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Elephant *Loxodonta africana* driven woodland conversion to shrubland improves dry-season browse availability for impalas *Aepyceros melampus*

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Along the Chobe Riverfront in northern Botswana, elephants *Loxodonta africana* have reduced woodland cover and modified woody species composition, forming shrublands. We tested the hypothesis that this has favoured the impala *Aepyceros melampus* population and contributed to the observed population increase by creating more available dry-season browse. Our results suggest that the increasing *Capparis* shrubland represents a key browsing habitat. The mixed *Combretum* shrubland was a less important browsing habitat, as female impalas browsed proportionally to the time spent feeding, but this habitat has more than doubled in extent, to almost 60% since 1962, thus providing much more available browse. The *Baikiaea* woodland, which has declined to less than half of its extent during 1962-1998 mainly due to elephant impacts, provided the least amount of dry-season browse for impalas. Impalas browsed mostly below 70 cm and conversion of woodland to shrubland has increased the availability of browse at this height. Our study suggests a three-way ecological interaction, with elephants changing the vegetation, and impalas increasing in number due to greater food availability.

Key words: Botswana, browsing ecology, habitat modification, savanna woodland

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The African elephant *Loxodonta africana* can convert woodlands from one state to another (Dublin et al. 1990, Hobbs 1996) by causing changes in vegetation structure and composition (Jachmann & Bell 1985, Calenge et al. 2002). This influences the availability and distribution of resources for other animals (Barnes 1996). Along the Chobe Riverfront in northern Botswana, elephants have reduced woodland cover (Simpson 1975, Mosugelo et al. 2002) and modified woody species composition (Child 1968, Simpson 1975, Moroka 1984). This may have favoured the impala *Aepyceros melampus*, because populations have increased with the opening of the woodland (Rutina 2004). However, it is not clear whether the observed increase is a response to elephant-induced habitat changes.

A number of studies have investigated seasonal changes

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in impala diet (Van Rooyen & Skinner 1989, Dunham 1980, 1982, Meissner et al. 1996, Omphile 1997). Impalas select a wide variety of herbaceous and woody plants within a number of plant communities (Van Rooyen & Skinner 1989, Dunham 1980, 1982, Meissner et al. 1996, Omphile 1997, Wronski 2002), and grasses and forbs comprise a larger proportion of the diet during the wet season than during the dry season (Dunham 1980, 1982, Van Rooyen 1992). During the dry season, when food is limited (Sinclair 1975), woody species are the primary food resource (Dunham 1980, Omphile 1997, Wronski 2002). In Sengwa Wildlife Research Area, Zimbabwe, browse comprised 6% of impalas' diet during the wet season and 82% during the dry season (Dunham 1980). Van Rooyen (1992) found that browse comprised 19% of the diet in the wet season and 52% in the dry season in Natal, South Africa. In our study area along the Chobe Riverfront, Omphile (1997) recorded an increase in the proportion of browse from 30% in the wet season to 82% in the dry season. Impalas respond to reduced food abundance during the dry season by selecting different plant parts and changing feeding heights (Dunham 1982, Van Rooyen 1992). Dunham (1982) showed that the proportion of browse in the impala diet was not correlated with the proportion of time spent feeding at different height levels. During the dry season, impalas fed mostly at the ground level (Dunham 1982). Considering the poor grass cover during the dry season, this suggests that browse is more abundant at the ground level during this period. Furthermore, Dunham (1980) reported that impalas select more for leaves than other browse parts, because of their high protein content.

The shift from grasses to woody species entails a shift in feeding strategies from primarily grazing in the wet season to primarily browsing in the dry season. The effect of season on proportion of time spent either browsing or grazing relative to forage availability by impalas is less understood. It has been shown, however, that impalas devote relatively more time to grazing while feeding (grazing and browsing) during the wet season and relatively more time to browsing while feeding during the dry season (Van Rooyen & Skinner 1989, Dunham 1980, 1982, Meissner et al. 1996, Omphile 1997). Accordingly, time spent feeding is likely to be conditional on time spent grazing in the wet season and conditional on time spent browsing in the dry season. In habitats with adequate acceptable woody browse species during the dry season, the ratio of time spent browsing in the dry season relative to time spent browsing in the wet season should be proportional to the ratio of time spent feeding in the dry season relative to time spent feeding in the wet season (matching response). When woody species are scarce, the ratio of time spent browsing during the dry season in relation to the wet season will be less than the ratio of time spent feeding during the dry season in relation to the wet season (under-matching response). When woody species are abundant, the ratio of time spent browsing during the dry season in relation to the wet season will exceed the ratio of time spent feeding during the dry season in relation to the wet season (over-matching response).

The aim of our paper was to test the hypothesis that the observed increase in impalas is related to elephant-induced conversion of woodland cover to shrublands (Mosugelo et al. 2002), through increasing the availability of acceptable browse for impalas during the dry season, which we assume is important for impala survival (Scoones 1995). Specifically, we tested the following predictions:

1) If there is no change in acceptable browse in elephant-impacted areas, there should be no response in feeding behaviour by impalas, and the ratio of time spent browsing in the dry season (B_{dry}) to time spent browsing in the wet season (B_{wet}) should equal the ratio of time spent feeding in the dry season (F_{dry}) to time spent feeding in the wet season (F_{wet}) for both habitats heavily and lightly impacted by elephants ($B_{dry}/B_{wet} = F_{dry}/F_{wet}$).
2) If dry-season browse has increased in heavily elephant-impacted habitats, we expect $B_{dry}/B_{wet} > F_{dry}/F_{wet}$ in heavily elephant-impacted habitats and $B_{dry}/B_{wet} = F_{dry}/F_{wet}$ or $B_{dry}/B_{wet} < F_{dry}/F_{wet}$ in habitats lightly impacted by elephants.
3) If elephant impact has had a negative effect on dry-season browse, we expect $B_{dry}/B_{wet} < F_{dry}/F_{wet}$ in heavily elephant-impacted habitats and $B_{dry}/B_{wet} = F_{dry}/F_{wet}$ or $B_{dry}/B_{wet} > F_{dry}/F_{wet}$ in habitats lightly impacted by elephants.

In addition, we documented how feeding heights changed with season in different habitats, in order to examine whether there was a shift in feeding patterns. We also documented the plant parts browsed by impalas in different habitat types during the dry season.

Methods

Study area

The study was conducted in a 30 km × 2 km area adjacent to the Chobe River, within Chobe National Park, northern Botswana (Skarpe et al. 2004). Soils in the

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study area can be grouped into two distinct classes, the nutrient-poor Kalahari sands (Ben-Shahar & McDonald 2002) and the nutrient-rich alluvial soils in areas earlier covered by floodplains (Simpson 1975). The study area was divided into four distinct woody habitat types, of which two resembled the original habitat in the area (Selous 1998). These were the riparian and *Baikiaea* woodlands. The other two vegetation types were mixed *Combretum* shrublands and *Capparis* shrublands. These shrublands are mainly transformations of the two woodland types following elephant impact (Simpson 1975, Mosugelo et al. 2002). The riparian woodland forms a 40-70 m strip on both soil types along the edge of the Chobe River or floodplain grasses. It varies from closed canopy relics of the original tall trees, dominated by evergreen species, to more open woodland. The *Baikiaea* woodland is open savanna dominated by Zambezi teak *Baikiaea plurijuga* occurring on Kalahari sand. The *Combretum* shrublands occur mainly on Kalahari sand soils and are dominated by *Combretum* species. The *Capparis* shrublands are dominated by woolly caperbush *Capparis tomentosa* and located on alluvial soils. The *Capparis* shrublands are located mainly on areas previously dominated *Acacia* woodland (Selous 1998). The riparian and *Baikiaea* woodlands were lightly impacted by elephants and the mixed *Combretum* and *Capparis* shrublands were heavily impacted. Skarpe et al. (2004) described the vegetation of the study area in more detail.

The rainy season lasts from November to May (Botswana Meteorological Service Department, unpubl. data) and most plant growth takes place during this time (Omphile 1997). Annual rainfall in the area is about 600 mm (Botswana Meteorological Service Department, pers. comm.). Temperatures range within 6-34°C, with June and July being the coldest months and September to November the hottest (Botswana Meteorological Service Department). Many ungulates congregate along the Chobe River during the dry season and disperse into *Baikiaea* woodland during the wet season. However, impalas remain along the riverfront throughout the year (Child 1968, Sheppe & Haas 1976).

Data collection

Browsing response patterns

Female impalas were selected for study because of their comparatively high nutritional requirements (Dunham 1980, 1982, Van Rooyen & Skinner 1989, Wronski 2002), their importance in population dynamics and their higher impact on woody vegetation due to the relative abundance of females compared to males. A scan-sampling technique (Altmann 1974) was used to record activities of female impalas sighted in the four woody habitat types from November 1998 to August 2001. Scan-sampling was conducted from a vehicle, to which impalas were habituated, at distances of 20-50 m with the help of binoculars and spotting scopes. In each woody vegetation habitat, scan observations were spread throughout the day from 06:00 to 19:00 and were conducted at least 10 days each month. At each sighting of an impala breeding herd, individual females were recorded as either feeding or non-feeding. Feeding included only handling and eating of food items and excluded searching time. Feeding was further recorded as either browsing or grazing, and for the purpose of this study browsing included only woody species, i.e. feeding on forbs was considered grazing.

Browsing heights and woody plant parts browsed

In 2000, we recorded the height at which impalas browsed in the *Capparis* shrublands, *Combretum* shrublands and riparian woodlands, using the scan observation technique (Altmann 1974). There were very few browsing observations in the *Baikiaea* woodlands in 2000, so this habitat was not included in the analysis. Browsing height was categorised into three classes using the angle subtended by the feeding impala's neck in relation to its forelegs (du Toit 1990). The browsing height classes were recorded as closest to 45°, 90° or ≥ 135°. These correspond to 0-40 cm, 41-70 cm and 71-145 cm, respectively (du Toit 1990).

During the dry season (June-August) in 2001, woody plant parts browsed by impalas in these three habitats were also recorded using a continuous focal animal method (Altmann 1974). The focal animals were radio-collared adult females. Parts browsed were recorded as intact leaves on plants, shoot/twigs or fallen leaves. No collared adult females were located in the *Baikiaea* woodlands from June to August 2001.

Data analyses

Browsing response patterns

The proportion of time spent feeding by impalas was the percentage of the feeding observations of the total observations. Similarly, proportion of time spent browsing was the percentage of browsing observations of the total feeding observations. Both parameters were calculated separately for each month for each habitat. The data were grouped into wet season (November-April) and dry season (May-October). The proportion of time spent feeding during the dry season (F_{dry}) in relation to the proportion of the time spent feeding in the wet season (F_{wet}) was modelled as a function of the proportion of time spent browsing in the dry season (B_{dry}) in relation to the

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proportion of time spent browsing in the wet season (B_{wet}) using the logit model (Agresti 1996):

$$\ln (F_{dry}/F_{wet}) = \alpha + \beta \ln (B_{dry}/B_{wet}),$$

where α is the intercept describing bias in any changes in the proportion of time spent feeding in the dry season relative to the wet season not accounted for by the proportion of time devoted to browsing in the dry season relative to the wet season. When $\alpha = 0$ there was no difference, if $\alpha < 0$ there was a browsing bias in the wet season compared to dry season, and when $\alpha > 0$ there was a browsing bias in the dry season compared to wet season. The slope, β, describes the sensitivity of the impalas' browsing response to changes in the time devoted to feeding. It describes the change in the proportion of time spent feeding in relation to the change in the proportion of time spent browsing between the dry and wet seasons. When $\beta = 0$ the proportion of time spent browsing is proportional to (matches) the proportion of time spent feeding between the two seasons. When $\beta < 0$ the proportion of time spent browsing is lower (under-matches) and when $\beta > 0$ the proportion of time spent browsing is higher (over-matches) than the proportion of time spent feeding between the two seasons.

Browsing heights and woody plant parts browsed

The proportion of browsing observations at each height class was the number of observations of browsing at that height class as a percent of total number of browsing observations. Similarly, the proportion of each woody plant part browsed was the number of observations of that part browsed in relation to the total number of observations of browsed woody plant items. To test for an association between browsing heights and seasons, a χ^2 test for homogeneity by vegetation type was performed using Proc freq in SAS. Seasons were ordered in relation to impalas' browsing preference, with dry season being superior to wet season. The non-zero correlation (M^2; Agresti 1996) was used to test for linear trends between season and feeding height in each habitat type. To test for differences in woody plant parts browsed by impalas in different habitat types, we performed an analysis of variance (ANOVA) with a generalised linear model (GLM), with habitat types and plant parts as the independent factors and angular transformed proportions of each part as the dependent variables.

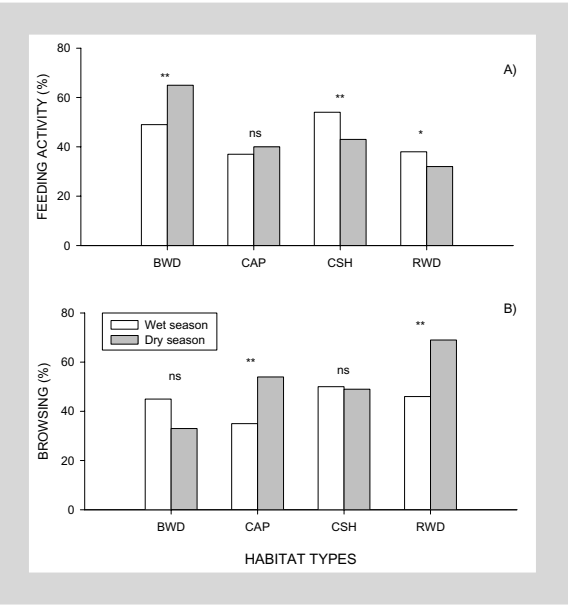


Figure 1. Proportion of observations spent feeding (A) and browsing (B) by female impala along the Chobe Riverfront. BWD denotes *Baikiaea* woodland (N = 436), CAP *Capparis* shrubland (N = 3,208), CSH mixed *Combretum* shrubland (N = 1,265) and RWD riparian woodland (N = 2,696). The results from χ^2 tests; ns indicates no significant difference, * significance at 5% and ** significance at 1%.

Results

Browsing response patterns

Overall, the proportion of time spent feeding in the dry season in relation to the wet season was positively related to the proportion of time spent browsing in the dry season in relation to the wet season (Logit model: Z = 3.87, P < 0.001). The increased probability of feeding in the dry season in relation to the wet season with increasing probability of browsing in the dry season in relation to the wet season was 1.48 (95% C.I.: 1.21-1.81), suggesting that the proportion of time spent browsing in

Table 1. Browsing response patterns of female impala along the Chobe Riverfront, northern Botswana. The results are from the logistic analysis, and P values are associated with the β estimates. N is the number of feeding observations.

Habitat	N	α	β	SE of β	Probability	Response pattern
Baikiaea woodlands	334	-0.64	-2.03	0.37	< 0.001	Under-matching
Capparis shrublands	1806	-0.17	0.75	0.12	< 0.001	Over-matching
Mixed *Combretum* shrublands	890	0.27	-0.26	0.16	0.10	Matching
Riparian woodlands	1514	-0.44	0.97	0.14	< 0.001	Over-matching

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the dry season in relation to the wet season exceeded the proportion of time spent feeding in the dry season in relation to the wet season. In the *Baikiaea* woodlands time spent feeding increased during the dry season in relation to the wet season (Fig. 1A). In contrast, time spent browsing between the dry and wet seasons did not differ (see Fig. 1B). The relationship between the relative time spent feeding and time spent browsing was not proportional (odds ratio = 0.13, 95% C.I.: 0.06-0.27; Logit model: Z = -5.43, P < 0.001), suggesting an under-matching response (proportional time spent browsing is less than proportional time spent feeding; Table 1). In the *Capparis* shrublands time spent feeding did not differ between the two seasons (see Fig. 1A). However, time spent browsing increased during the dry season in relation to the wet season (see Fig. 1B). A large disproportionate relation between time spent feeding and time spent browsing was observed (odds ratio = 2.12, 95% C.I.: 1.68-2.66; Logit model: Z = 6.42, P < 0.001), suggesting an over-matched response (proportional time spent browsing is greater than proportional time spent feeding; see Table 1). Time spent feeding in the *Combretum* shrublands decreased during the dry season in relation to wet season (see Fig. 1A), whereas time spent browsing between the two seasons did not change (odds ratio = 0.77, 95% C.I.: 0.57-1.05; Logit model: Z = -1.63, P = 0.10), suggesting a matching response (proportional time spent browsing equals proportional time spent feeding; see Table 1). In the riparian woodlands, time spent feeding decreased in the dry season in relation to wet season (see Fig. 1A), whereas time spent browsing increased during the same period (see Fig. 1B). Changes in proportion of time spent feeding in the dry season in relation to the wet season showed a large disproportionate change in relation to proportion of time spent browsing in the dry season in relation to wet season (odds ratio = 2.63, 95% C.I.: 2.01-3.45; Logit model: Z = 7.03, P < 0.001), suggesting an over-matching response (see Table 1).

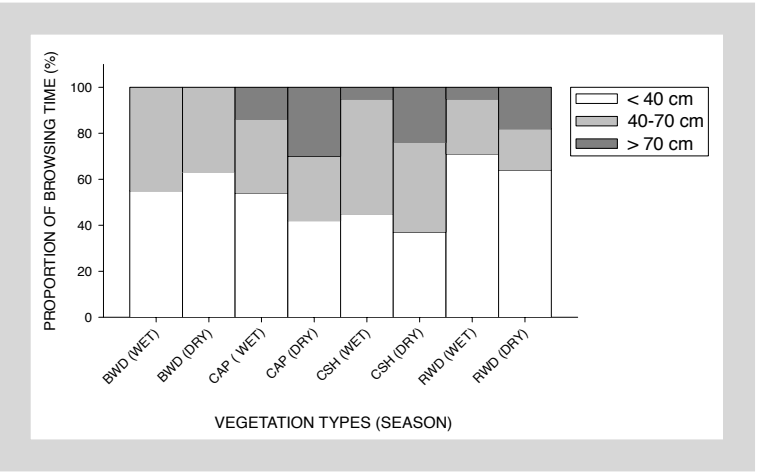


Figure 2. Proportions of female impalas observed browsing at heights of < 40 cm (□), 40-70 cm (▒) and > 70 cm (■) along the Chobe Riverfront. BWD denotes *Baikiaea* woodland, CAP *Capparis* Shrubland, CSH mixed *Combretum* shrubland, and RWD riparian woodland; WET denotes the wet season and DRY the dry season.

Browsing heights and woody plant parts browsed

Female impalas spent > 30% of their browsing time browsing at heights of < 40 cm in all habitats throughout the year, with no seasonal difference (χ^2 test: P > 0.05 in all habitat types; Fig. 2). Time spent browsing between 40-70 cm and > 70 cm differed between seasons (χ^2 tests: P < 0.001 in all habitat types; see Fig. 2). Female impalas spent more time browsing at heights of 40-70 cm than at heights of > 70 cm in the wet season in all habitat types (see Fig. 2). Time spent browsing at heights of 40-70 cm declined and time spent browsing at heights of > 70 cm increased in all habitat types in the dry season relative to the wet season (χ^2 tests: P < 0.001

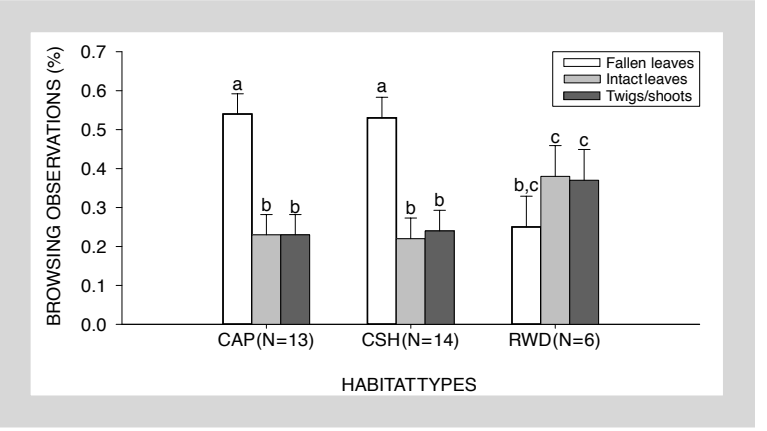


Figure 3. Proportions of woody plant parts browsed by female impalas along the Chobe Riverfront in the dry season (June/July 2001). CAP denotes *Capparis* shrubland, CSH mixed *Combretum* shrubland and RWD riparian woodland. Different letters indicate significant differences and similar letters no differences at 0.05 significance levels.

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in all habitat types; see Fig. 2). The proportion of time devoted to browsing during the dry season in relation to the wet season increased with increasing browsing height in the mixed *Combretum* shrublands and riparian woodland ($M^2 = 20.06$, $P = 0.001$ for mixed *Combretum* shrubland, and $M^2 = 15.23$, $P = 0.001$ for riparian woodland) and did not change significantly in the *Capparis* shrublands ($M^2 = 3.02$, $P = 0.082$). During the dry season, fallen leaves formed 50% of female impalas' diet in the mixed *Combretum* and *Capparis* shrublands and 25% in the riparian woodland. Leaves and shoot/twigs were browsed equally in the *Capparis* and *Combretum* shrublands, but at a higher rate in the riparian woodland than the shrublands (ANOVA, interaction for parts browsed and habitat, $F_{2, 90} = 6.42$, $P = 0.002$; Fig. 3).

Discussion

We tested the hypothesis that the observed increase in impalas was related to elephant-induced loss of woodland cover, which increased the availability of acceptable browse for impalas during the dry season. Our results indicated, as expected, that the availability of browse in the dry season increased in the heavily elephant-impacted *Capparis* shrubland, but not in the lightly impacted *Baikiaea* woodland. However, no response was found for the heavily impacted *Combretum* shrubland, where we expected an increase in dry season browse availability response, and we found an unexpected positive response in dry season browse availability in the lightly impacted riparian woodland.

Although the changes in availability of dry season browse were not totally consistent with our predictions, our results, in combination with observed elephant-induced changes in extent of the habitats, can explain the observed increase in the impala population. The *Baikiaea* woodland was a poor habitat for dry-season browse, and its extent declined from 60.5% of the study area in 1962 to only 22.9% in 1998 (Mosugelo et al. 2002). This habitat has been replaced by the *Combretum* shrubland (termed mixed woodland and shrubland in Mosugelo et al. 2002), which was intermediate in available dry-season browse. This habitat type has increased more than two-fold from 23.8% in 1962 to 58.7% in 1998 (Mosugelo et al. 2002). The area of *Capparis* shrubland, which had high availability of dry-season browse, increased from 2.4 to 4.8%. Although the riparian woodland had a high availability of dry-season browse, it was a minor habitat in the area, covering 0.6% in 1962 and only 0.07% in 1998 (Mosugelo et al. 2002). Thus, the observed elephant-induced habitat changes in the area have resulted in an overall increase in available dry-season browse for impalas.

These browsing response patterns partly confirmed impala habitat preferences found by Omphile & Powell (2002), who found that impalas along the Chobe Riverfront were sighted more in *Capparis* and *Combretum* shrublands. They attributed these preferences to medium to low vegetation height, availability of water and drained soils. We suggest that, in addition, availability of acceptable browse also influenced impala habitat use during the dry season. Dunham (1980) documented that *Capparis tomentosa* and *Combretum mossambicense* were both among the plants with the highest use by impalas during the dry season in the nearby Sengwa Wildlife Research Area, Zimbabwe. In addition, woody species in the *Capparis* shrublands have higher total nitrogen, digestible dry matter and phosphorus contents than those in other habitats along the Chobe Riverfront during the dry season, and many of the woody species in the *Baikiaea* woodland were low in nutrients (Omphile 1997).

Impalas browsed 35-40% of the time < 40 cm height throughout the year and during the dry season fallen leaves formed 50% of their diet in the *Capparis* and *Combretum* shrublands. Browsing height in the *Capparis* and *Combretum* shrublands increased in the dry season relative to the wet season, suggesting that impalas were selecting for twigs and attached leaves, in addition to fallen leaves. Unlike the shrublands, in the riparian woodland fallen leaves formed only 25% of the diet, and impalas spent 60% of their browsing time < 40 cm during the dry season. This suggested that acceptable browse was still reachable during the dry season. The riparian woodland was dominated by evergreen to semi-deciduous species and the *Capparis* and *Combretum* shrublands were dominated by deciduous species (L. Rutina, pers. obs.). Thus, fallen leaves would have been more abundant in the *Capparis* and *Combretum* shrublands than in the riparian woodlands.

We conclude that the elephant-driven conversion of *Baikiaea*-dominated woodland to shrublands has increased dry-season browse availability for impalas along the Chobe Riverfront. This has probably contributed to the observed population increase of impalas in the area.

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