Elephant diet at the edge of the Fynbos Biome, South Africa

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Abstract

Qualitative observations of the diet of the African elephant near Knysna over the decade 1990–2000 made by forest guards Wilfred Oraai and Karel Maswati are presented and discussed. The elephants studied were the last three native elephants and two introduced juveniles. This is the first evidence that elephants routinely eat the nutrient-poor, heathy shrubs and wiry grasslike plants of fynbos. The introduced juveniles generally ignored the relatively nutrient-rich, soft shrubs and herbaceous plants, including legumes and tuberous monocotyledonous plants regenerating after fire. Fynbos appears to be a far more attractive food resource than were the saplings of the tallest species of forest trees. *Pterocelastrus tricuspidatus* (Celastraceae) and species of *Acacia* introduced from Australia were among the most palatable trees to elephants near Knysna. Even the introduced juveniles routinely broke far more trees of *Acacia* spp. than they could eat. Seeds of these species seldom germinated from their faeces, suggesting that elephants may be useful in controlling invasive exotic trees in the south-western Cape. Barring of the original routes to the coast may have left the Knysna elephants deficient in iodine and selenium, explaining their slow reproduction and avoidance of plants potentially aggravating deficiency of these elements. This study provides encouragement for renewed attempts to conserve the African elephant in the Fynbos Biome.

Résumé

Ici sont présentées et discutées les observations qualitatives du régime alimentaire des éléphants de la région de Knysna, qui ont été faites par les gardes forestiers Wilfred Oraai et Karel Maswati entre 1990 et 2000. Les éléphants étudiés étaient les trois natifs derniers de l'endroit et deux juvéniles qui ont été introduits. C'est la première preuve du fait que les éléphants mangent habituellement les arbustes rabougris et les plantes herbeuses drues pauvres en nutriments du fynbos. Les juvéniles introduits ignorent généralement les arbustes plus tendres et les plantes herbeuses relativement riches en nutriments, y compris les légumineuses et les monocotylédones tubéreuses qui repoussent après les feux. Le fynbos semble être une ressource alimentaire bien plus appréciée que ne le sont les repousses des plus grandes espèces d'arbres. *Pterocelastrus tricuspidatus* (Celastraceae) et les espèces d'*Acacia* introduites d'Australie comptent parmi les espèces les plus appréciées des éléphants de la région de Knysna. Les juvéniles introduits cassent même régulièrement plus de troncs d'*Acacia* spp. qu'ils n'en pourraient manger. Les semences de ces espèces germent rarement à partir de leurs excréments, ce qui suggère que les éléphants peuvent être utiles pour le contrôle des arbres exotiques envahissants dans le sud-ouest de la province du Cap. La fermeture des voies d'accès originales vers la côte pourraient avoir entraîné chez les éléphants de Knysna une déficience en iode et en sélénium, ce qui expliquerait la lenteur de leur reproduction et leur aversion pour des plantes qui pourraient éventuellement aggraver leur déficience dans ces éléments. Cette étude constitue un encouragement pour de nouvelles tentatives destinées à maintenir l'éléphant d'Afrique dans le biome du Fynbos.

Introduction

The most southerly survivors of the African elephant (*Loxodonta africana* Blumenbach) today occur inland of Knysna, a town on the south coast of South Africa. An attempt was made in July 1994 to increase the relict population by introducing three orphaned female juveniles from Kruger National Park. One died soon after release, and although the two surviving

juveniles were healthy and grew normally, they were removed in July 1999 (Withers 2001).

The nutrition of the African elephant in the Fynbos Biome of the south-western Cape (from Cape Town to Port Elizabeth) is of interest, in view of the nutrient-poor local soils. The Knysna elephants have reproduced too slowly to maintain their population, despite excellent body condition and a lack of competing species of large herbivores (Carter 1971; Koen 1984; Seydack et al. 2000; Milewski 2002). Fynbos is a complex of shrubby, evergreen, nutrient-poor vegetation. It varies from tall thickets through heathlands to low, open vegetation dominated by wiry grasslike plants, according to soil moisture and depth, and stage of regeneration after fire. Knysna is marginal to the Fynbos Biome, because fynbos is here interrupted by the largest area of indigenous evergreen afromontane forest (hereafter referred to as forest) in South Africa.

The diet of native and introduced individuals of the African elephant was documented from opportunistic observations made by forest guards Wilfred Oraai and Karel Maswati near Knysna from 1990 to 2000. Several lines of investigation suggest that attempts should be renewed to conserve the African elephant in the Fynbos Biome.

History of the population

The African elephant was common near Knysna during the 19th century and was hunted for ivory until approximately 1900 (Seydack et al. 2000). The population declined to approximately 20 animals in 1908, to 10 in 1970, and 3 in 1983. For half a century (1920–1970), the Knysna elephants failed to increase despite minimal losses to hunting and the continual presence of sexually mature females (Seydack et al. 2000). During the present study (1990–2000), only one individual (a female now more than 50 years old, and probably post-reproductive) was thought to remain. Subsequently, it was realized that the population still comprises three sexually mature individuals (Withers 2001). Since I cannot be sure which of the three native individuals was trailed and occasionally glimpsed during fieldwork, I refer to these collectively as the last native elephants.

The African elephant has survived in the south-western Cape long after the extermination of the two largest species of African bovids, the African buffalo (*Syncerus caffer*) and the eland (*Tragelaphus oryx*) (Phillips 1925; Skead 1980). The last native elephants have been extremely secretive, confining themselves largely to forest and fynbos on government land.

The introduced juveniles were 5 to 12 years old during the study period, attaining 90% of mature female shoulder height by the time they were removed, in good condition. Authorities decided to capture them because they remained outside government land, out of contact with the last native elephants. The introduced juveniles are now sexually mature females residing in Shamwari Game Reserve, east of Port Elizabeth (Withers 2001).

Study area

The study area of 250 km^2 extends approximately 25 km from west to east, north-east of Knysna, and consists partly of natural vegetation straddling the poorly defined edge of the Fynbos Biome (fig. 1). The home ranges of the last native elephants are cut off from

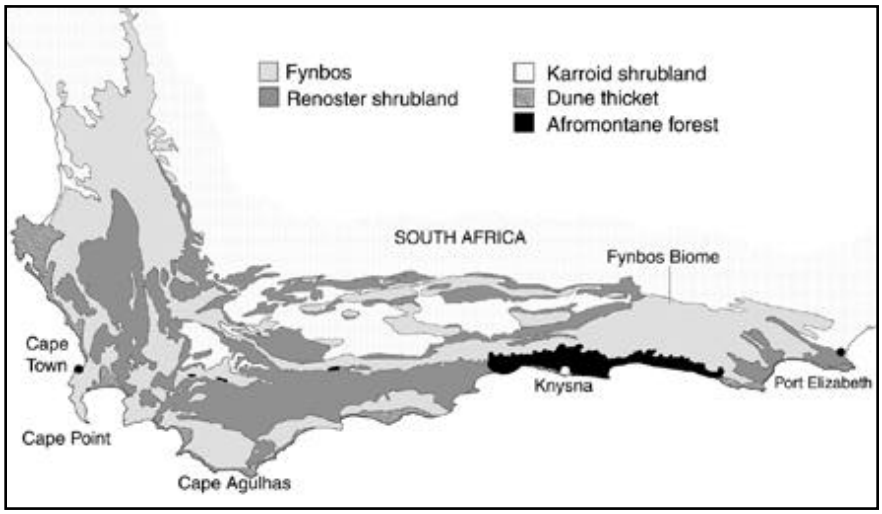

Figure 1. The Fynbos Biome showing various shrubby vegetation types within this biome and the strip of afromontane forest that forms an enclave between fynbos and the coast near Knysna (map adapted from that kindly supplied by Thomas Köhler, Redhouse).

the coast by cleared and built-up areas, a national highway and sea cliffs approximately 100 m high in the Harkerville area (Carter 1971). The south-west of the study area is a nutrient-poor coastal plain, with forest and tall, dense fynbos similar to the thickets of *Erica* and other shrubs characteristic of mountains in East Africa. The north-east of the study area includes foothills of the east–west sandstone range of the Outeniqua Mountains, covered with low fynbos, rich in plant species. Dry, north-facing slopes of the Keurbooms River gorge have grassy vegetation with aloes, repeatedly crossed by the introduced juveniles in 1998–1999. Forest is mainly on government land, whereas fynbos is most extensive on private land, some of which serves as rough pasture for cattle.

Forest and fynbos differ greatly in vegetation height, floristic composition, and fire regime. Forest is essentially free of fire, whereas most plants of fynbos depend on fire for regeneration. The genus *Acacia*, although native to the south-western Cape, is represented near Knysna only by several species introduced from Australia. One of these, *A. melanoxylon*, has valuable timber but is not confined to plantations.

Methods

Information accumulated by observant game guards has value, even if it is not collected systematically. Unless recorded by scientists, such data are likely to be lost when personnel retire.

The information used in this study was gathered by W. Oraai and K. Maswati, employed by the South African Department of Water Affairs and Forestry (DWAF), and based in the Diepwalle forest block. Over the study decade, these two forest guards routinely spent several days at a time locating and following both the last native elephants and the introduced juveniles as part of their official duties in monitoring the Knysna elephants. W. Oraai spent most of his working time following the introduced juveniles over five years (1994–1999). The last native elephants remained shy despite repeated attempts to approach them. Therefore, their diet could be assessed only indirectly from damage to vegetation, disturbance of earth and contents of fresh faeces. The introduced juveniles became habituated to the point of allowing the two guards to approach within 50 m. This permitted direct observations of the diet of these fast-growing elephants as they approached sexual maturity.

My role was to record and interpret the observations after the fieldwork was complete. The guards shared their knowledge in three interviews in the Afrikaans language at Diepwalle Forest Station in July and September 2000. I first interviewed both guards together for seven hours and then interviewed W. Oraai alone 45 days later for three hours. Several published field guides to trees and shrubs and a compendium of colour photographs of most of the herbaceous plants of forest and forest edge in the study area (Baard 1994) were used to identify plant species. The guards supplied information from memory, since they had not made written notes. No quantitative data emerged from this study. However, I checked the consistency of replies by repeating many questions during the second interview. Less than 3% of all replies were inconsistent. During the first interview, I was told that *Chasmanthe*, *Clutia*, *Gymnosporia*, and *Solanum* were not eaten, whereas during the second interview I was told that these taxa were eaten. The third interview took the form of a one-day visit (17 Sept. 2000) by four-wheel-drive vehicle to foraging sites of the introduced juveniles in fynbos and farmland. This was led by W. Oraai, at a time when most species of herbaceous plants were apparent in the spring of 2000. Results (including all tables) refer collectively to the introduced juveniles and last native elephants, except where stated otherwise. Although several differences between the diets of the introduced juveniles and the last native elephants emerged in the course of the interviews, it will require further interviews to resolve these differences for the whole list of plant taxa eaten.

In addition, seven juvenile elephants are now kept in a large enclosure of fynbos and forest at the Knysna Elephant Park, outside the study area. Accompanied by W. Oraai, I noted the dietary preferences of the three elephants present at the time, in September 2000. The proprietors, I. and L. Withers, conducted my visit. Since the three elephants are not free living and are artificially provided with much of their food, they are excluded from the Results but are discussed where appropriate.

Results

The last native elephants remained in the south-west of the study area. During the study decade (1990–2000), they appear to have spent approximately 80% of their time in forest, 19% in low-altitude fynbos, and 1% in

plantations of exotic but non-invasive tree species.

The introduced juveniles initially spent less than two months with the last native elephants, mainly in forest (Seydack et al. 2000). They then left the home range of the Knysna elephants and spent years in fynbos in the north-east of the study area, wandering on the foothills of the Outeniqua Mountains. The introduced juveniles and last native elephants alike were attracted to fynbos, which was regenerating freshly less than six months after the few and localized fires recorded during the study period. However, the juveniles spent most of their time in mature fynbos with varied densities of Australian species of *Acacia* and *Hakea,* which are invasive exotics over much of the south-western Cape. They appeared to be most strongly attracted to fynbos in winter.

During the five years of their stay (1994–1999), the introduced juveniles spent more than 80% of their time in fynbos and rough pasture, 10% in patches of forest, 5% in well-grown plantations, and less than 5% near croplands, where they occasionally raided pumpkins, cabbages, tomatoes and oats. Attempts were made in 1999 to attract the introduced juveniles to a capture site with bales of lucerne, molasses and oranges. These foods were accepted but did not prove attractive enough. The capture was thus delayed and was eventually made in fynbos elsewhere (Withers 2001).

Forest plants eaten

Only 11 of more than 35 species of forest trees and shrubs available in their home range were eaten by the last native elephants (tables 1–4). The introduced juveniles apparently ate mainly bark (possibly for the cambium and phloem layers) when in forest. *Pterocelastrus tricuspidatus* (Celastraceae) was the indigenous tree species most conspicuously damaged by the introduced juveniles and the last native elephants alike, and its intact seeds were found in elephant faeces (table 1). Mistletoe from several species of trees was eaten, often by breaking the host branch and sometimes by breaking the entire host plant.

Fynbos plants eaten

Most of the common genera of shrubs and grasslike plants of fynbos, particularly *Erica*, were routinely eaten (table 2). *Leucadendron* was the only indigenous member of the Proteaceae observed to be eaten. The elephants pulled out the mature tussocks of wiry, grasslike plants, particularly *Bobartia*, and ate the pale stem bases, discarding the green parts. Foliage was likewise discarded when they were eating the bases, rhizomes and corms of Iridaceae. Very few of the many indigenous species of legumes were eaten, despite luxuriant growth of *Virgilia* and *Aspalathus* after fire. The introduced juveniles and last native elephants ignored most herbaceous plants common after fire, eating mainly grasses and grasslike plants (including their leaves) at this stage of regeneration.

Exotic plants eaten

The elephants occasionally damaged eucalypts and pines growing in plantations, eating mainly bark. The introduced juveniles, and to a lesser degree the last native elephants, frequently ate invasive exotic *Acacia* species (table 3), which were available in forest, fynbos and disturbed vegetation. The introduced juveniles frequently destroyed juvenile-form trees of *Acacia mearnsii* up to 8 m high, breaking the bole and leaving most of the plant to decay, although some of the bark, foliage and pods were eaten.

Earth eaten

Although the introduced juveniles and last native elephants ignored most geophytes (for example,

Table 1. Species of ripe fruits eaten by free-living elephants near Knysna, 1990–2000

INDIGENOUS (FLESHY FRUITS)	*Rhus chirindensis*, possibly *R. lucida*
Burchellia bubalina	*Solanum hermannii**
*Cassine papillosa**	INVASIVE EXOTICS (PODS)
Ilex mitis	*Acacia mearnsii* (arils in some cases still brightly coloured in faeces)
Maytenus acuminata	*Acacia melanoxylon* (arils in some cases still brightly coloured in faeces)
Pterocelastrus tricuspidatus	
*Rapanea melanophloeos**	

* species found germinating in old faeces of elephant

Haemanthus, Ornithogalum, Scadoxus, Wachendorfia), they excavated the tubers and rhizomes of herbaceous plants such as Iridaceae and bracken fern (*Pteridium*) in forest and fynbos (table 4). The introduced juveniles also excavated sites for dust bathing. However, there is no evidence that the elephants ate earth as a nutritional supplement.

Table 2. Indigenous plant species of which foliage was eaten by free-living elephants near Knysna, 1990–2000

FOREST TREES

Celtis africana
*Ilex mitis**
Kiggelaria africana
Maytenus acuminata†
Platylophus trifoliatus
*Pterocelastrus tricuspidatus**†
*Rapanea melanophloeos**
Rhus chririndensis
Sideroxylon inerme

FOREST UNDERSTOREY/EDGE SHRUBS

Brachylaena neriifolia
Burchellia bubalina
Canthium inerme
Clutia pulchella
Diospyros dichrophylla (not preferred)
Grewia occidentalis
Gymnosporia buxifolia
Hibiscus ludwigii
Rubus fruticosus
Scutia myrtina†
Trichocladus crinitus†

FOREST HERBACEOUS PLANTS

Cyathea capensis (rosette of tree-fern destroyed to obtain pith; recorded also by Carter 1971)
Secamone alpini† (pulled from *Podocarpus latifolius*, which was sometimes felled to obtain this high-climbing vine)
Viscum obscurum and *Viscum.* sp. (mistletoe) on *Virgilia* and *Cunonia* (which were damaged only to obtain mistletoe), and on *Pterocelastrus* and *Acacia melanoxylon*

FYNBOS SHRUBS

Berzelia intermedia
Brunia nodiflora
Chrysanthemoides monilifera (after fire)
Cliffortia odorata†
Cliffortia sp. or spp.
Colpoon compressum (introduced juveniles)
Cyclopia subternata
Erica hebecalyx, E. lanata, E. scabriuscula (preferred, although *E. cerinthoides* and *E. densifolia* not eaten)
Euryops virgineus (not preferred)
Gnidia denudata
Laurophyllus capensis
Leucadendron spp.
Metalasia muricata (not preferred)
Passerina falcifolia and spp.
Phylica paniculata and spp.
Rhus lucida
Struthiola sp.

FYNBOS HERBACEOUS PLANTS

Aloe ferox (introduced juveniles; stem pith eaten, by breaking whole plant and discarding leaves and flowers)
Aloe striata (introduced juveniles; leaves of this procumbent species eaten)
Blechnum spp. (fern rosette pith, after fire)
Carpobrotus spp. (introduced juveniles)
Polygonum salicifolium
Rhoicissus digitata
Solanum hermannii

GRASSLIKE PLANTS

Bobartia sp. or spp. (mainly stem-bases and rhizomes, but also flowers)
Ehrharta rehmannii (in fynbos regenerating after fire)
Juncus sp. or spp.
Panicum maximum
Stipa dregeana (grass in forest)
Tetraria involucrata (pale shoot-bases only where tussocks mature; greens where tussocks regenerating after fire)
several unidentified tussock grasses and sedges

Trees of *Podocarpus latifolius* and *Canthium mundianum* were broken without being eaten.
* species whose boles were broken and stripped of bark, which was eaten
† species recorded eaten by elephant near Knysna by Phillips (1925), who also recorded *Clematis brachiata, Sparmannia africana, Maytenus peduncularis*, and the exotic *Quercus pedunculata*

Table 3. Exotic plant species (excluding agricultural crops) eaten by free-living elephants near Knysna, 1990–2000

*Acacia melanoxylon**† (mainly in forest)
*Acacia mearnsii**† (mainly in fynbos)
Hakea sp. (foliage, in fynbos)
Eucalyptus diversicolor and spp. (bark, in plantations)
Pinus spp. (introduced juveniles; bark, in plantations)
Pennisetum clandestinum (lawn grass; *Trifolium* also recorded by Koen 1983)

Albizia lophantha and *Sesbania punicea* were not eaten
* species of which boles were broken and bark stripped and eaten, in addition to the foliage and pods being eaten
† species recorded by Phillips (1925), who also listed *Quercus pedunculata* and *Physalis* sp. as eaten by the Knysna elephants; Carter (1971) recorded *Rosa* sp. and the seeds of *Quercus* (in elephant faeces) as eaten by the Knysna elephants

Table 4. Indigenous plant species excavated by free-living elephants near Knysna, 1990–2000

TREES
Ocotea bullata (shallow roots excavated in forest)
HERBACEOUS PLANTS (LEAVES, FLOWERS AND GREEN STEMS DISCARDED; ONLY STEM-BASES, RHIZOMES OR CORMS EATEN)
Chasmanthe aethiopica (forest edge)
Dietes iridioides (forest)
Pteridium aquilinum (rhizomes, in disturbed areas; recorded also by Carter 1971)
Tritoniopsis caffra (corms, in fynbos)
Typha capensis (introduced juveniles; rhizomes)
Watsonia spp. (introduced juveniles; corms, in fynbos regenerating after fire)

The elephants sometimes ate the pale stem bases of the Iridaceae in the above list by pulling up the shoots with the trunk, without excavating corms on these occasions.

Discussion

Knowledge of the diet of the Knysna elephants in forest has accumulated for many years (Phillips 1925). However, this appears to be the first record of free-living individuals of the African elephant eating many of the common genera in fynbos, which are nutrient poor (Koen 1984; Seydack et al. 2000). As both forest and fynbos are extensive in the study area, it is noteworthy that the introduced juveniles chose fynbos as their main habitat. However, this refers to only two, largely self-educated individuals, and it remains unsure how representative their behaviour is of the Knysna elephants in their original state.

Selective foraging

The popular perception has been that the Knysna elephants eat most of the plants available in forest (Carter 1971). However, it is now clear that the elephants prefer *Pterocelastrus*, *Ilex* and *Rapanea* over many similar indigenous genera of trees, and exotic *Acacia melanoxylon* over indigenous forest species. Foliage is not eaten from the four tallest species of indigenous trees (*Podocarpus falcatus, P. latifolius, Olea capensis, Ocotea bullata*), although saplings and boles of *P. latifolius* are routinely broken, trees of *O. capensis* are sometimes pushed over, shallow roots of *O. bullata* are excavated and eaten, and fallen fruits of *P. latifolius* and *O. capensis* are infrequently eaten (Phillips 1925; Carter 1971; Von Gadow 1973; Koen 1983).

Several common species of forest edge and understorey have not been recorded in the diet. For example, the fast-growing, tall shrub *Halleria lucida* is ignored by the Knysna elephants (Von Gadow 1973). The protein-rich foliage of nitrogen-fixing indigenous plants appears to be discarded even where the associated mistletoe is eaten. For example, the only part of *Virgilia, Psoralea* and *Podalyria* definitely recorded as eaten is the seed pods (Phillips 1925; Koen 1983). Most species of vines are apparently ignored, including *Asparagus*, known elsewhere

to be eaten by kudu (*Tragelaphus strepsiceros*) and giraffe (*Giraffa camelopardalis*) (A. V. Milewski, unpublished), and Cucurbitaceae. The elephants apparently avoid plants defended by oxalate (for example, *Oxalis, Achyranthes, Rumex*), most Asteraceae, and aromatic plants (for example, *Leonotis, Plectranthus*). The only member of the Rutaceae known to be preferred by the Knysna elephants is *Zanthoxylum davyi*. The only trees with stout spines on the trunk, suggesting defence specifically against elephants, are *Z. davyi* and *Scolopia zeyheri*, both of which are uncommon in the study area (Von Gadow 1973). Spinescence is at best weakly correlated with dietary choices of elephants at the edge of the Fynbos Biome.

Pterocelastrus *as a food plant*

Pterocelastrus tricuspidatus dominates certain types of forest near Knysna (Seydack 1990) and occurs as a shrub in fynbos elsewhere in the south-western Cape, particularly on coastal dunes (Pierce 1984). The palatability of *P. tricuspidatus* is considerable, despite its content of flammable resin (Von Breitenbach 1974). The introduced juveniles ate this species mainly in the form of bark, possibly because they could not easily break the trees. Elsewhere in the south-western Cape, bovids (for example, eland, bushbuck *Tragelaphus scriptus* and common duiker *Sylvicapra grimmia*) eat fruits and foliage of *P. tricuspidatus* (A.V. Milewski, unpublished). Elephants apparently prefer *P. tricuspidatus* over other indigenous trees near Knysna, and possibly compensate for their damage by propagating this species.

The fruit of *P. tricuspidatus* is fleshy when ripe and contains 1–3 seeds, each covered by a thin but lipid-rich aril (Von Breitenbach 1974). The fruits generally retain their seeds after falling to the ground. *Cassine, Chionanthus, Ficus, Olea, P. latifolius, Rapanea, Rubus, Scutia* and *Solanum* all have succulent fruits and are disseminated by elephants and birds (Phillips 1925; Koen 1983; Rowan 1983). However, *P. tricuspidatus* differs from many other coexisting trees with fleshy fruits, because neither the bushpig (*Potamochoerus larvatus*) nor the local species of primates and fruit bat have been recorded consuming its ripe fruit (Seydack 1990; C.J. Skead, pers. comm.; C.J. Vernon, pers. comm.). Fruit production of *P. tricuspidatus* is asynchronous with that of bird-disseminated species (Pierce 1984). Although the yellow colour of the fruit suggests consumption by birds (J. Koen, pers. comm.), the only direct evidence for this appears to be an old list of fruits eaten by the Knysna loerie (*Tauraco corythaix*), which includes the genus *Pterocelastrus* (Rowan 1983). The germination of seeds recovered from faeces of the Knysna elephants should be studied, to test the hypothesis that *P. tricuspidatus* is disseminated by this large herbivore.

Diets of other herbivores

The Knysna elephants appear to provide food for, rather than compete with, the bushbuck. In forest, the bushbuck relies partly on coppice regrowth of *P. tricuspidatus, Platylophus trifoliatus, Ilex mitis* and *A. melanoxylon* (broken and eaten by elephants) and *O. bullata* (not broken or eaten by elephants) (Von Gadow 1973; Von Breitenbach 1974). Facilitation may also occur in the case of the blue duiker (*Cephalophus monticola*), which eats leaves of trees broken down to within reach by the elephants (for example, *Canthium* spp.), or shrubs unrecorded in the diets of the elephants (for example, *Carissa*) (Von Gadow 1973; H. Herd, pers. comm.). The grey rhebuck (*Pelea capreolus*) occurs in low fynbos and prefers shrubs of Asteraceae and *Aspalathus* although also eating Bruniaceae regenerating after fire (Beukes 1988; R. Knight, pers. comm.). The grysbuck (*Raphicerus melanotis*), like the grey rhebuck, may differ from the elephants in preferring Asteraceae (D. Gibbs, pers. comm.).

The African buffalo browses many species of shrubs, although it prefers grasses (De Graaff et al. 1973). The buffalo was formerly common near Knysna (Phillips 1925; Skead 1980) and may have filled the gap in foraging height and dietary preferences between the Knysna elephants and small bovids.

The eland probably did not penetrate forest but was important in open fynbos. The eland was temporarily reintroduced near Tsitsikamma, east of Knysna, but its diet was not recorded. Elsewhere in the south-western Cape, the eland eats, for example, Celastraceae, *Chrysanthemoides monilifera, Rhus, Viscum* and (sparingly) *Carpobrotus* spp. and *Sideroxylon inerme* while ignoring *Cassytha, Chironia, Cynanchum* and Urticaceae. These choices concur with those of the elephants near Knysna. However, the eland differs from the elephants in eating herbaceous Asteraceae, and the leaves and inflorescences of toxic geophytes such as *Brunsvigia* (Amaryllidaceae) (V. Deverson, pers. comm.).

The Knysna elephants facilitate the bushpig and the baboon (*Papio ursinus*) as well as competing with them (Phillips 1925). The Knysna elephants ignored oranges offered in the Harkerville area (Carter 1971) and do not compete with the bushpig for the fallen fruits of *P. falcatus* and most other species of forest trees (Seydack 1990). The elephants and the bushpig both eat ferns and grasslike plants, in fynbos as well as forest. However, the elephants appear to prefer *Bobartia*, whereas the bushpig appears to prefer the rhizomes of *Pteridium* and the fronds of other ferns (Seydack 1990). The geophytes chosen by the elephants are mainly the same cormous Iridaceae (for example, *Watsonia*) preferred by the bushpig and the baboon. Tubers of Aponogetonaceae, Araceae, Hyacinthaceae, Hypoxidaceae, Orchidaceae, Oxalidaceae, and Vitaceae are preferred by the bushpig but not the elephants (Seydack 1990; Baard 1994; I. and L. Withers, pers. comm.; A.V. Milewski, unpublished). Confirmation is required of the eating of fungi by the Knysna elephants, which is suggested by their having tilled the earth over several square metres at a time using tusks and feet (Carter 1971), and foraging for fungi by enclosed juveniles in Knysna Elephant Park (I. and L. Withers, pers. comm.). However, fungi are likely to contribute more to the diet of the bushpig than to that of the elephants (Seydack 1990). The baboon overlaps in diet with the elephants, eating the foliage of *Erica*, Proteaceae, and grasslike plants, the shoots, flowers and pods of invasive exotic *Acacia* as well as indigenous *Virgilia*, the corms and pale shoot-bases of Iridaceae, and the bark (cambium) of indigenous and exotic trees (Erasmus 1993). However, baboons excavate corms of Hypoxidaceae near Knysna, and root-tubers of ground orchids elsewhere in the Fynbos Biome (S. Privett, pers. comm.), which has not been recorded for the elephants.The bushpig and the baboon also differ from the elephants in supplementing their diets with animal matter.

Control of invasive exotics by herbivores

Large wild herbivores have a largely unexplored potential as agents for the control of invasive exotic trees and shrubs in forest and fynbos in conservation areas in the south-western Cape. The elephants apparently prefer invasive exotic *Acacia* to indigenous legumes and fast-growing trees at the edge of the Fynbos Biome. Invasive exotic species of *Acacia* all lack spines and contain tannins but vary from soft, bipinnate leaves to straplike phyllodes, which in the case of *A. melanoxylon* are as fibrous as the leaves of any indigenous tree species near Knysna. Enclosed juveniles in Knysna Elephant Park accept a staple diet of freshly cut branches of invasive exotic *Acacia*, collected by their keepers between Knysna and Plettenberg Bay (I. and L. Withers, pers. comm.) and have been observed eating a sapling of *Eucalyptus* growing in their enclosure (S. Privett, pers. comm.). They eat mainly *A. mearnsii* and *A. longifolia* but also accept *A. cyclops, A. pycnantha*, and *A. saligna* (I. and L. Withers, pers. comm.). Australian species of *Acacia* appear to be less defended by cyanogenic compounds than are African legumes, including indigenous species of *Acacia* (Conn et al. 1985).

The introduced juveniles frequently broke the boles of invasive exotics, in many cases eating only a small part of the tree before moving on. *Acacia mearnsii* does not survive if its bole is broken within 0.5 m of the ground; *A. melanoxylon* resprouts but is suppressed by the bushbuck, which prefers shoots of this species over most indigenous trees near Knysna (Von Breitenbach 1974). The Knysna elephants broke down *A. melanoxylon* frequently enough to prevent economic harvesting of its timber by DWAF in the study area (Von Gadow 1973). Mature phyllodes of invasive exotic *Acacia* spp. do not appear to be palatable to ruminants in the fresh state, but the eland and the grysbok eat the soft shoots, unripe pods and phyllodes that have dried on damaged branches (M. J. D'Alton, pers. comm.; D. Gibbs, pers. comm.). Germination of invasive exotic *Acacia* spp. from elephant faeces has been negligible (Koen 1983). The elephants, in combination with other indigenous herbivores, thus appear capable of reducing populations of invasive exotics without doing corresponding damage to ecologically similar indigenous plants.

Micronutrient deficiency?

The introduced juveniles and last native elephants at the edge of the Fynbos Biome have shown that after weaning, even vegetation on nutrient-poor soils is sufficient for body maintenance and growth. Ericaceae are also routinely eaten by the walia ibex (*Capra ibex walie*) in Ethiopia and the red deer (*Cervus elaphus*) in Scotland. It is unclear which is more attractive to the African elephant: forest regrowth after clearing or fynbos regenerating after fire.

The critical question is why the Knysna elephants

have reproduced so poorly, in contrast to the population in Addo National Park, just east of the Fynbos Biome. Micronutrient deficiency has been suspected for many years (Carter 1971; Koen et al. 1988). Although copper and zinc may be deficient to some degree (Koen 1984; Seydack et al. 2000), the elements with potentially the greatest effects on reproduction are iodine and selenium (Milewski 2000). Despite proximity to the coast, forestry workers in the study area risk iodine deficiency unless they supplement their diet with seafood (Steyn 1955). Iodine deficiency can repress reproduction of domestic livestock even when all other nutrients are sufficient (Milewski and Diamond 2000). Avoidance by the elephants of various apparently nutritious plants may possibly be owing to cyanogenic compounds (legumes), nitrate (Asteraceae), and oxalate (certain herbaceous plants), all of which indirectly aggravate deficiencies of iodine and selenium (Coleby 2002).

The Knysna elephants originally moved over a wide area (Phillips 1925), balancing their nutrition over the course of the year. Forest elephants in East Africa are known to make and maintain deep excavations for nutrient supplements of a quality probably unavailable near Knysna (Milewski 2000). Extensive low open fynbos apparently provides nutrients sufficient for the growth of juveniles, at least in combination with certain forest plants and protein-rich invasive exotics. However, the confinement of the last native elephants to forest and fynbos has possibly denied them the micronutrients required for pregnancy and lactation. Seaweed cast up after storms might have originally provided the necessary iodine and selenium, but the Knysna elephants no longer have access to the shore. Artificial supplementation of the elephants may be required for successful breeding on a diet of forest and fynbos plants near Knysna. This might be partly accomplished by means of occasional injections of iodized oil.

It is premature to accept the extermination of the last population of the African elephant appropriate to the Fynbos Biome. Various regimes of supplementation of micronutrients have yet to be attempted. Further reintroductions may not only perpetuate this symbolic animal of Knysna but also contribute towards the recruitment of an underestimated ally in the control of invasive exotic plants in conservation areas elsewhere in the south-western Cape.

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