

Elephant both Increase and Decrease Availability of Browse Resources for Black Rhinoceros

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ABSTRACT

Despite the apparent dual role of elephant *Loxodonta africana* in shaping the food niches of large herbivores, empirical studies focus on their role in facilitating foraging opportunities, while declining resource opportunities (a necessary requirement for competition) are rarely quantified. Our study investigates the relative importance of elephant in these processes by quantifying potential browsing opportunities (using total and preferred biomass, between-bite distances and bite mass) for black rhinoceros *Diceros bicornis* along a gradient of elephant utilization in the succulent thickets of the Addo Elephant National Park, South Africa. We show that browse biomass and potential between-bite harvest rates initially increase with the intensity of elephant utilization through the formation and spread of elephant pathways in otherwise impenetrable thicket. At the maximum, modeled estimates of total and preferred biomass are on average 223 percent and 254 percent higher, respectively, than that recorded in the absence of elephant (Exclosures); potential between-bite harvest rates are 75 percent higher. With continued elephant utilization, however, browse biomass declines and between-bite distances increase as the pathways expand and coalesce and canopy height declines. Our model of the change in potential browsing opportunities for rhinoceros reflects the accumulated effects of elephant over time, *i.e.*, the effects accumulate until the relationship switches from increased to reduced availability. With this we demonstrate the key role of elephant for rhinoceros foraging, linked to a potential loss of this role at higher levels of utilization.

Key words: Addo Elephant National Park; browse availability; foraging opportunities; impacts; succulent thicket; trophic interactions.

ALTHOUGH THE SHARED IMPORTANCE OF FACILITATION AND COMPETITION IN SHAPING LARGE herbivore communities is widely accepted (Sinclair 1985, Murray & Illius 1996, Putman 1996), the relative occurrence of these processes is little studied (Hobbs *et al.* 1996, Young *et al.* 2005, Odadi *et al.* 2011). In African large herbivore assemblages, elephant *Loxodonta africana* typically utilize the greatest share of the available resources and play a key role in the structure and functioning of these communities (Fritz *et al.* 2002, 2011). These trophic interactions are mediated mostly by effects on vegetation composition and structure (reviewed in Kerley *et al.* 2008), which intensify as elephant densities increase. For some herbivores the effects facilitate access to habitat (Parker 1983, Valeix *et al.* 2011, see Pringle 2008 for effects on other vertebrates) and increase the availability and quality of food (*e.g.*, Rutina *et al.* 2005, Makhabu *et al.* 2006, Kogi *et al.* 2011). As an example, the conversion of tall woodlands to shrub coppice improves access to nutrient-rich regrowth for browsers. Where elephant are abundant, competition may intensify as the impacts reduce browse availability and alter habitats unfavorably (Owen-Smith 1988, Kerley *et al.* 2008, Landman *et al.* 2013). In these cases, elephant limit browser abundances as woodlands are transformed to open habitat (Parker 1983). Despite the apparent dual role of elephant in shaping the food niches of large herbivores, empirical studies focus on their role in facilitation, while declining

foraging opportunities (a necessary requirement for competition) are rarely quantified (Young *et al.* 2005). Identifying the relative importance of elephant in these processes is significant given their status as keystone species (thus maintaining key processes), and the need to manage elephant effects on biodiversity by reducing competition (Owen-Smith 1988, Kerley & Landman 2006, Kerley *et al.* 2008).

In the succulent thickets of the Addo Elephant National Park, South Africa, elephant effects on the woody community are dramatic, such that significant declines in plant species richness, density and biomass have been recorded (reviewed in Kerley & Landman 2006). Consequently, recent evidence suggests that elephant and black rhinoceros *Diceros bicornis* compete for browse resources, causing rhinoceros to shift their foraging along the browse-grass continuum and in relation to availability (Landman *et al.* 2013). Opposing this competitive interaction is the hypothesis of Kerley *et al.* (1999) that the formation of elephant pathways may facilitate access to habitat and food for herbivores in otherwise impenetrable thicket. It is also likely, however, that the role of elephant in these processes may be linked, varying with the intensity of utilization. We tested this by quantifying potential browsing opportunities for rhinoceros along a gradient of elephant utilization in the Addo Elephant National Park. With this approach, we contrasted two alternative hypotheses with our null hypothesis of no change: (1) given the evidence for competition, elephant consistently reduce browsing opportunities for rhinoceros; or (2) elephant initially facilitate access to browse

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through path formation, but these foraging opportunities decline (increasing the potential for competition) with intensive utilization. As the structure of the canopy shrubs continue to decline with elephant utilization (*sensu* Landman *et al.* 2012), we did not test the unlikely scenario that browsing opportunities may increase toward equilibrium. We expected elephant to influence the biomass, spatial distribution and structure (*i.e.*, the responses of leaves and shoots to browsing – *e.g.*, Bergstrom 1992) of browse (*e.g.*, Rutina *et al.* 2005, Kohi *et al.* 2011), affecting potential harvest rates and consequently foraging effort (Spalinger & Hobbs 1992, Shipley & Spalinger 1995, Shipley *et al.* 1998, Shipley 2007). Thus, we quantified potential browsing opportunities using browse biomass, between-bite distances and bite mass, for potential between- and within-bite harvest rates. Elephant herbivory is considered the key determinant of thicket structure (as opposed to rainfall or fire; Kerley *et al.* 1995, Hayward & Zawadzka 2010), and so we discuss our results in terms of the role of elephant in driving herbivore foraging opportunities.

METHODS

Addo Elephant National Park (33°31'S, 25°45'E) is situated in the Eastern Cape, South Africa. The park comprises several fenced sections with the majority of the elephant population confined to the Addo Main Camp section (AMC; 120 km² at the time of the study). AMC was originally fenced in 1954 (23.3 km²) to enclose the elephant of the region and incrementally expanded to accommodate the steadily growing population (from 22 individuals in 1954 to nearly 400 in 2003; Kerley & Landman 2006). Three sites (Exclosures; covering 4.3, 4.2 and 1.9 km²) that have excluded elephant for >50 yr, but are accessible to other large herbivores (*e.g.*, kudu *Tragelaphus strepsiceros*, bushbuck *Tragelaphus scriptus*, common duiker *Sylvicapra grimmia*), were established for monitoring purposes. While only 11 black rhinoceros occurred in AMC during the study, the area previously supported more than 40 individuals.

The region is semi-arid with 260–530 mm rainfall annually. In the absence of natural permanent surface water, various pumped water points maintain water availability year-round (Landman *et al.* 2012). The area comprises a series of low, undulating hills (60–350 m in height) in the Sundays River valley where nutrient-rich soils give rise to succulent thicket habitats (covering *ca* 70% of the area). These thickets are typically evergreen, 2–4 m high, dense and characterized by a high diversity of growth forms (Vlok *et al.* 2003). The tree succulent *Portulacaria afra* is locally dominant and occurs in a matrix of spinescent shrubs (*e.g.*, *Azima tetraacantha*, *Capparis sepiaria*, *Carissa bispinosa*, *Searsia* spp.) and low trees (*e.g.*, *Euclea undulata*, *Schotia afra*, *Sideroxylon inerme*). Couch grass *Cynodon dactylon* is seasonally abundant in areas where intensive utilization by elephant has removed the canopy shrubs (Landman *et al.* 2012).

EXPERIMENTAL DESIGN.—We used the incremental expansion of AMC between 1954 and 2003 to establish a gradient of elephant utilization and quantify potential browsing opportunities for rhi-

noceros. Thus, following Lombard *et al.* (2001), our approach assumed that areas utilized for an extended period experienced relatively higher impacts, due to higher mean elephant densities, when compared with areas utilized for shorter periods; *i.e.*, we (initially) assumed an even distribution of elephant and substituted space for time. We estimated elephant density for each site as the mean over 49 yr, using population numbers from Gough and Kerley (2006) for every year. Forty-three, 30 m line-transects were located at five sites (6–13 transects per site, separated sufficiently [>1 km] to be considered independent) exposed to elephant, representing mean densities between 0.4 and 2.3 elephant/km² (Table 1). We also placed 12 transects at the Exclosures and used these as a control against which to measure elephant effects (Lombard *et al.* 2001).

Surface water availability is a key limiting resource for elephant, and so their impacts intensify in the vicinity of water (Chamaille-Jammes *et al.* 2007, Landman *et al.* 2012). In succulent thicket, this results in the near complete replacement of the thicket shrub community with grasses (Landman *et al.* 2012), and therefore the near loss of browsing opportunities. Thus, to contextualize our gradient of elephant utilization and quantify the upper-limit of impacts on potential browsing opportunities for rhinoceros, we also surveyed eight transects placed within 300 m of Hapoor water point. Hapoor is located in the area of AMC originally fenced in 1954 (Site 1), and is one of only two water points that have maintained water availability for elephant since the initial fencing. All other experimental transects were located >1000 m from permanent water (*i.e.*, the distance at which elephant effects tend toward an asymptote in thicket – Landman *et al.* 2012) to reduce the effect of water. As our experimental transects were generally placed on even terrain with similar soils (*a proxy* for food quality; Kohi *et al.* 2011, Pretorius *et al.* 2011), we expected surface water availability to be the primary determinant of elephant effects at this scale.

Our approach assumed that elephant were the principle drivers of vegetation structure (and hence browsing opportunities),

TABLE 1. Characteristics of sample sites incrementally exposed to elephant in the Addo Main Camp section.

Site	Area (km ²)	Total time (yr) utilized by elephant	Mean no. of elephant/km ² (range) [†]
1	23.3	49	2.3 (0.9–4.0)
2	14.4	26	1.3 (1.8–3.2)
3	10.6	21	1.1 (1.8–3.2)
4	22.9	19	1.0 (1.8–3.2)
5	31.0	8	0.4 (2.3–3.2)
Exclosure	10.4	0	0 (0)

[†]Estimated as the mean over 49 yr (1954–2003) using population numbers from Gough and Kerley (2006) for every year. Note that because mean densities were standardized to 49 yr, these are generally smaller than the range estimated according to the time each site was utilized by elephant.

dominating the effects of other herbivores (*e.g.*, kudu, bushbuck, common duiker). While this assumption should be treated with caution (Landman *et al.* 2008), it reflected the fact that elephant dominate large herbivore biomass in AMC (South African National Parks, unpubl. data) and have been managed at densities that exceed recommended levels for 50 yr (Kerley & Landman 2006). We recognize that the effects of rhinoceros on vegetation structure may be comparable with that of elephant (*e.g.*, O’Kane *et al.* 2011), but presumed that these were offset in AMC through differences in population density.

POTENTIAL BROWSING OPPORTUNITIES.—As we were interested in browsing opportunities for rhinoceros specifically, we sampled at a scale that matched their foraging behavior. Thus, we used available information on black rhinoceros bite sizes (quantified as the stem diameter in millimeters at point of browsing) and foraging heights (max.: 175 cm) in succulent thicket (Wilson 2002) to define our sample units (*i.e.*, bites) and sampling range. Along each transect, we sampled rhinoceros browsing opportunities by clipping and collecting all potential bites within the estimated foraging height range that intersected the line. All canopy shrubs (27 spp.: 5 succulents, 22 woody shrubs) encountered along transects were sampled and we used species-specific mean bite sizes where possible (Wilson 2002). Collected material was oven-dried to constant mass. As succulent thicket is a seasonal habitat with an evergreen shrub community (Stuart-Hill & Aucamp 1993), we ignored seasonal variations in browse availability.

We quantified potential browsing opportunities in terms of browse biomass (g dry mass/m), between-bite distances (calculated as the inverse of the number of bites/m) and bite mass (g dry mass). Bite mass and bite distances were used to estimate potential within- (*i.e.* instantaneous) and between-bite harvest rates, and hence foraging effort. For browse biomass, we used available data on black rhinoceros food preferences in succulent thicket (quantified where elephant were absent; Landman *et al.* 2013) to differentiate between preferred and non-preferred items; preferred items are typically utilized more frequently when alternative foods are available on an equal basis (Johnson 1980). Bite mass was investigated by selecting 10 bites per site for each of the five canopy dominants with adequate data, *i.e.*, *P. afra*, *E. undulata*, *S. afra*, *A. tetracontba* and *C. sepiaria*; these species are important food items for rhinoceros in succulent thicket, contributing a portion of the bulk of the diet (Landman *et al.* 2013). Data for Hapoor water point were excluded from these analyses because most canopy shrubs were characteristically severely reduced (or completely removed) following intensive utilization by elephant (Landman *et al.* 2012).

CORRELATES OF POTENTIAL BROWSING OPPORTUNITIES.—To identify the likely correlates of the change in potential browsing opportunities, we used the hypothesis of Kerley *et al.* (1999) to predict that this will be associated with the formation and spread of elephant pathways. That is, path formation (reflecting the movement and foraging effects of the entire population) may initially facilitate access to browse in otherwise impenetrable thicket, but with

continued utilization these paths gradually replace the canopy shrubs (Landman *et al.* 2012), causing the loss of browsing opportunities. Thus, at each experimental transect we counted (for no. pathways/m) and measured the width (for path area/m) of each elephant path that intersected the line. In addition, because the top-down foraging of elephant reduces canopy height in thicket (Stuart-Hill 1992), presumably with implications for herbivore foraging height, we also recorded these heights at 50 cm intervals along each transect (calculated as the mean of 61 points per transect).

DATA ANALYSIS.—We modeled trends in browse biomass and potential harvest rates using ordinary least-squares regressions. Using our conceptual understanding of the effect of elephant on thicket structure, and hence potential browsing opportunities, we tested three candidate models: a null hypothesis (no effect), $y = \beta_0$; linear model (constant decline), $y = \beta_0 - \beta_1 x$; quadratic model (browsing opportunities reach a maximum at intermediate elephant densities, but decline toward the extremes), $y = \beta_0 + \beta_1 x + \beta_2 x^2$. In these models, y = potential browsing opportunity, x = intensity of utilization expressed as mean elephant density (Table 1), and β are constants. We evaluated model fit by testing for a significant contribution ($\alpha = 0.05$) of the quadratic term to the linear model on the basis of an *F*-test (Crawley 2007). Because we had no information on realized elephant numbers (hence mean densities) at Hapoor water point, we excluded the data for this site from the regressions; these data are presented as the mean \pm SD.

We further used multiple regression analysis to assess whether the number or area of elephant pathways or canopy height was associated with potential browsing opportunities for rhinoceros (using total browse biomass as the response variable). Model selection proceeded by systematically removing non-significant terms (*i.e.*, terms with the smallest non-significant partial *F*-statistic) from the full-model, comprising all explanatory variables and their interactions (Crawley 2007). Because multiple regression analysis is sensitive to co-linearity between the explanatory variables (Wetherill *et al.* 1986), we used hierarchical partitioning procedures (package hier.part in R2.14.0; R Development Core Team 2011) to confirm model fit and evaluate the relative independent contribution of each explanatory variable to the minimal adequate model (Mac Nally 2000). In all instances, diagnostic plots of observed and fitted values and residuals were inspected for deviations from model assumptions.

RESULTS

POTENTIAL BROWSING OPPORTUNITIES.—Nearly two-thirds of the canopy shrub species that we recorded at our sites are important food items for black rhinoceros in succulent thicket (Landman *et al.* 2013), comprising both dominant and preferred foods. We detected no change in the incidence of these species between sites (total: mean = 18 spp., $R^2 = 0.27$, $F_{1,5} = 1.50$, $P = 0.289$; preferred: mean = 12 spp., $R^2 = 0.05$, $F_{1,5} = 0.23$, $P = 0.656$), but recorded noticeably fewer species at Hapoor water point (total: 6

spp., preferred: 4 spp.). Thus, with the exception of Hapoor, we concluded that the predicted change in potential browsing opportunities was likely associated with a change in species abundance, rather than richness.

For all regression models of browse biomass and between-bite distances, model fit improved significantly when we added a quadratic term to the linear model (total biomass: $SS_{linear-quadratic} = 3718.70$, $P < 0.001$; preferred biomass: $SS_{linear-quadratic} = 3048.80$, $P < 0.001$; between-bite distances: $SS_{linear-quadratic} = 1.19$, $P < 0.001$). Browse biomass (total and preferred) and potential between-bite harvest rates initially increased with the intensity of utilization, reaching a maximum at the equivalent impact of roughly 1.6 elephant/km² (Fig. 1; Table 2). At the maximum, modeled estimates of total and preferred biomass were on average 223 percent and 254 percent higher, respectively, than that recorded in the absence of elephant (Exclosures), while potential between-bite harvest rates were 75 percent higher (*i.e.*, on average, distances between bites decreased from 0.84 m to 0.21 m toward the maximum). With continued utilization, however, browsing opportunities declined and presumably followed a trend toward the minimum recorded near water (Fig. 1). Here, browse biomass was 17 (total) and 43 (preferred) times lower than the estimated maximum, while between-bite distances reached 2.6 m.

Generally, bite mass for the canopy dominants varied little with mean elephant density (Table 2). For *P. afra* and *S. afra*, however, bite mass (log transformed) declined linearly such that potential within-bite harvest rates were 89 percent (*P. afra*) and

159 percent (*S. afra*) lower at their minimum than harvest rates at the Exclosures.

CORRELATES OF POTENTIAL BROWSING OPPORTUNITIES.—As expected, the number ($R^2 = 0.41$, $F_{1,54} = 36.84$, $P < 0.001$) and area ($R^2 = 0.33$, $F_{1,54} = 26.49$, $P < 0.001$) of elephant pathways increased with the intensity of utilization, eventually replacing the canopy shrubs near water (Fig. 2). Canopy height declined steadily along the same gradient ($R^2 = 0.33$, $F_{1,54} = 25.66$, $P < 0.001$).

Results from the multiple regression analysis showed that 40 percent ($F_{2,52} = 17.26$, $P < 0.001$) of the change in total browse biomass could be explained by elephant path area (coefficient = 26.47, SE = 9.87) and canopy height (coefficient = -11.97, SE = 3.78). Hierarchical partitioning confirmed our model selection and determined that for the best-model, canopy height contributed more of the variation (54.1%) in browse biomass.

DISCUSSION

While the keystone role of elephant in shaping large herbivore communities is widely accepted (*e.g.*, Owen-Smith 1988; Fritz *et al.* 2002, 2011; Kerley *et al.* 2008), the scale at which this manifests is not understood. By describing a unimodal relationship between potential browsing opportunities for black rhinoceros and elephant effects, our study provides insights into the dual

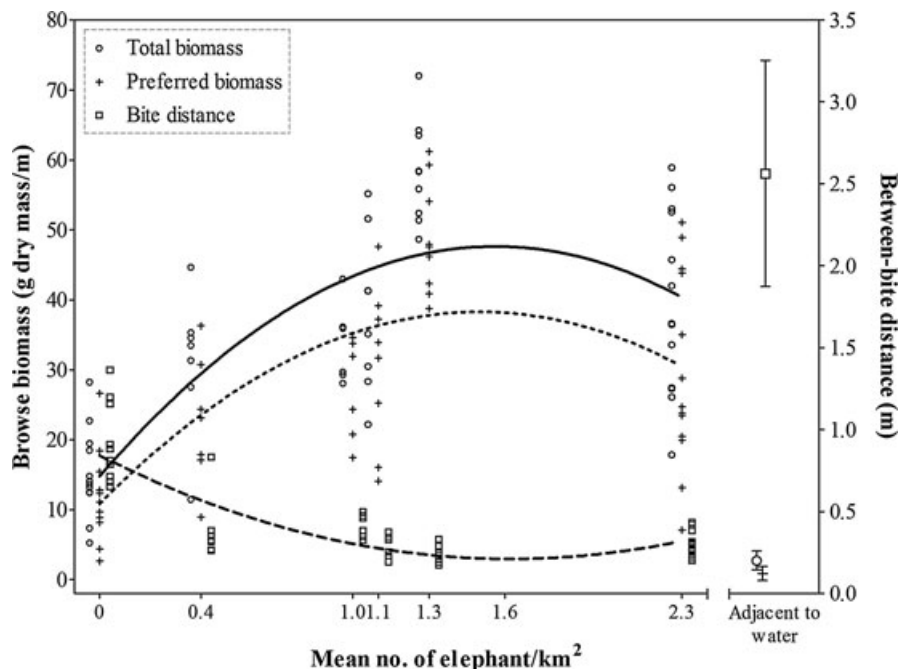


FIGURE 1. Relationship between potential browsing opportunities for black rhinoceros, expressed as browse biomass and between-bite distances, and the intensity of elephant utilization. Solid and dotted lines show total and preferred biomass, respectively; dashed lines show bite distances. Data for Hapoor water point are presented as the mean \pm SD.

TABLE 2. Regression model equations and ANOVA tests of the relationship between browse biomass and potential within- and between-bite harvest rates and the intensity of elephant utilization.

Variable	Preferred model equation	R ²	F	df	p
Browse biomass (g dry mass/m)					
Total biomass	$y = 14.76 + 42.07x - 13.46x^2$	0.54	30.42	2, 52	<0.001
Preferred biomass	$y = 10.81 + 36.58x - 12.19x^2$	0.45	21.19	2, 52	<0.001
Potential harvest rate					
Bite distance (m)	$y = 0.84 - 0.78x + 0.24x^2$	0.70	60.01	2, 52	<0.001
Bite mass (g dry mass)					
<i>Portulacaria afra</i>	$\text{Log}(y) = 1.42 - 0.12x$	0.07	4.68	1, 59	0.035
<i>Enclea undulata</i>	No effect	0.02	1.19	1, 59	0.281
<i>Schottia afra</i>	$\text{Log}(y) = 0.93 - 0.18x$	0.20	14.05	1, 59	<0.001
<i>Azima tetraacantha</i>	No effect	0.04	2.34	1, 59	0.132
<i>Capparis sepiaria</i>	No effect	0.06	2.14	1, 59	0.149

x, Potential browsing opportunity; x, Mean elephant density (Table 1).

role of elephant in herbivore foraging. This may be particularly significant as elephant typically regulate resource utilization in local communities, with consequences for herbivore dynamics

and ecosystem functioning (Fritz *et al.* 2002, 2011). That is, at high densities elephant monopolize resources and limit herbivore abundances through competition, while at low elephant densities, these herbivores are unable to compensate entirely (causing reduced herbivore abundances); we presume that the latter partly reflects a loss of the role of elephant in facilitation. Thus, we expand on the studies that demonstrated increased browsing opportunities due to elephant (*e.g.*, Rutina *et al.* 2005, Makhabu *et al.* 2006, Kohi *et al.* 2011) and those that inferred reduced availability as herbivore numbers declined (*e.g.*, Fritz *et al.* 2002), by suggesting that the role of elephant in these processes scales with the intensity of their effects. Our study is matched only by that of Young *et al.* (2005), showing increased and reduced grass cover (the former mediated by interactions with cattle) in the presence of elephant, with consequences for zebra *Equus burchelli* abundances.

At our study site, more than 50 percent (and up to 70%) of the variance in potential browsing opportunities could be explained by the intensity of elephant utilization (expressed as mean densities). Elephant effects on preferred browse for rhinoceros appeared to be more complex (*i.e.*, only 45% of the variance explained), which probably reflects the interplay of their food preferences and the differential responses of the canopy shrub species to the impacts (Kerley & Landman 2006, O'Connor *et al.* 2007, Kerley *et al.* 2008). Nevertheless, our results partly supports the hypothesis of Kerley *et al.* (1999) that elephant initially facilitate access to browse as pathways are formed through

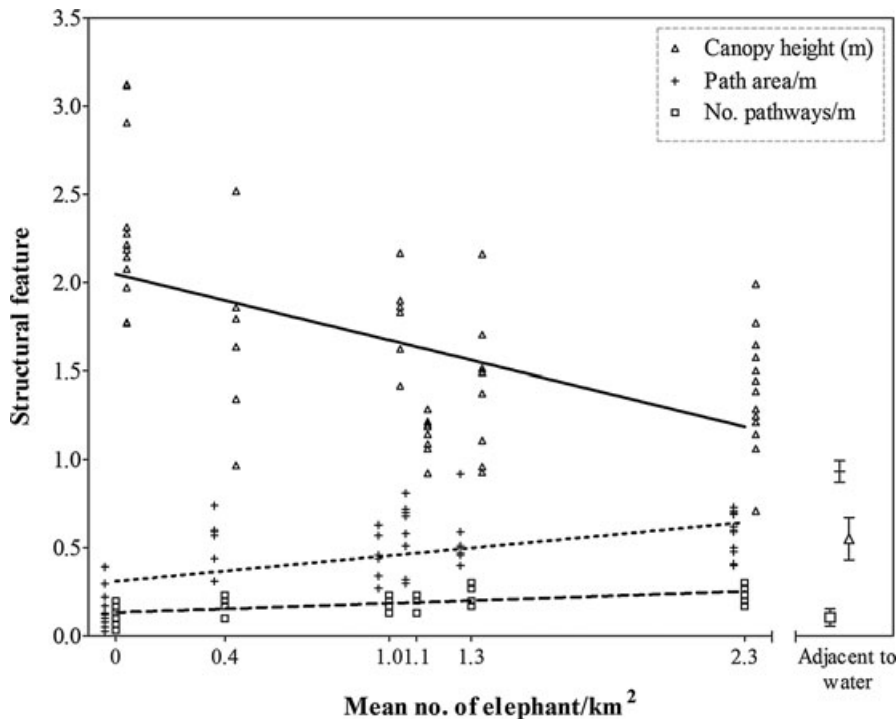


FIGURE 2. Structural features of the thicket shrub community that respond to the effects of elephant, and likely correlate with potential browsing opportunities for rhinoceros. Solid, dotted and dashed lines show canopy height and the area and number of elephant pathways, respectively. Data for Hapoor water point are presented as the mean ± SD.

impenetrable thicket. This coincides with a decrease in the distances between bites, which we predict may increase potential harvest rates and reduce foraging effort (Spalinger & Hobbs 1992). These patterns are broadly similar to the patterns of browse facilitation described by Makhabu *et al.* (2006) using individual trees in *Combretum-Capparis* shrublands; *i.e.*, trees with high accumulated elephant impacts had a greater number of twigs available for re-browsing, than trees with no or low impacts. The consequence of this was an increase in the abundance of browsing impala *Aepyceros melampus* (Rutina *et al.* 2005) and kudu (Makhabu *et al.* 2006). With continued elephant utilization, however, we show that browse biomass gradually declines and between-bite distances increase as the pathways expand and coalesce (shown by a decline in the number of elephant pathways with continued utilization; Fig. 2) and canopy height declines. At the end-point near water, the canopy shrubs are virtually completely replaced with paths (*cf.* Landman *et al.* 2012), causing the near loss of browsing opportunities. We thought that the predicted decline in between-bite harvest rates at higher elephant densities could be offset by rhinoceros potentially taking larger bites that would require less handling time and may be chewed more efficiently (Spalinger & Hobbs 1992, Shipley 2007). For example, moose *Alces alces* select larger bites as tree and stem densities decline and the distances between food patches increase (Shipley & Spalinger 1995, Shipley *et al.* 1998). Instead, we show that available bite sizes for the five canopy dominants either did not vary with mean elephant density, or were significantly lower at higher densities. This suggests that rhinoceros may have limited opportunity to compensate for potentially reduced harvest rates at high levels of impact, causing a further increase in foraging effort. Although our predictions follow the functional response relationships of other browsers (*e.g.*, Trudell & White 1981, Wickstrom *et al.* 1984, Spalinger *et al.* 1988), it will be important to explore how rhinoceros foraging responds, particularly as their selection of browse may be modified by factors other than food availability (*e.g.*, landscape topography, habitat heterogeneity, etc.; Lent & Fike 2003, Morgan *et al.* 2009).

Our model of the change in potential browsing opportunities reflects the accumulated effects of elephant over time; *i.e.*, the effects accumulate until the relationship switches from increased to reduced availability. The decline in browse availability is closely associated with habitat transformation in succulent thicket, as ephemeral grasses gradually replace the canopy shrubs removed by elephant (Stuart-Hill 1992, Stuart-Hill & Aucamp 1993, Kerley *et al.* 1995, Landman *et al.* 2012). Importantly, this transformation brings about a loss of resources (*e.g.*, organic matter, soil material) and ecological functioning that is nearly irreversible without active restoration (Vlok *et al.* 2003, Landman *et al.* 2012). This suggests that browsing opportunities might not recover following intensive utilization by elephant, such that our model may be dominated by declining availability and an increased potential for competition (*sensu* Pringle *et al.* 2007, Odadi *et al.* 2011). We speculate that this implies a loss of the keystone role of elephant for rhinoceros foraging in succulent thicket. Elsewhere, however, the relative importance of elephant for herbivore foraging may be more dynamic

on the basis of the seasonal availability of resources. In savanna habitats, for example, we expect elephant effects on browse availability to decline during the wet season when grasses dominate the diet, while the reverse may be true during the dry season when the diet is characterized by browse (Owen-Smith 1988, Kerley *et al.* 2008). Thus, analogous to the interactions within grazing herbivore assemblages (Arsenault & Owen-Smith 2002, Odadi *et al.* 2011), facilitative effects may dominate during the growing season, while competition between elephant and coexisting browsers may be more apparent during the dormant season. These ideas, however, require further exploring by contrasting seasonal effects and by establishing the mechanisms through which these processes are expressed (*e.g.*, Arsenault & Owen-Smith 2002, Young *et al.* 2005, Odadi *et al.* 2011). Specifically, resource facilitation and competition may manifest through interactions between food availability and quality. For example, Hobbs *et al.* (1996) show that competition between elk *Cervus elaphus canadensis* and cattle arise as elk densities increases and grass biomass declines; these grazing effects cause an increase in the nitrogen content and digestibility of the available food, which enhance cattle diet quality. We predict that changes in food quality brought about by the effects of elephant (Holdo 2003, Kohi *et al.* 2011) may modify our model of changing browse availability along a gradient of elephant utilization. Thus, the hypothesis of Musgrave and Compton (1997) that increased feeding damage by insects is a consequence of declining plant phenolics in AMC provides circumstantial evidence that browse quality varied with elephant effects in our study. This suggests that quantifying the role of elephant in herbivore foraging requires a broader integrated approach that incorporates both food availability and quality.

While our study is limited by a lack of replication across sites and assumes an even distribution of elephant (but modified locally in relation to the availability of surface water) to estimate the intensity of their effects, we provide insights into the relative importance of elephant for rhinoceros foraging in succulent thicket. Thus, it is important to recognize that elephant densities in AMC have consistently exceeded recommended levels (Kerley & Landman 2006) and our estimated threshold (*i.e.*, the equivalent utilization of roughly 1.6 elephant/km²) for declining browse availability. On the basis of our model, this implies that maintaining elephant at these densities may compromise the foraging-, and conservation opportunities of rhinoceros through increased competition. This is supported by evidence that elephant and rhinoceros compete for browse resources in AMC, causing rhinoceros to change their foraging strategies (Landman *et al.* 2013) and activity patterns (C. J. Tambling, unpubl. data). We predict that the threshold between increased and reduced browsing opportunities will vary between herbivores, and in relation to species-specific food preferences. For rhinoceros, the estimated threshold is similar for total and preferred browse, but it is unlikely that this will be the case among more selective foragers. This highlights the need to quantify the importance of elephant in the foraging of other large herbivores. Thus, our study demonstrates the role of elephant for rhinoceros foraging, linked to a potential loss of this role at higher densities.

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LITERATURE CITED

- ARSENAULT, R., AND N. OWEN-SMITH. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97: 313–318.
- BERGSTROM, R. 1992. Browse characteristics and impact of browsing on trees and shrubs in African savannas. *J. Veg. Sci.* 3: 315–324.
- CHAMAILLE-JAMMES, S., M. VALEIX, AND H. FRITZ. 2007. Managing heterogeneity in elephant distribution: Interactions between elephant population density and surface-water availability. *J. Appl. Ecol.* 44: 625–633.
- CRAWLEY, M. J. 2007. *The R Book*. John Wiley & Sons, Ltd, England.
- FRITZ, H., P. DUNCAN, I. J. GORDON, AND A. W. ILLIUS. 2002. Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia* 131: 620–625.
- FRITZ, H., M. LOREAU, S. CHAMAILLE-JAMMES, M. VALEIX, AND J. CLOBERT. 2011. A food web perspective on large herbivore community limitation. *Ecography* 34: 196–202.
- GOUGH, K. F., AND G. I. H. KERLEY. 2006. Demography and population dynamics in the elephants *Loxodonta africana* of Addo Elephant National Park, South Africa: Is there evidence of density dependent regulation? *Oryx* 40: 434–441.
- HAYWARD, M. W., AND B. ZAWADZKA. 2010. Increasing elephant *Loxodonta africana* density is a more important driver of change in vegetation condition than rainfall. *Acta Theriol* 55: 289–299.
- HOBBS, N. T., D. L. BAKER, G. D. BEAR, AND D. C. BOWDEN. 1996. Ungulate grazing in sagebrush grassland: Mechanisms of resource competition. *Ecol. Appl.* 6: 200–217.
- HOLDO, R. M. 2003. Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. *J. Trop. Ecol.* 19: 189–196.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65–71.
- KERLEY, G. I. H., M. H. KNIGHT, AND M. DE KOCK. 1995. Desertification of Subtropical Thicket in the Eastern Cape, South Africa: Are there alternatives? *Environ. Monit. Assess.* 37: 211–230.
- KERLEY, G. I. H., AND M. LANDMAN. 2006. The impacts of elephants on biodiversity in the Eastern Cape Subtropical Thickets. *S. Afr. J. Sci.* 102: 395–402.
- KERLEY, G. I. H., M. LANDMAN, L. KRUGER, N. OWEN-SMITH, D. BALFOUR, W. F. DE BOER, A. GAYLARD, K. LINDSAY, AND R. SLOTOW. 2008. Effects of elephant on ecosystems and biodiversity. In R. J. Scholes, and K. G. Mennell (Eds.). *Elephant Management: A Scientific Assessment for South Africa*, pp. 146–204. Wits University Press, Johannesburg.
- KERLEY, G. I. H., M. C. MASON, A. WEATHERBY, AND W. R. BRANCH. 1999. The role of tortoises in the Thicket biome, South Africa: Important meso-herbivores in a mega-herbivore dominated landscape? In B. Bartholemew (Ed.). *The Desert Tortoise Council Proceedings of the 1997–1998 Symposium*, pp. 34–40. Desert Tortoise Council, Wrightwood, CA.
- KOHI, E. M., W. F. DE BOER, M. J. S. PEEL, R. SLOTOW, C. VAN DER WAAL, I. M. A. HEITKONIG, A. SKIDMORE, AND H. H. T. PRINS. 2011. African elephants *Loxodonta africana* amplify browse heterogeneity in African Savanna. *Biotropica* 43: 711–721.
- LANDMAN, M., G. I. H. KERLEY, AND D. S. SCHOEMAN. 2008. Relevance of elephant herbivory as a threat to important plants in the Addo Elephant National Park, South Africa. *J. Zool. (Lond)* 274: 51–58.
- LANDMAN, M., D. S. SCHOEMAN, A. J. HALL-MARTIN, AND G. I. H. KERLEY. 2012. Understanding long-term variations in an elephant piosphere effect to manage impacts. *PLoS ONE* 7: e45334.
- LANDMAN, M., D. S. SCHOEMAN, AND G. I. H. KERLEY. 2013. Shift in black rhinoceros diet in the presence of elephant: Evidence for competition? *PLoS ONE* 8: e69771.
- LENT, P., AND B. FIKE. 2003. Home ranges, movements and spatial relationships in an expanding population of black rhinoceros in the Great Fish River Reserve, South Africa. *S. Afr. J. Wildl. Res.* 33: 109–118.
- LOMBARD, A. T., C. F. JOHNSON, R. M. COWLING, AND R. L. PRESSEY. 2001. Protecting plants from elephants: Botanical reserve scenarios within the Addo Elephant National Park, South Africa. *Biol. Conserv.* 102: 191–203.
- MAC NALLY, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: The distinction between, and reconciliation of, predictive and explanatory models. *Biodivers. Conserv.* 9: 655–671.
- MAKHABU, S. W., C. SKARPE, AND H. HYTTEBORN. 2006. Elephant impact on shoot distribution on trees and rebrowsing by smaller browsers. *Acta Oecol.* 30: 136–146.
- MORGAN, S., R. L. MACKAY, AND R. SLOTOW. 2009. A priori evaluation of land use for the conservation of black rhinoceros (*Diceros bicornis*). *Biol. Conserv.* 142: 384–393.
- MURRAY, M. G., AND A. W. ILLIUS. 1996. Multispecies grazing in the Serengeti. In J. Hodgson, and A. W. Illius (Eds.). *The Ecology and Management of Grazing Systems*, pp. 247–272. CAB International, Wallingford, UK.
- MUSGRAVE, M. K., AND S. G. COMPTON. 1997. Effects of elephant damage to vegetation on the abundance of phytophagous insects. *Afr. J. Ecol.* 35: 370–373.
- O'CONNOR, T. G., P. S. GOODMAN, AND B. CLEGG. 2007. A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biol. Conserv.* 136: 329–345.
- ODADI, W. O., M. K. KARACHI, S. A. ABDULRAZAK, AND T. P. YOUNG. 2011. African wild ungulates compete with or facilitate cattle depending on season. *Science* 333: 1753–1755.
- O'KANE, C. A. J., K. J. DUFFY, B. R. PAGE, AND D. W. MACDONALD. 2011. Are the long-term effects of mesobrowsers on woodland dynamics substitutive or additive to those of elephants? *Acta Oecol.* 37: 393–398.
- OWEN-SMITH, N. 1988. *Megaherbivores – The Influence of Very Large Body Size on Ecology*. Cambridge University Press, Cambridge.
- PARKER, I. S. C. 1983. The Tsavo story: An ecological case history. In R. N. Owen-Smith (Ed.). *Management of Large Mammals in African Conservation Areas*, pp. 37–50. Haum, Pretoria.
- PRETORIUS, Y., W. F. DE BOER, C. VAN DER WAAL, H. J. DE KNEGHT, R. C. GRANT, N. M. KNOX, E. M. KOHI, E. MWAKIWA, B. R. PAGE, M. J. S. PEEL, A. K. SKIDMORE, R. SLOTOW, S. E. VAN WIEREN, AND H. H. T. PRINS. 2011. Soil nutrient status determines how elephant utilize trees and shape environments. *J. Anim. Ecol.* 80: 875–883.
- PRINGLE, R. M. 2008. Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology* 89: 26–33.
- PRINGLE, R. M., T. P. YOUNG, D. I. RUBENSTEIN, AND D. J. MCCAULEY. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *PNAS* 104: 193–197.
- PUTMAN, R. H. 1996. *Competition and Resource Partitioning in Temperate Ungulate Assemblies*. Chapman Hall, London.
- R DEVELOPMENT CORE TEAM. 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- RUTINA, L. P., S. R. MOE, AND J. E. SWENSON. 2005. Elephant *Loxodonta africana* driven woodland conversion to shrubland improves dry-season browse availability for impalas *Aepyceros melampus*. *Wildl. Biol.* 11: 207–213.

- SHIPLEY, L. A. 2007. The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. *Oikos* 116: 1964–1974.
- SHIPLEY, L. A., S. BLOMQUIST, AND K. DANELL. 1998. Diet choices by free-ranging moose in relation to plant distribution, chemistry, and morphology in northern Sweden. *Can. J. Zool.* 76: 1722–1733.
- SHIPLEY, L. A., AND D. E. SPALINGER. 1995. Influence of size and density of browse patches on intake rates and foraging decisions of young moose and white-tailed deer. *Oecologia* 104: 112–121.
- SINCLAIR, A. R. E. 1985. Does interspecific competition or predation shape the African ungulate community? *J. Anim. Ecol.* 54: 899–918.
- SPALINGER, D. E., T. A. HANLEY, AND C. T. ROBBINS. 1988. Analysis of the functional response in foraging in the Sitka black-tailed deer. *Ecology* 69: 1166–1175.
- SPALINGER, D. E., AND N. T. HOBBS. 1992. Mechanisms of foraging in mammalian herbivores: New models of functional response. *Am. Nat.* 140: 325–348.
- STUART-HILL, G. C. 1992. Effects of elephants and goats on the Kaffrarian Succulent Thicket of the Eastern Cape, South Africa. *J. Appl. Ecol.* 29: 699–710.
- STUART-HILL, G. C., AND A. J. AUCAMP. 1993. Carrying capacity of the succulent valley bushveld of the Eastern Cape. *Afr. J. Range For. Sci.* 10: 1–10.
- TRUDELL, J., AND R. G. WHITE. 1981. The effect of forage structure and availability on food intake, biting rate, bite size, and daily eating time of reindeer. *J. Appl. Ecol.* 18: 63–81.
- VALEIX, M., H. FRITZ, R. SABATIER, F. MURINDAGOMO, D. CUMMING, AND P. DUNCAN. 2011. Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biol. Conserv.* 144: 902–912.
- VLOK, J. H. J., D. I. W. EUSTON-BROWN, AND R. M. COWLING. 2003. Acocks' Valley Bushveld 50 years on: A new perspective on the delimitation, characterization, and origin of Subtropical Thicket vegetation. *S. Afr. J. Bot.* 69: 27–51.
- WETHERILL, G. B., P. DUNCOMBE, M. KENWARD, J. KOLLERSTROM, S. R. PAUL, AND B. J. VOWDEN. 1986. *Regression Analysis with Applications*. Chapman and Hall, London.
- WICKSTROM, M. L., C. T. ROBBINS, T. A. HANLEY, D. E. SPALINGER, AND S. M. PARISH. 1984. Food intake and foraging energetic of elk and mule deer. *J. Wildl. Manag.* 48: 1285–1301.
- WILSON, S. L. 2002. *Body Size Influences on Foraging Behavior of Thicket Biome Browsers*. PhD Dissertation. University of Port Elizabeth, Port Elizabeth, South Africa.
- YOUNG, T. P., T. M. PALMER, AND M. E. GADD. 2005. Competition and compensation among cattles, zebras, and elephant in a semi-arid savanna in Laikipia, Kenya. *Biol. Conserv.* 122: 351–359.