ELEPHANT IMPACT IN THE LITTLE KAROO, SOUTH AFRICA

by

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Abstract

This study investigated the impact of five introduced elephant on trees after one year in Sanbona Wildlife Reserve, a 54 000 ha game reserve in the Little Karoo. The study was initiated following concern over the potential degradation caused by elephant in an area with an annual rainfall of 300 mm. *Euclea undulata* and *Nymania capensis* were virtually unutilised, while over 20% of all *Acacia karroo* and *Schotia afra*, and almost 50% of *Rhus spp.* were utilised. Utilisation of available shoots, branches and bark of *A. karroo* and *S. afra* increased on average by 3%, while *Rhus spp.* shoot and bark utilisation decreased by the same amount over 12 months. Height class utilisation was zero for all species in the < 1 m height class, and was spread evenly between the taller height classes. Excessive damage was rare and heavy utilization of trees was largely confined to a 100 ha portion of the reserve around the Bellair Dam. The study provides a basis for ongoing monitoring of the elephant population and its impact.

Key words: arid, historical, key resource, trees, utilisation

Introduction

African elephants (*Loxodonta africana* (Blumenbach)) are conspicuous and important role-players in ecosystems. They act as seed dispersers (Dudley, 2000), release nutrients into the environment by pushing over trees and through their waste products, and contribute disproportionately to the structure of their habitat (Laws, 1970; Ben-Shahar, 1998; Mosugelo *et al.*, 2002). They can also negatively affect ecosystems by shifting plant communities towards domination by less palatable species (Wiseman *et al.*, 2004), or by causing a general decrease in species abundance (Johnson *et al.*, 1999), resulting in local extinctions (Moolman & Cowling, 1994; Lombard *et al.*, 2001). Most studies that have measured the impact of elephants have been carried out in the relatively mesic environments where most elephant populations occur. In Malawi for example, Jachmann and Bell (1985) investigated their effect on *Brachystegia* woodlands, and in South Africa's succulent thicket their impact on vegetation was measured in comparison to that of goats (Stuart-Hill, 1992). Few studies have assessed the impact of elephants in arid environments. Arid systems such as South Africa's Karoo, are likely to be less resilient than mesic systems. Resilience of an ecosystem is dependent upon the speed at which it is able to cycle energy or matter (DeAngelis, 1980). Plants need water to grow and therefore ecosystems that are relatively rainfall-deprived, are likely to be less resilient due to the slower speed at which they cycle energy or matter. Consequently they are at greater risk of long-term degradation following disturbance than are mesic environments. Studies on elephant impact in arid areas have either investigated populations which range over vast tracts of land, thereby compensating for aridity with space (Viljoen & du P Bothma, 1990), or semi-arid study sites (Smallie & O'Connor, 2000; MacGregor & O'Connor, 2004). In the latter cases permanent populations of elephants were believed to occur historically (Smithers, 1983). Studies of the impact of elephants in the Karoo, or in any range-restricted area as arid as the Karoo, have thus far not taken place.

In pre-colonial times elephants occurred in large numbers in South Africa, estimated at around 100 000 (Hall-Martin, 1992). In the Karoo however, there are scant records of their presence (Skead, 1980; Vernon, 1990). Dean & Milton (2003) found that although names of mapped features and farms in the Karoo did reflect the historical distribution of large herbivores, no close relationship existed between historical records of large herbivores and herbivore-adapted defence and dispersal traits of plants. This may suggest that these animals were not permanent residents, but rather migrants through the area. Evidence also exists that the Karoo may formerly have been better able to sustain large herbivores, and has become less grassy (Bond *et al.*, 1994) and more desertified (Dean & Milton, 2003) since pre-colonial times. Therefore, the question of whether elephants occurred in the Karoo should be separated from how well the area is currently suited to their presence. Despite their migratory status, an interest has been expressed in settling elephant in the Karoo, particularly as a draw-card for tourists. Sanbona Wildlife Reserve, a 54 000 hectare fenced game reserve in the Little Karoo of south western South Africa, has done just that. In September 2003 two juvenile and three adult elephants were introduced into this Reserve, with the intention of eventually increasing the population to 20 elephants with further introductions.

The combination of relatively small size of the fenced Reserve, and the aridity of the area, has caused concern over the potential impact of the introduced elephants. The local conservation authority, CapeNature, stipulated that the Reserve conduct studies to quantify this impact. This experiment measured the impact of elephant on Sanbona's most widespread tree species. These trees were *Acacia karroo, Euclea undulata, Nymania capensis, Rhus spp.* (*Rhus lancea* and *Rhus pendulina)*, and *Schotia afra*. Percentage of trees visited, percentage of shoot, browse and bark utilised per tree, and preference for different height classes was investigated. The area was sampled three months after the arrival of the elephants and again one year later, and the results from the second survey were compared with the first. Shortly after their arrival on Sanbona, it was noticed that the elephants spent the majority of their time in the lush vegetation in the area of the Bellair Dam. In order to quantify their dependence on this area, the amount of trees visited per transect was also compared with the distance of transects from the Dam. This study acts as the basis for ongoing research and monitoring of the elephant population and its impact on the landscape. Central to this is the issue of establishing and re-calibrating thresholds of probable concern (TPCs) (Rogers & Biggs, 1999) so that management action can moderate elephant impact based on environmental indicators.

Methods

Study Area

Sanbona Wildlife Reserve (Fig. 1) is a of 54 000 hectare private game reserve north-west of Barrydale in South Africa's Western Cape province. The reserve lies between 33°35′ and 33°55′ South, and 20°25′ and 20°50′ East. The topography is variable but seldom flat, with large tracts of land taken up by mountainous terrain. Approximately two thirds of the Reserve, to the south, is covered largely by Renosterveld vegetation, while the northern parts are dominated by Little Succulent Karoo (Low & Rebelo, 1996). Rainfall in Barrydale is 300 mm per year. In the north of the Reserve drainage lines, as well as the area surrounding Bellair Dam, support concentrations of *Acacia karroo*, *Rhus spp.*, and *Schotia afra* trees. The dam broke its walls in November 2003, but pools remain and the fertile alluvium in and around it still supports lush vegetative growth. The dam is currently being rebuilt. *Euclea undulata* and *Nymania capensis* are not dependent on these moister habitats and the distribution of the former is uniformly distributed over the north of the Reserve.

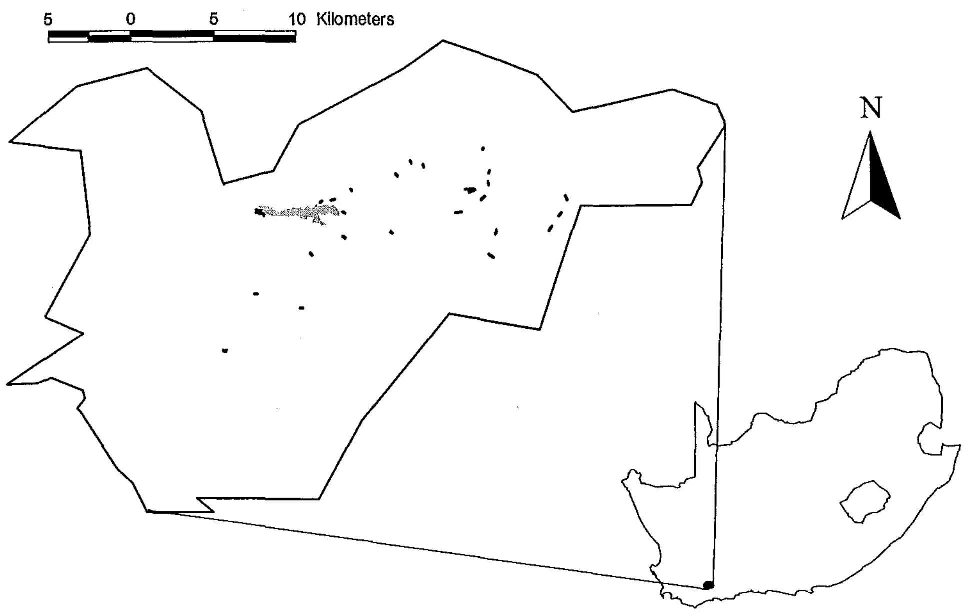


Fig 1 Location of Sanbona Wildlife Reserve within South Africa, showing the distribution of 34 transects sampled, and the location of Bellair Dam

Fieldwork

A baseline survey was conducted in December 2003, three months after the introduction of the five elephants. The site was again surveyed in December 2004 to establish how much elephant utilisation had taken place during the year that had passed.

The tree species studied were often multi-stemmed and occurred either singly or in clusters. Within such clusters, distinguishing of individual trees was difficult. Clusters rather than individual trees were therefore sampled, unless individuals stood alone. A cluster was defined as vegetation of the same species with more than 30% canopy overlap, or with main stems that clearly grew from the same rootstock. For the sake of convenience both solitary trees and clusters are hereafter referred to as trees.

Just over 1 000 trees were sampled in 34 transects in each survey. Using the "wandering quarter" sampling method (Catana, 1963), the next tree sampled on a transect, was the closest tree within a 45^{o} angle either side of a pre-determined compass bearing. The bearing was usually directed into the middle of a clump of trees, and the same bearing was maintained throughout the course of the particular transect. Transect length varied from about 50 m to about 500 m, and the number of trees per transect varied from four to 65, with an average of 29.2 (± 16.6). Species, size (height and average diameter), and degree of utilisation were recorded. Degree of utilisation was measured by scoring each tree according to the amount of shoot, branch, and bark utilization it had sustained, categorized into increments of 10 percent of the available material. Branches that were completely broken, were not given shoot or bark utilisation scores. Four height classes were used: < 1 m, 1 – 3 m, 3 – 5 m, and > 5 m.

Analysis

The number of trees visited in 2003 was compared to the number visited in 2004, as was the average percentage of shoot, branch and bark utilisation. These utilisation categories were also split into height classes for the trees surveyed in 2004 to detect preferences. A regression was performed to determine the elephants' dependence on the Bellair Dam area, whereby the number of trees visited in a transect and the percentage utilisation of trees per transect were compared to the distance of each transect from the Bellair Dam.

Results

Percentage of trees visited

The percentage of trees that showed signs of elephant utilisation between 2003 and 2004 is shown in Fig. 2. Most striking was the near lack of visitation to *Euclea undulata* and *Nymania capensis. Rhus spp.* visitation was highest, at roughly twice that of *Acacia karroo* and *Schotia afra* for both 2003 and 2004. The sample size for *Rhus spp.*, however, was an order of magnitude smaller than that of *A. karroo* and *S. afra* due to the relative scarcity of these trees.

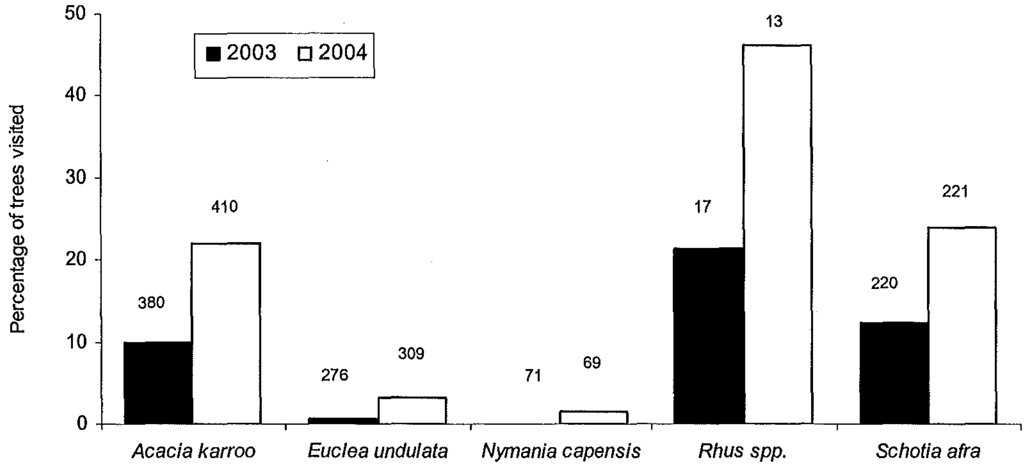
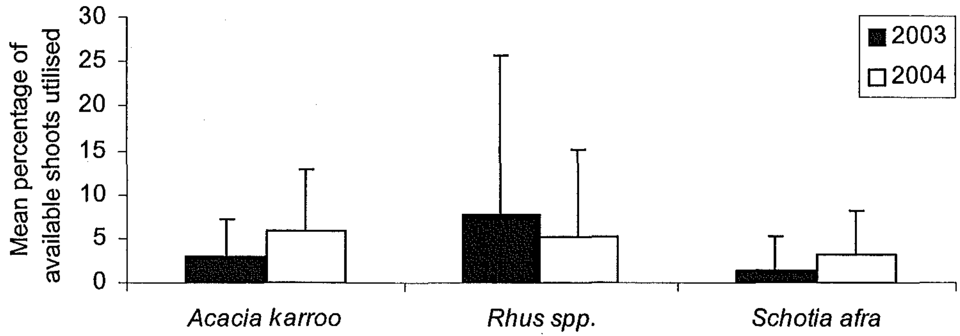


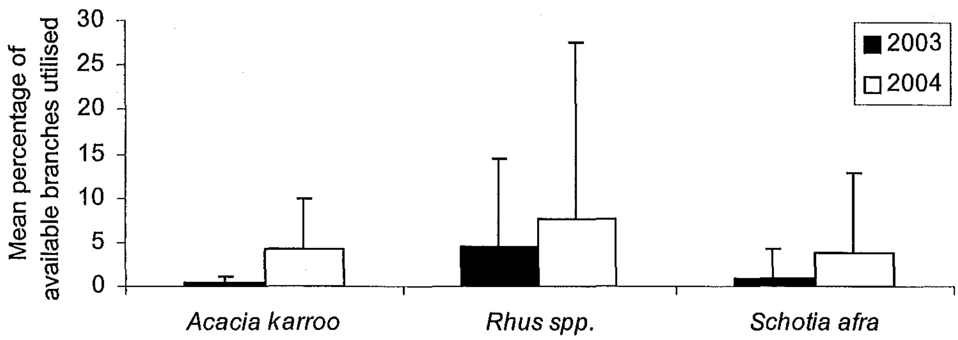
Fig 2 The percentage of trees visited by elephants in 2003 and 2004 for five tree species at Sanbona Wildlife Reserve. The number above each bar is the number of trees recorded

Percentage utilisation

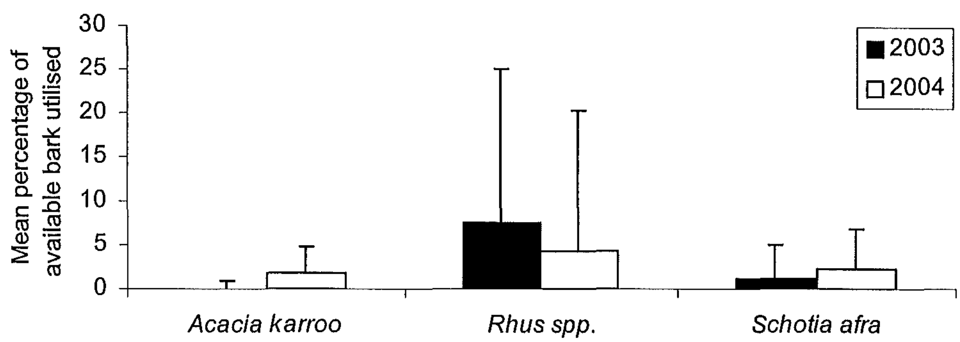
Due to the low levels of utilisation experienced by *E. undulata* and *N. capensis*, percentage shoot, branch and bark utilisation was not analysed for these species. The greatest percentage of available shoots (Fig. 3a), branches (Fig. 3b) and bark (Fig. 3c) in 2003 was for *Rhus spp.*, but in 2004 the species most utilised were *A. karroo* (shoot and branch) and *S. afra* (bark). The change in mean utilisation of *A. karroo* shoot (P = 0.0028), branch (P = 0.0037) and bark (P = 0.0342) was found to be significant, but due to the relatively small proportion of trees sampled that were utilised by the elephants, the changes from one year to the next were not significant for *Rhus spp.* shoot (P = 0.5165), branch (P = 0.1672) or bark (P = 0.3330), nor *S. afra* shoot (P = 0.1932), branch (P = 0.0943) or bark (P = 0.1936) utilisation. A Mann-Whitney U test (Zar, 1999) was used to test for significance.



(a)



(b)



(c)

Fig 3 Mean percentage utilisation (plus standard deviation) of (a) shoot, (b) branch and (c) bark of the three species that sustained noteworthy levels of utilisation by elephants at Sanbona Wildlife Reserve between 2003 and 2004. Sample sizes for each species are the same as for Fig. 2

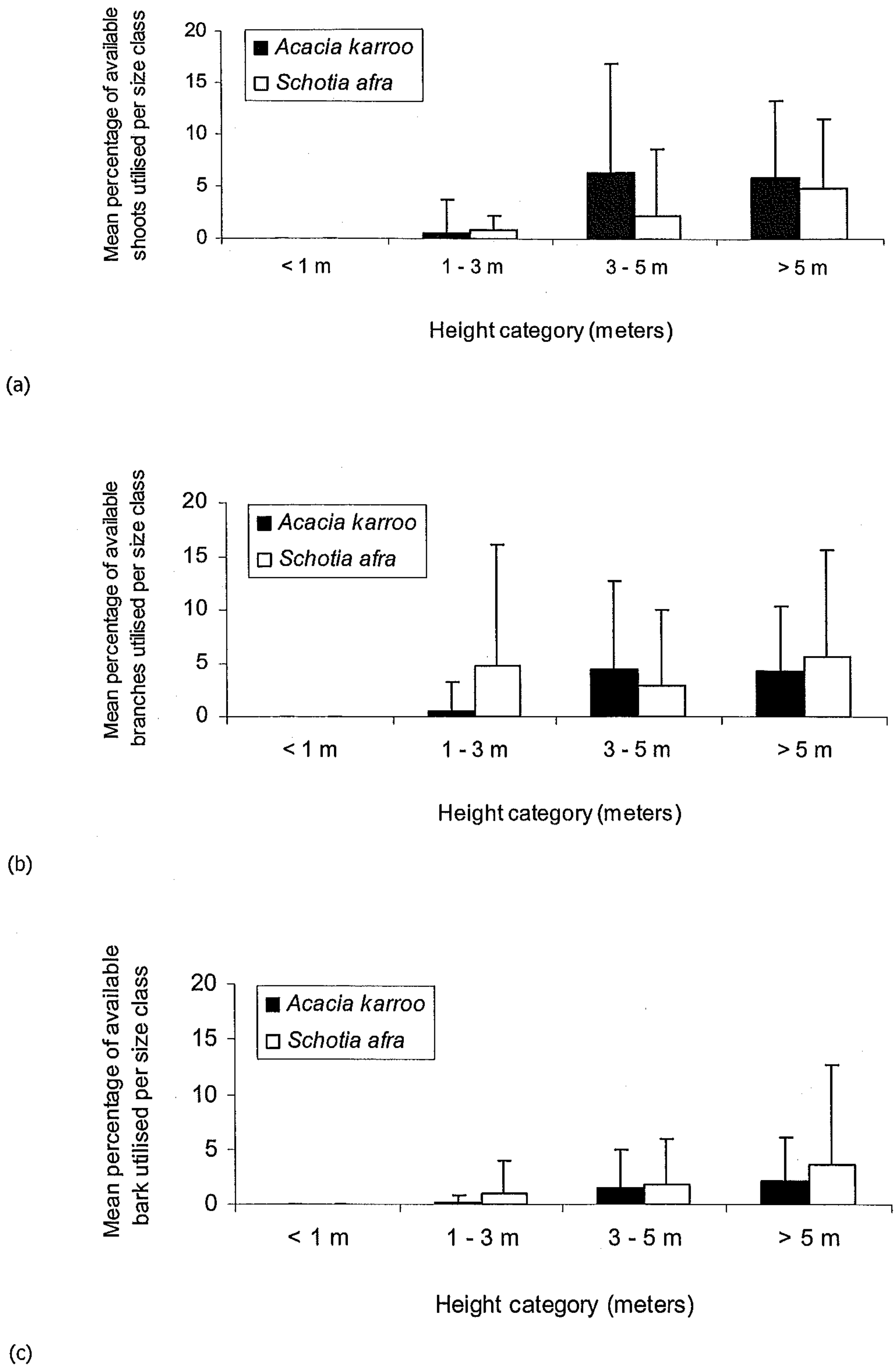


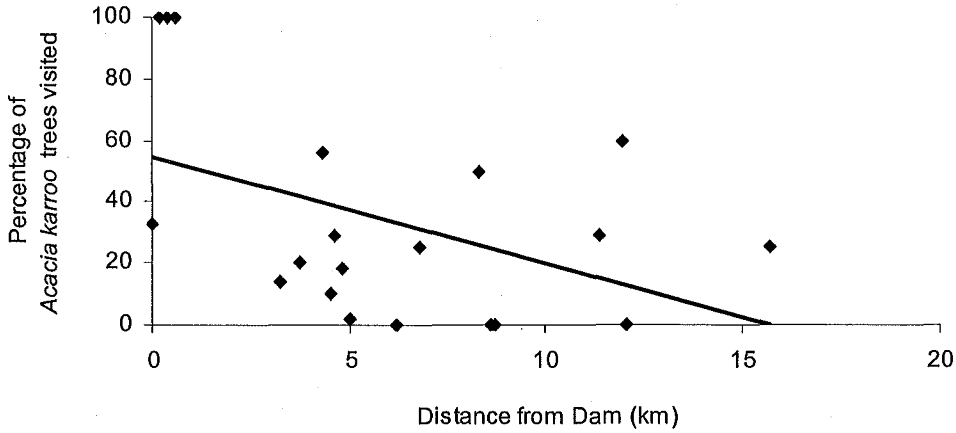
Fig 4 Mean percentage utilisation (plus standard deviation) per height class for (a) shoot, (b) branch and (c) bark for *Acacia karroo* and *Schotia afra* between 2003 and 2004

Utilisation of different height classes

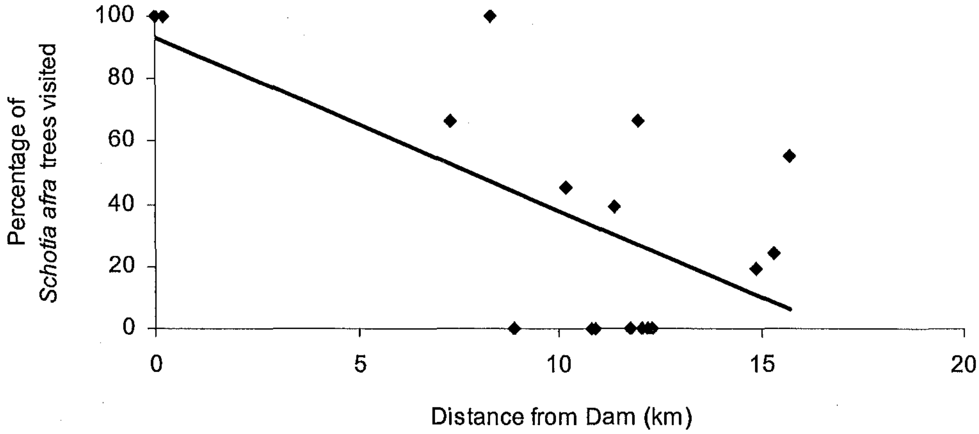
Due to small sample size the height class utilisation of *Rhus spp.* was not analysed, nor was that of *E. undulata* or *N. capensis*, because of negligible utilisation by the elephants. Most noticeable in *A. karroo* and *S. afra* (Fig. 4) was the complete lack of selection for the smallest (< 1 m) height class, followed by the next-shortest (1 - 3 m) class except in the case of *S. afra* branch utilisation. Results revealed a preference for *S. afra* bark over *A. karroo* bark, in both cases increasing with an increase in tree height. Again, due to the large number of unutilised trees sampled, the differences in utilisation between the two species was non-significant ($P > 0.05$) with the exception of shoot utilisation, where *A. karroo* was significantly more utilised than *S. afra* ($P = 0.0360$) (Mann-Whitney U test, Zar, 1999).

Proximity to Bellair dam

The number of *A. karroo* and *S. afra* trees visited by the elephants decreased significantly with increasing distance from Bellair Dam (Fig. 5). However, both regressions were affected by the high number of trees visited by the elephants in the immediate vicinity of the Dam, while further away distance appeared to be a poor predictor of visitation frequency. The same was the case for percentage utilisation of *A. karroo* shoots ($y = -0.7596x + 10.084$, $r^2 = 0.44$, $P = 0.0009$), branches ($y = -0.5826x + 7.6108$, $r^2 = 0.30$, $P = 0.0097$) and bark ($y = -0.2769x + 3.3962$, $r^2 = 0.45$, $P = 0.0012$), and for *S. afra* shoots ($y = -0.7451x + 10.475$, $r^2 = 0.4064$, $P = 0.0053$), branches ($y = -1.2493x + 17.115$, $r^2 = 0.4246$, $P = 0.0041$) and bark ($y = -0.444x + 7.0935$, $r^2 = 0.2624$, $P = 0.0333$). In all cases, for both visitation and utilisation of *A. karroo* and *S. afra* trees, the regression equations would not have been significant without the inclusion of the transects that were located within 500 m of the Dam.



(a)



(b)

Fig 5 Relationship between frequency of tree visitation per transect, and distance of transects from Bellair Dam for (a) *Acacia karroo* ($y = -3.5502x + 54.838$, $r^2 = 0.2219$, $P = 0.02$) and (b) *Schotia afra* ($y = -5.5083x + 92.674$, $r^2 = 0.4023$, $P = 0.006$)

Discussion

Overall results revealed preference by the Sanbona elephants for particular species, height classes and area on the Reserve, while the comparison of successive years showed roughly expected increases in visitation and utilisation.

Utilisation of different tree species

The near-absence of utilisation of *Euclea undulata* and *Nymania capensis* was one of the most striking results of the study. The literature cites varying degrees of elephant utilisation of other *Euclea* species in savanna (Guy, 1976; Steyn & Stalmans, 2001; Wiseman *et al.*, 2004), although Stuart-Hill (1992) noted an increase in *E. undulata* frequency in the Eastern Cape in areas where elephant were present relative to areas where goats were grazed. Perhaps preferred sources of food were merely sufficient, but it is more likely that elephants regard this species as unpalatable. In support of this assumption, several cases were observed in which *Schotia afra* shoots, bark or branches were extracted from amidst clusters of *E. undulata*, with no damage inflicted on the latter. *N. capensis* is documented as being highly palatable to domestic livestock (Hobson *et al.*, 1975; van Breda & Barnard, 1991), but the specimens on Sanbona were generally small and straggly with little browse to offer, and were not abundant.

There was a surprisingly small increase in shoot utilisation of *Acacia karroo* and *Schotia afra* between 2003 and 2004, and in the case of *Rhus spp.*, both shoot and bark utilisation actually decreased from one year to the next. This may be accounted for by new growth rapidly covering old damage, and the possibility that *Rhus spp.* are faster-growing than *Acacia karroo* and *S. afra* (Holmes & Cowling, 1993). Shoot utilisation of *A. karroo* and of *S. afra* increased by similar amounts, but their branch and bark utilisation differed, with *A. karroo* increasing by a larger extent. This could suggest more shoot utilisation of *A. karroo* than of *S. afra*, but a faster response than that of *S. afra*, resulting in roughly equal observed increases in shoot utilisation for both species. *A. karroo* is a fast growing species, capable of an annual increase in height of around 0.6 meters (Aref *et al.*, 2003).

For analysis of height class utilisation, only *A. karroo* and *S. afra* were investigated, due to a combination of substantial utilisation and sufficient sample size. Most striking here was the complete lack of utilisation of the smallest (< 1 m) height class. This lack of selection for smaller trees has been reported for other species (Jachmann & Bell, 1985; Gadd, 2002). The next-shortest height class (1 – 3 m) followed suit as next least utilised, with the notable exception of branch utilisation of *S. afra*. The reason for this anomaly lies in the differentiation of architecture between the two species. *A. karroo* of this height were generally spindly trees - probably saplings - and provided very little browse. *S. afra* of the same height were much thicker-stemmed and had more leafy canopies. However, the mean branch utilisation score for these short *S. afra* trees was also higher than for any other height class of either species except for the tallest (> 5 m) *S. afra*. This was probably due to the brittleness of *S. afra* branches and the fact that the 1 – 3 m trees had fewer branches than larger specimens. When elephants fed on the trees, even if only shoots were targeted, the *S. afra* branches would be more easily broken. On the smaller trees there were fewer branches, thus damage to only one or two would be reflected by a relatively high utilisation score. With regard to shoot utilisation, the overall preference for *A. karroo* over *S. afra* may be explained by the softness of their shoots relative to the woody growth of *S. afra*. Bark utilisation seemed relatively independent of other forms of utilisation, and the pattern was simpler, with *S. afra* bark being preferred to *A. karroo* bark and the bark of taller trees preferred to that of shorter trees.

Bellair Dam as a key resource area

In the Kaokoveld it was found that a significantly small proportion of trees were utilised by elephant further than 20 km from water (Viljoen & du P Bothma, 1990). On Sanbona the relatively lush area around Bellair dam appear to be of similar importance to the elephants for water as well as food. Although there are permanent watering points in the south of the Reserve, these areas have so far been largely avoided by the elephants. None are nearly as large as Bellair Dam, nor are they endowed with noteworthy quantities of vegetation. Distance of transects from Bellair dam was significantly negatively correlated with the number of trees visited per transect despite the presence of vast quantities of alternative forage in the area of the Dam. Personal observations and reports by management showed that the elephants regularly feed on grass, reeds and *Tamarix* scrub in this area, and preliminary analysis of dung suggests that these food sources may contribute more to the elephants diet on Sanbona than the woody flora. The spatial gap between transects within 500 m of the dam and those further than that, was at least three kilometres for *A. karroo* and at least seven kilometres for *S. afra.* Beyond these distances utilisation was not correlated with distance from the dam, suggesting that once the elephants leave the Dam area, they are willing to forage some distance away.

The Dam may be acting as an artificially-created key resource area (KRA) (Illius & O'Connor, 1999), which has been heavily utilised by the five Sanbona elephants over the 15 months since their introduction. The rest of the Reserve provides only limited resources for the elephants. This suggests that the carrying capacity of the Reserve and the carrying capacity of the KRA are one and the same. Consequently, as long as the KRA sustains the elephants, their impact on the rest of the reserve will not be mediated by external factors such as drought, which would otherwise buffer their effect by causing mortality. This demonstrates the care that needs to be taken when managing heterogeneous habitat. The carrying capacity of the Reserve as a whole is not the same as that of the most vulnerable areas, and managers need to base animal stocking rates on the capacity of the vulnerable areas (Steyn & Stalmans, 2001). An area of dry savanna the size of Sanbona can reportedly support a maximum of 270 elephants (Cumming *et al.*, 1997), while the same size area in the Kaokoveld can support only five individuals (Viljoen& du P Bothma, 1990). As far as aridity is concerned, Sanbona falls somewhere between these two, but the heterogeneity of resource distribution on the Reserve is much more akin to the latter area.

General implications of elephant impact

The net impact on any ecosystem must take into account the response capability of the system. Recruitment is important for the survival of a species under pressure from disturbance, and *S. afra* has been noted to recruit very rarely in semi-arid thicket vegetation South Africa's Eastern Cape Province, possibly because this species may have established in a wetter climatic phase (Midgley & Cowling, 1993). Sanbona is more arid than the Eastern Cape thicket, and represents the western-most extent of the range of *S. afra*. These trees may thus be in danger of decline with the advent of time and an increase in the elephant population.

Results, however, indicate that at current levels of utilisation, the woody component of Sanbona's vegetation is not at risk of serious decline in the foreseeable future. No uprooted or pushed trees, and no elephant-induced tree mortalities were noted on any of the transects. Elsewhere on the Reserve, and in two cases close to transects, personal observations and reports by Reserve staff revealed that only two *A. karroo* and two *S. afra* trees have so far been uprooted or pushed over during the year and a half subsequent to the elephants' introduction. However, elephant behaviour is notoriously complex, and patterns of behaviour, including feeding behaviour, can change suddenly (De Boer *et al.*, 2000; MacGregor & O'Connor, 2004). Days before the second survey began, one of the elephants gave birth. Consequently all movement out of the Dam area ceased, and the single adult male began to distance himself from the herd more often. Adult bulls have been known to cause a disproportionate amount of damage to their environment (Guy, 1976), and there is no guarantee that this will not begin to happen with Sanbona's bull, or future bulls. The impact measured so far seems essentially feeding-oriented, and should therefore be regarded as an approximate minimum of which this number of elephants are capable in this environment. Rainfall during the time they have so far spent on the Reserve was also not particularly low, and drought could exacerbate the effect they have on their environment.

Although conducted over a short time interval and with a small population of elephants, it was intended that this study would contribute to a detailed management plan, and that Reserve staff would continue monitoring of elephant impact after its completion. This is particularly important in view of the fact that the Reserve intends to increase its elephant population. Some degree of impact is inevitable - the central issue is merely how much should be tolerated. Considering the importance of nature-based tourism in South Africa's economy (van der Waal & Dekker, 2000; Tomlinson *et al.*, 2002; Reilly *et al.*, 2003), it may be worthwhile comparing elephant impact in the Little Karoo with that of small stock farming, the probable alternative land use, which has been found to be more problematic for plant diversity conservation (Stuart-Hill, 1992; Moolman & Cowling, 1994) than the presence of elephants. Using freshwater ecosystems as an example, Rogers and Biggs (1999) advocate endpoints, values and indicators to allow for strategic rather than reactive management. They term these guidelines "thresholds for probable concern" (TPCs). Prior to this study, the TPCs proposed by Sanbona management was that no more than a 50% loss of any tree species was acceptable near Bellair Dam, and no more than 30% away from the Dam. Beyond these thresholds measures would be sought to reduce impact. Such measures could include fencing the elephants into a certain portion of the Reserve, or fencing in botanical reserves. This study provides data to evaluate the validity of thresholds so far established, and in the broader context, to begin to understand the impact of which elephant are capable in the Little Karoo.

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References

AREF, I.M., EL-JUHANY, L.I. & HEGAZY, S.S. (2003) Comparison of the growth and biomass production of six acacia species in Riyadh, Saudi Arabia after 4 years of irrigated cultivation. *Journal of Arid Environments* **54(4),** 783-792.

BEN-SHAHAR, R. (1998) Changes in structure of svanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecology* **136,** 189-194.

BOND, W.J., STOCK, W.D. & HOFFMAN, M.T. (1994) Has the Karoo spread? A test for desertification using carbon isotopes from soils. *South African Journal of Science* **90,** 391-397.

CATANA, A.J. (1963) The wandering quarter method of estimating population density. *Ecology* **44,** 349-360.

CUMMING, D.H.M., FENTON, M.B., RAUTENBACH, I.L., TAYLOR, R.D., CUMMING, G.S., CUMMING, M.S., DUNLOP, J.M., FORD, A.G., HAVORKA, M.D., JOHNSTON, D.S., KALCOUNIS, M., MAHLANGU, Z. & PORTFORS, C.V.R. (1997) Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science* **93,** 231-236.

DE BOER, W.F., NTUMI, C.P., CORREIA, A.U. & MAFUCA, J.M. (2000) Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology* **38,** 188-201.

DEANGELIS, D.L. (1980) Energy flow, nutrient cycling, and ecosystem resilience. *Ecology* **61(4),** 764-771.

DEAN, W.R.J. & MILTON, S.J. (2003) Did the flora match the fauna? Acocks and historical changes in Karoo biota. *South African Journal of Botany* **69(1),** 68-78.

DUDLEY, J.P. (2000) Seed dispersal by elephants in semiarid woodland habitats of Hwange National Park, Zimbabwe. *Biotropica* **32(3),** 556-561.

GADD, M.E. The impact of elephants on the marula tree *Sclerocarya birrea. African Journal of Ecology* **40,** 328-336.

GUY, P.R. (1976) The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwe area, Rhodesia. *South African Journal of Wildlife Research* **6(1),** 55-63.

HALL-MARTIN, A.J. (1992) Distribution and status of the African elephant *Loxodonta africana* in South Africa, 1652-1992. *Koedoe* **35(1),** 65-86.

HOBSON, N.K., JESSOP, J.P., GINN, VD R. M.C. & KELLY, J. (1975) *Veld plants of southern Africa*. Johannesburg: Macmillan South Africa.

HOLMES, P.M. & COWLING, R.M. (1993) Effects of shade on seedling growth, morphology and leaf photosynthesis in six subtropical thicket species from the Eastern Cape, South Africa. *Forest Ecology and Management* **61(3-4),** 199-220.

ILLIUS, A.W. & O'CONNOR, T.G. (1999) On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications* **9(3),** 798-813.

JACHMANN, H. & BELL, R.H.V. (1985) Utilization of elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology* **23,** 245-258.

JOHNSON, C.F., COWLING, R.M. & PHILLIPSON, P.B. (1999) The flora of the Addo Elephant National Park, South Africa: are threatened species vulnerable to elephant damage? *Biodiversity and Conservation* **8,** 1447-1456.

LAWS, R.M. (1970) Elephants as agents of habitat and landscape change in East Africa. *Oikos* **21,** 1-15.

LOMBARD, A.T., JOHNSON, C.F., COWLING, R.M. & PRESSEY, R.L. (2001) Protecting plants from elephants: botanical reserve scenarios within the Addo Elephant National Park, South Africa. *Biological Conservation* **102,** 191-203.

LOW, A.B. & REBELO, A.G. (1996) Vegetation of South Africa, Lesotho and Swaziland. Pretoria: Department of Environmental Affairs and Tourism.

MACGREGOR, S.D. & O'CONNOR, T.G. (2004) Response of *Acacia tortilis* to utilization by elephants in a semi-arid African savanna. *South African Journal of Wildlife Research* **34(1),** 55-66.

MIDGLEY, J.J. & COWLING, R.M. (1993) Regeneration patterns in Cape subtropical transitional thicket; where are all the seedlings? *South African Journal of Botany* **59(5),** 496-499.

MOOLMAN, H.J. & COWLING, R.M. (1994) The impact of elephant and goat grazing on the endemic flora of South African succulent thicket. *Biological Conservation* **68,** 53-61.

MOSUGELO, D.K., MOE, S.R., RINGROSE, S. & NELLEMAN, C. (2002) Vegetation changes during a 36-year period in northern Chobe National Park, Botswana. *African Journal of Ecology* **40,** 232-240.

REILLY, B.K., SUTHERLAND, E.A. &HARLEY, V. (2003) The nature and extent of wildlife ranching in Gauteng province, South Africa. *South African Journal of Wildlife Research* **33(2),** 141-144.

ROGERS, K.H. & BIGGS, H. (1999) Integrating indicators, endpoints and value systems in strategic management of the rivers of the Kruger National Park. *Freshwater Biology* **41,** 439-451.

SKEAD, C.J. (1980) *Historical mammal incidence in the Cape Province, Vol. I.* Cape Town: Dept. of Nature and Environmental Conservation.

SMALLIE, J.J. & O'CONNOR, T.G. (2000) Elephant utilization of *Colophospermum mopane*: possible benefits of hedging. *African Journal of Ecology* **38,** 352-359.

SMITHERS, R.H.N. (1983) *The mammals of the southern African subregion.* Pretoria: University of Pretoria.

STEYN, A. & STALMANS, M. (2001) Selective habitat utilisation and impact on vegetation by African elephant within a heterogeneous landscape. *Koedoe* **44(1),** 95-103.

STUART-HILL, G.C. (1992) Effects of elephants and goats on the Kaffrarian succulent thicket of the eastern Cape, South Africa. *Journal of Applied Ecology* **29,** 699-710.

TOMLINSON, K.W., HEARNE, J.W. & ALEXANDER, R.R. (2002) An approach to evaluate the effect of property size on land-use options in semi-arid rangelands. *Ecological Modelling* **149,** 85-95.

VAN BREDA, P.A.B. & BARNARD, S.A. (1991) *Veld plants of the winter rainfall region: a guide to the use of veld plants for grazing.* Cape Town: Cape & Transvaal Printers (Pty) Ltd.

VAN DER WAAL, C. & DEKKER, B. (2000) Game ranching in the Northern Province of South Africa. *South African Journal of Wildlife Research* **30(4),** 151-156.

VERNON, C.J. (1990) Famous hunters of the past – 1: the Krugers and the possibility of elephant in the Karoo. *Pelea* **9,** 115-117.

VILJOEN, P.J. & DU P BOTHMA, J. (1990) The influence of desert-dwelling elephants on vegetation in the northern Namib Desert, South West Africa/Namibia. *Journal of Arid Environments* **18,** 85-96.

WISEMAN, R., PAGE, B.R. & O'CONNOR, T.G. (2004) Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *South African Journal of Wildlife Research* **34(1),** 25-37.

ZAR, J.H. (1999) *Biostatistical analysis, 4th Edition.* Upper Saddle River: Prentice-Hall International.