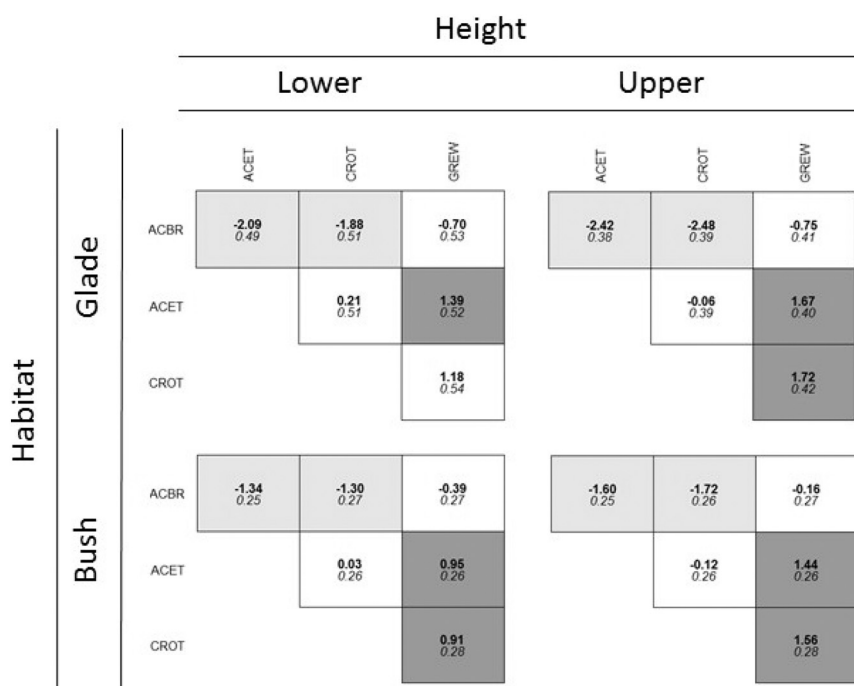
### 2.3. Data analyses

We used linear-mixed effects models to test for the effects of habitat type on leaf loss and leaf persistence from each of the four tree species at each foraging height. We used a linear mixed effects model with log transformed (+ 0.01) leaf persistence as the response variable, with an offset term (also log transformed, + 0.01) for initial leaf biomass at the start of the trial, fixed effects for habitat type, and a random effect of trial nested in site. The offset term is needed because the initial biomass of each branch differed within and between species, such that the initial biomass could affect how many leaves were left at the end of the trial and confound the response to herbivory per se.

To quantify leaf consumption, we used a similar analytical structure to the leaf persistence analysis, but examined the log transformed biomass removed (+ 0.01) as the response variable and did not include an offset term. This analysis quantifies the diet preference of dik-dik and impala; however, we do not have data on which individual leaves

**Table 1**  
The effect of habitat type on leaf persistence (g/cm) after two nights of exposure to ungulate foraging.

Branch height	Tree species	$\beta$	SE	P	Interpretation
Lower	<i>Acacia etbaica</i>	0.142	0.172	0.411	No effect of habitat type.
	<i>Acacia brevispica</i>	-0.068	0.401	0.865	No effect of habitat type.
	<i>Croton dichogamus</i>	-0.044	0.064	0.501	No effect of habitat type.
	<i>Grewia bicolor</i>	-0.546	0.347	0.123	No effect of habitat type.
Upper	<i>Acacia etbaica</i>	-0.397	0.159	0.016	Less leaf biomass remaining in glade
	<i>Acacia brevispica</i>	-0.838	0.406	0.044	Less leaf biomass remaining in glade
	<i>Croton dichogamus</i>	-0.024	0.023	0.295	No effect of habitat type.
	<i>Grewia bicolor</i>	-1.042	0.342	0.004	Less leaf biomass remaining in glade



**Fig. 2.** Tukey's posthoc comparisons of herbivore-removed leaf biomass for tree species within each habitat and foraging height. Bold numbers indicate the mean difference in coefficient estimates (columns minus rows). Italicized values show standard errors. Dark gray shading indicates that species listed in the column had significantly more ( $P < 0.05$ ) biomass removed than the species in the row. Light gray shading indicates that species listed in the column had significantly less biomass removed than the species in the row. White cells indicate no significant differences in biomass removal between species. Species codes are as follows: ACBR (*Acacia brevispica*), ACET (*Acacia etbaica*), CROT (*Croton dichogamus*), GREW (*Grewia bicolor*).

were consumed by which species of herbivore.

To quantify foraging activity of dik-dik and impala, we compared the number of photos from camera traps showing foragers actively consuming leaves from each branch cutting in each plot, accounting for the nested experimental design of the plots within trials. We used generalized linear mixed models with a Poisson distribution because the response variable was counts (number of photos x number of individuals per branch cutting). Only data involving the consumption of leaves by dik-dik or impala was used. All statistical analyses were performed using R (v 3.4.3) package 'lme4' v1.1-15 (Bates et al., 2015) with statistical significance determined at the level of  $P < 0.05$ .

### 3. Results

We documented a mean biomass consumption of 0.62 g ( $\pm 0.9$  SD) per 10 cm of branch per night, with 45% of consumption consisting of *A. brevispica* and 33% consisting of *G. bicolor*. Using camera traps, we detected a mean foraging activity of 10.0 impala ( $\pm 19.0$  SD) and 0.63 dik-dik ( $\pm 1.9$  SD) per branch per night.

Leaf persistence varied by all three foraging dimensions – height, defenses, and habitat (Table 1). At lower branch heights, there was no effect of habitat on leaf persistence for any tree species. At upper branch heights, leaves of all species had lower persistence in the glade than in the bushland, with the exception of *Croton dichogamus* (in which leaf persistence did not vary across habitats).

Leaf consumption was influenced by habitat ( $F = 9.47$ ;  $P < 0.001$ ) and tree species ( $F = 62.11$ ;  $P < 0.001$ ), but not by height ( $F = 0.32$ ;

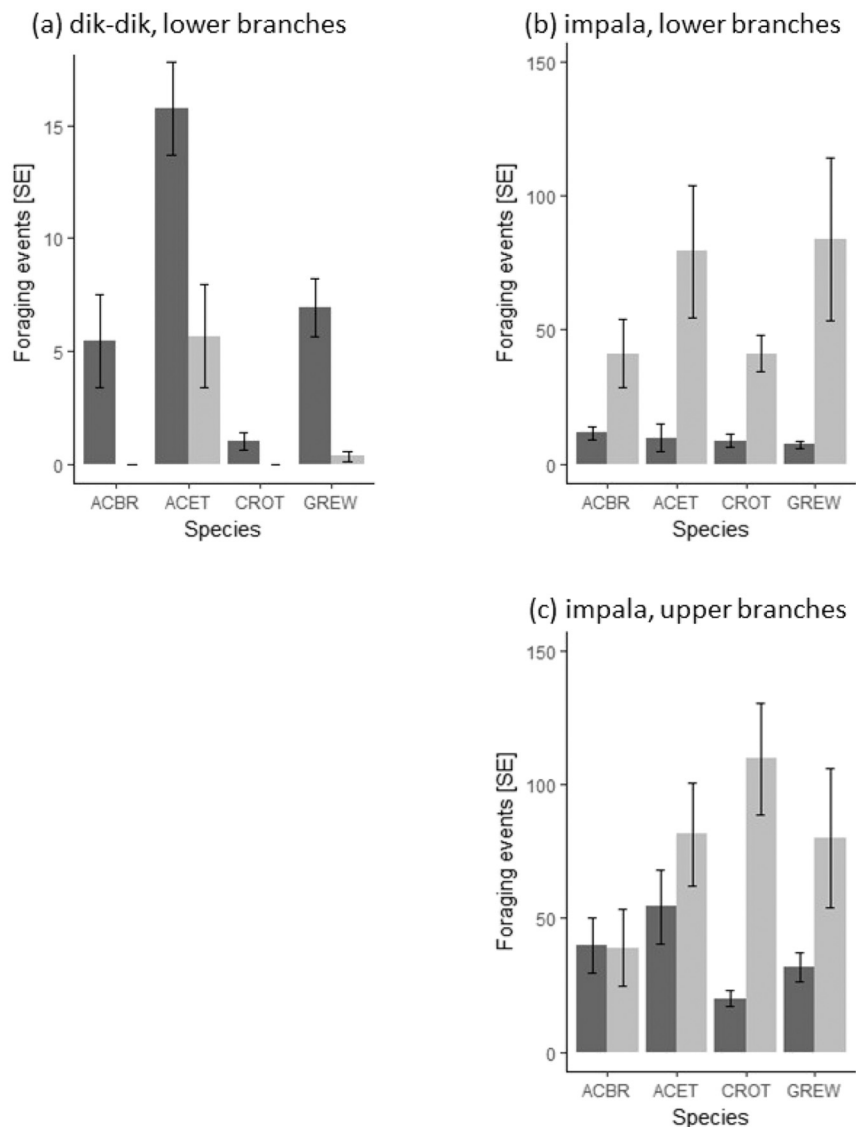
$P = 0.570$ ). A post-hoc analysis for differences in leaf consumption between tree species indicated comparable amounts of leaf consumption between foraging heights for a given habitat (Fig. 2). An exception was a non-significant difference between *C. dichogamus* and *G. bicolor* in glades at lower branch heights. At the remaining habitats and heights, *G. bicolor* was preferred to *C. dichogamus*.

Foraging activity varied by herbivore and habitat. We recorded 9748 foraging events, of which 94% were by impala. Of the impala foraging events, 69% ( $n = 6353$ ) occurred in glades, of which 56% ( $n = 3570$ ) were at upper branch heights. Conversely, only 5% ( $n = 518$ ) of all impala foraging events were detected at lower branch heights in the bushland. Dik-dik foraging activity was restricted to lower branches, and occurred primarily in the bushland (86% of dik-dik foraging events).

There was a significant effect of habitat type on the foraging activity recorded for each tree species. Dik-dik foraged more on *A. etbaica* and *G. bicolor* than *A. brevispica* and *C. dichogamus* in the bushland habitat; we did not record dik-dik foraging on *A. brevispica* and *C. dichogamus* in the glade habitat (Fig. 3A). Foraging by impala for all tree species and at all heights was greater in the glade than in the bushland habitat (Fig. 3B, C).

### 4. Discussion

Despite strong overlap in preference for the same species of tree between dik-dik and impala, distinct use of other foraging dimensions (risk-induced habitat use and foraging height) gave rise to spatial



**Fig. 3.** Foraging activity (number of photos) of (a) dik-dik at lower branch heights; (b) impala at lower branch heights; and (c) impala at upper branch heights for four species of trees in experimental plots. Dark gray bars indicate mean foraging activity in the bushland and light gray bars indicate mean foraging activity in glades. Species codes are as follows: ACBR (*Acacia brevispica*), ACET (*Acacia etbaica*), CROT (*Croton dichogamus*), GREW (*Grewia bicolor*).

variation in browsing pressure. Dik-dik consumed leaves primarily in the bushland, occasionally in glades, and exclusively at lower branches. Impala consumed leaves primarily in the glades, occasionally in the bushland, and rarely from lower branches in the bushland. As a result of partitioning risk avoidance by impala and dik-dik, leaf persistence was: 1) homogenized among habitat types at lower branch heights; 2) heterogenized on higher branches because leaves persisted longer in the bushland than in the glade.

We believe that distinction between dik-dik and impala in these foraging dimensions arises from differences in how each species perceives risk of predation. Through a combination of GPS tracking and field experiments, Ford et al. (2014) showed that impala avoid woody cover because it is associated with higher per capita risk of mortality from predation by leopards and wild dogs. Conversely, dik-dik typically avoid glades and other open areas (Ford and Goheen, 2015a), presumably because they rely on crypsis to minimize predation (Brashares et al., 2000). Risk-mediated habitat segregation has been observed elsewhere in sympatric ungulates (Lingle et al., 2011) and other taxa (Orrock et al., 2013; Werner et al., 1983), but usually as short-term responses to an immediate encounter with a single predator (Montgomery et al., this issue). Here, we showed that such segregation borne

out over longer periods (via persistent response to woody cover) affects the distribution of plant-herbivore interactions across space.

Resource partitioning among herbivores was also influenced by the manner in which perceived risk of predation influences foraging height. Dik-dik cannot access upper branches, while impala are able to access leaves on both upper and lower branches. However, impala generally forewent browsing at lower branch heights in the bushland. A raised head posture is often associated with higher alertness and risk-aversion in ungulates, especially in habitats with low visibility (Makin et al., 2017; Smith and Cain, 2009; Underwood, 1982). Thus, impala can remain vigilant while feeding at upper branch heights, even in the risky bushland. In glades, where visibility is 50–100 m and grass is cropped to < 30 cm, the lowered head position may not incur any more risk than a raised head position. In contrast, in the bushland, a lowered head likely incurs a greater reduction in visibility than a raised head position. The change in visibility along a vertical axis may explain why impala foraging activity was influenced by habitat type at lower branches but not upper branch heights (Fig. 3).

We found that plant defense strategy (mechanical vs chemical defenses) interacted weakly with habitat to affect both leaf removal and foraging activity. Generally, diet preferences are narrower in risky

habitats (animals focus on higher-quality foods) while food preferences weaken in safer habitats (Brown, 1999; Fryxell and Doucet, 1991; Sinclair and Arcese, 2009). In habitat that dik-dik perceived as risky (glades), they consumed trees that either were poorly defended altogether (*G. bicolor*) or mechanically defended (*A. etbaica*), and avoided eating trees defended by tannins (*A. brevispica*, *C. dichogamus*; Fig. 3a). In habitats that dik-dik perceived as safe (bushland), they broadened their diet to include these chemically-defended trees. Similarly, impala avoided both species of thorny trees (*Acacia* spp.) at lower branch heights in risky habitats (bushland), but foraged on both lower and upper branches within the safety of glades (Fig. 3b and c). Although dik-dik and impala have distinct perceptions of which habitat type is riskiest, each species relaxed its diet preferences in the habitat it perceives as safe.

The general pattern of aversion by dik-dik to chemically-defended trees, and by impala to mechanically-defended trees, is consistent with research showing that chemical defenses are more effective for smaller-sized herbivores and mechanical defenses are more effective for larger-sized herbivores (Demment and Van Soest, 1985; Cooper and Owen-Smith, 1986). Moreover, these results indicate that the effectiveness of plant defense depends not only on the size of the herbivore, but on the perceptions of risk by the herbivore – an outcome also documented in squirrels (Schmidt, 2000), bush babies (McArthur et al., 2012), rabbits (Camp et al., 2015), and monkeys (Emerson and Brown, 2015).

Our use of a cafeteria-style feeding experiment to quantify the interaction between consumptive and non-consumptive interactions builds on a legacy of studies using ‘giving up densities’ conducted elsewhere that have largely focused on rodents (e.g., Brown, 1988; Brown, 1989; Bowers and Dooley, 1993; Brown, 1999; Halliday and Morris, 1993). To the best of our knowledge, ours is the first study to use natural food sources in a GUD-like approach to understand how risk of predation and plant defense impacts browsing pressure by ungulates. GUDs have been used to quantify perceived risk of predation in other ungulates (e.g., Abu Baker, 2015; Abu Baker and Brown, 2013; Bleicher and Rosenzweig, 2017; Druce et al., 2009; Iribarren and Kotler, 2012), but to our knowledge these studies have focused on consumer dynamics and no attempts have been made to link GUDs to resource heterogeneity per se. Although our study offers a novel way of using natural plant material in a field experiment, we acknowledge that the presentation of branch cuttings was not entirely natural. Glades are generally devoid of woody vegetation, and the sudden appearance of the ~2-m tall branch cuttings is an unusual context for ungulates to encounter food. A more natural presentation may include branch cuttings that more closely represent an earlier life history stage, such as a seedling or sapling, an approach that is worth exploring in future studies. There is also substantial room to measure how other plant-based traits (i.e., chemical, mechanical defenses, nutrient densities) influence diet selection. The use of natural food sources in GUD studies for large mammals is an important advance in studies looking to quantify fear-mediated trophic cascades (Ford and Goheen, 2015b).

Our results provide insight into the mechanisms by which spatial heterogeneity in woody cover is maintained through herbivory. Previous work in our study area suggested that heterogeneity in woody cover was created by people (i.e., through cattle corrals or ‘bomas’) and maintained by wildlife (Augustine and McNaughton, 2010; Augustine, 2003b). Our results suggest that both dik-dik and impala may have an impact on the establishment and recruitment of trees in glades, and to a lesser extent, dik-dik may also have an impact on trees in bushland habitats. Herbivory by both species is capable of altering tree densities and suppressing woody vegetation (Ford et al., 2015, 2014). Understanding how herbivores influence the characteristic tree-grass codominance of savannas is an important consideration as woody encroachment continues to threaten grasslands in East Africa (Ford et al., 2016). Such considerations are also germane to understanding the consequences of herbivore population declines (Georgiadis et al., 2007a, 2007b; Young et al., 2013; Ali et al., 2017) and carnivore

recovery (Ford et al., 2015, Ng'weno et al., 2017) in coexistence landscapes (Schmitz et al., this issue).

## Declaration of authorship

TO, ATF, JRG conceived and designed the field experiments. TO conducted field work. TO and ATF analysed the data. IO and AM conducted lab work. TO, ATF, JRG, and PW wrote the manuscript, while other authors offered editorial guidance.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.01.028>.

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