Plant volatiles are a salient cue for foraging mammals: elephants target preferred plants despite background plant odour

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Highlights

- Elephants choose preferred plants using odour cues alone.
- Odour cues are useful even when mixed with odours from other plants.
- An abundant green leaf volatile fails to mask odour cues of preferred plants.
- Olfaction probably plays a key role in efficient foraging by mammalian herbivores.

Abstract

To forage non-randomly, animals must discriminate amongst food items. Foods differ in look, smell, and taste, providing cues for foragers with appropriate senses. Irrespective of the sensory modality, however, foragers can only use cues effectively if they can detect sensory signals above background noise. Recent evidence shows that foraging mammalian herbivores can detect plant odours, but their capacity to select preferred plants in a noisy olfactory background is unknown. Using choice trials, we tested whether the African elephant *Loxodonta africana* uses plant odour as a salient cue despite increasingly complex and challenging background odours. We first established their preference for familiar plant species. We then tested their capacity to discriminate and select preferred plants based on odour alone. We found that elephants successfully chose preferred species even when presented with complex background odours from non-preferred plants mimicking multi-species vegetation patches. Elephants also succeeded despite our attempt to mask distinguishing odours with large amounts of a synthetic green leaf volatile. GC-MS analysis confirmed that volatile organic compound profiles differed among plant species. In demonstrating that elephants exploit plant odours even when the signal from preferred plants is embedded in sensory noise of background odours, we provide crucial behavioural evidence that olfaction provides an efficient mechanism for selective, non-random foraging. Whether mammalian herbivores recognise novel odours, for example from newly invading plant species, or when air pollution degrades odours of familiar plants, needs investigating. Accounting for the capacity of mammalian herbivores to use plant odour cues will improve models of both their foraging behaviour and the ecosystem impacts of their foraging.

KEYWORDS diet choice, foraging, green leaf volatile, herbivory, mammal, odour, olfaction, volatile organic compound

To forage non-randomly, organisms need a mechanism to detect, discriminate then select food items of choice. This mechanism involves their senses — such as sight, smell, and taste — to recognise and interpret cues from the particular food they seek. Understanding which senses play a central role in food choice by different organisms helps us understand whether and how animals make efficient decisions when foraging in information-rich dynamic environments. Of all the senses, olfaction has the most ancient evolutionary roots and is probably the one most widely used across taxa (Firestein, 2001). Many animals exploit odour cues to seek mates and gain information about other conspecifics (Fleischer, Pregitzer, Breer, & Krieger, 2018; Johnston, 2003; Marneweck, Jurgens, & Shrader, 2017). Insects use odour to choose oviposition sites and find nectar (Schoonhoven, Van Loon, & Dicke, 2005). Odour cues are used by predators to locate prey, and by prey to avoid predators (Nevitt, Veit, & Kareiva, 1995; Parsons et al., 2018; Price & Banks, 2012). Natural odour landscapes are “noisy”, comprising complex and variable mixtures of volatile compounds emitted both from items that forager seek as well as any other, background, sources (Riffell et al., 2014; Wilson, Kessler, & Woods, 2015). Despite this chemical noise, theoretical models indicate that the use of odour cues substantially improves food detection rate and hence the efficiency of foragers (Hein & McKinley, 2012).

Despite a long history of research on foraging by mammalian herbivores, we know very little about the sensory mechanisms they use to detect and choose food plants.

Yet this matters because mammalian herbivores are a strongly interactive component of many ecological communities, and their influence is greatly amplified by the current apex predator crisis (Estes et al., 2011). Selective foraging by deer, moose, elephant and wallabies, for example, alters plant communities, abundance of other organisms and ecological processes (Cote, Rooney, Tremblay, Dussault, & Waller, 2004; Daskin, Stalmans, & Pringle, 2016; Dexter, Hudson, James, MacGregor, & Lindenmayer, 2013; Foster, Barton, & Lindenmayer, 2014; McInnes, Naiman, Pastor, & Cohen, 1992), sending ecosystems down new trajectories. Mammalian herbivores are also increasingly involved in human-wildlife conflict, causing damage to crops and other vegetation (Bayani et al., 2016; Bulinski & McArthur, 1999; Horsley, Stout, & DeCalesta, 2003), or having their movements restricted by humans in space and time (Coppes, Burghardt, Hagen, Suchant, & Braunisch, 2017; Pudyatmoko, 2017; Seidler, Long, Berger, Bergen, & Beckmann, 2015; Thurfjell, Ciuti, & Boyce, 2017). To effectively predict and possibly manage the broad ecological impacts of such interactions, it is therefore crucial to understand the behaviours involved in the foraging process. A major part of this understanding lies is elucidating how they select food in the first place.

Odour offers an important foraging cue that several mammalian herbivores have been shown to exploit. Both African elephants *Loxodonta africana* and Asian elephants *Elephas maximus* can discriminate artificial odours (Bates et al., 2007; Miller et al., 2015; Rizvanovic, Amundin, & Laska, 2013) and recent evidence shows that in the absence of background odour, African elephants can use leaf odour to distinguish and select plants (Melissa H. Schmitt, Shuttleworth, Ward, & Shrader, 2018). In Australia, the swamp wallaby *Wallabia bicolor* uses olfaction to locate

Eucalyptus leaves at night or when visual cues are otherwise absent (Bedoya-Perez, Issa, Isler, Banks, & McArthur, 2014; Finnerty, Stutz, Price, Banks, & McArthur, 2017; Stutz, Banks, Proschogo, & McArthur, 2016; Stutz, Croak, Banks, Proschogo, & McArthur, 2017); while common brushtail possums *Trichosurus vulpecula* use odour in deciding whether or not to visit artificial food patches (Mella, Possell, Troxell-Smith, & McArthur, 2018).

An important question, however, is whether background odour from non-target plants interferes with the capacity of mammalian herbivores to detect and choose preferred food plants. To rely primarily on plant odours to make efficient foraging decisions, foragers must be able to overcome or ignore the sensory noise in complex olfactory landscapes to detect and respond to the odour signal of their preferred foods. Background odour is a potential confounding factor in resource location by insects (Schröder & Hilker, 2008). Indeed, some plant odours effective at attracting insects in laboratory trials can become ineffective in the field due to background odours (Cai et al., 2017; Xu et al., 2017).

Here, our aim was to test the hypothesis that plant odour provides a salient cue for mammalian herbivores despite background odour. We tested whether a large herbivore – the African elephant – can detect, discriminate and choose preferred plants using leaf odour under increasingly challenging odour scenarios. We designed these scenarios to mimic food choice within a multi-species food patch, adding sensory noise to the signal provided by preferred plants. Such within-patch choice is one of the critical spatial scales in efficient foraging (Senft et al., 1987).

We chose this study system for several reasons. First, African elephants are mixed feeders (Codron et al., 2006) that shape ecosystems via their feeding (Beuchner & Dawkins, 1961; Daskin et al., 2016; Western & Maitumo, 2004). Yet, despite their enormous absolute food requirements, they forage selectively (Owen-Smith & Chafota, 2012; Shrader, Bell, Bertolli, & Ward, 2012). Second, their trunk is part of their olfactory apparatus but also a foraging tool, often reaching for and selecting plants out of sight. Third, many native plant species at our study site had very little odour (to us), representing many broad-leaf plant species globally. Finally, we could run rapid effective trials because elephants have excellent cognitive and rapid learning abilities (Plotnik, Lair, Suphachoksahakun, & de Waal, 2011; Plotnik, Shaw, Brubaker, Tiller, & Clayton, 2014).

METHODS

Study system

We used six semi-tame African elephants, 15–32 years old, four males, two females, three left- and three right-trunked. All trials were run at the *Elephant Whispers* facility, Hazyview, Mpumalanga Province, South Africa, with 12 of 17 professional elephant handlers at any time to ensure the comfort and safety of the elephants. Handlers were not assigned to individual elephants, but rather rotated among the elephants within and between days. Elephants foraged free-range daily in natural lowveld savanna and riverine thickets from which we harvested our native plant species.

Ethical Note

All experiments were performed in accordance with the Animal Ethics Committees of the University of Sydney (AEC Project #2014-717) and University of Kwa-Zulu Natal (AREC/106/015) and the Australian Code for the Care and Use of Animals for Scientific Purposes.

General protocol

We ran five choice trials using the same general protocol, modified from Melissa H. Schmitt et al. (2018), using plants familiar to the elephants. Within a trial, we presented each elephant with paired plant samples in a set of five consecutive tests over 5-10 minutes. The position of the two options was randomised (coin-toss) for each elephant with two constraints. First, a given option was on one side in no more than three consecutive tests, to prevent elephants using memory of position as a cue. Second, in each test, a given option was presented half on the left and half on the right positions among elephants, to balance other potential confounding effects.

We ran 1-2 sets per day, 3-4 hours apart, up to five days per week, with sets interspersed by natural foraging. We tested all elephants simultaneously. At the start of each test, the elephants stood ~4 m apart with one handler riding and another standing 5 m in front (Figure 1a, d). The standing handler presented the paired samples (~1 m apart in bins) and asked the elephant to “walk up”, “smell” and “choose” (depending on the trial), then rewarded the elephant from the bin it chose.

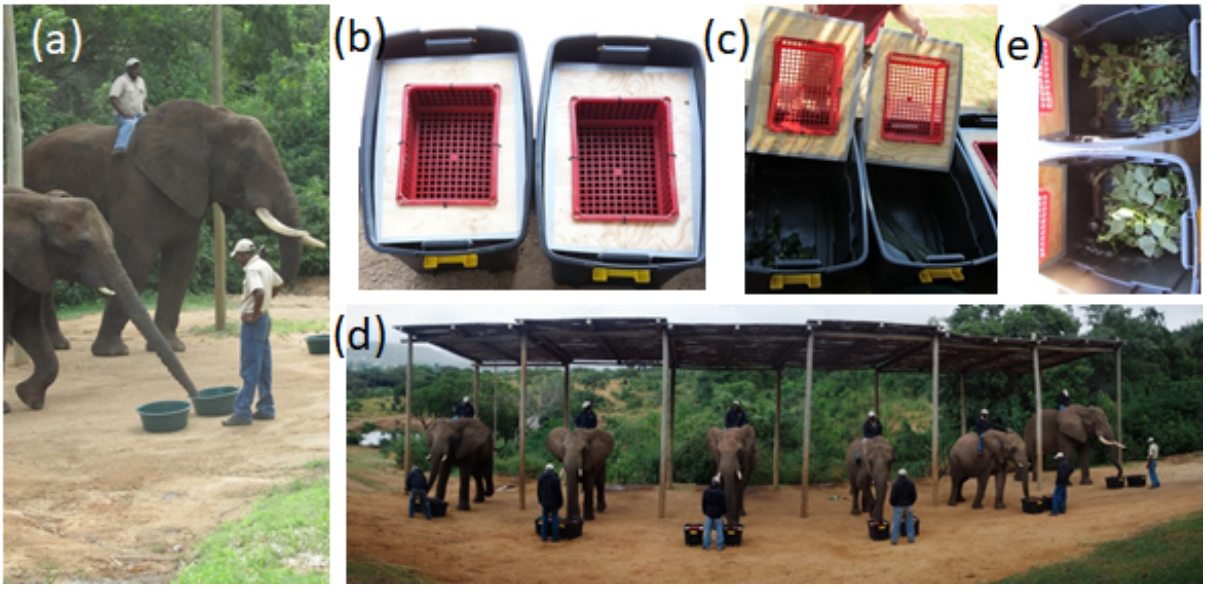

Figure 1. Setup for preference and odour trials with six elephants. (a) Preference Trial 1, elephant in foreground with trunk extended to assess and/or grasp her choice from a bin, with elephant handlers; (b) Odour Trials 2-5, bins with visually concealed plants covered by perforated lids; (c) Trial 2 bins with lids still open, with one plant species in each bin; (d) the six elephants during a Trial 2 odour test; (e) Trial 4 bins with lids still open, with the complex background odour of both low preference species in both bins, but only the high preference species in the lower bin.

Trials were run blind (plants not visible) to both elephants and handlers, except Trial 1. For all trials, leaf-stem samples (all ~30-45 cm stem length; fresh leaf weight 20–30 g in Trials 1 and 2, 10–20 g in Trials 3 - 5) were harvested fresh daily from at least two plants per species. These small clippings represent a “small trunkful”, which is their most common harvest size (M. H. Schmitt, Ward, & Shrader, 2016).

Defining high and low preference plants

In Trial 1, we sought to identify two high and two low preference plant species for use in odour trials. We initially tested 10 plant species in a pilot study (listed in Appendix A1); nine native tree/shrub species that lacked spines or thorns, were

reasonably common and could occur in the same patch where the elephants foraged free-range, and a fodder crop, Bana grass (hybrid of *Pennisetum glaucum* and *P. purpureum* Schum (Gupta & Mhere, 1997)) expected to be highly preferred. Based on the pilot study, we compared two high preference (Bana grass (Bg) and *Pterocarpus rotundifolius* (*Pr*)) against two low preference (*Gymnanthemum coloratum* (*Gc*) and *Euclea natalensis* (*En*)) species. Each elephant was always presented with two plant species, placing (usually two) similar sized pieces from each species in two identical 40 L plastic bins, one species per bin. On walking up, the elephants were able to smell each bin (Figure 1a) and the first plant option of the two provided that was grasped with its trunk was considered its choice.

Simple choice using plant odour cues

In Trial 2 we tested whether elephants could choose options based on odour cue alone, using the simplest scenario comparing two plant species, representing odour signal without sensory noise from background plant odour. We tested the same four pairs as in Trial 1. An elephant was presented with one piece of one plant species in a black plastic tote bin (110 L) and one piece of another plant species in a second bin. The plant samples were visually hidden by covering the bins with a ply-wood lid into which we had firmly inserted and secured a plastic “open-weave” basket (37 cm x 27 cm) containing 1 cm^2 holes (Figure 1b, c). The two bins were placed on the ground as in Trial 1. On approach, elephants smelled both bins before choosing, indicated by dominant sniffing and/or dragging the bin and/or lifting the lid (Figure 1d). The handler on the ground then rewarded the elephant with the plant sample from the chosen bin.

Choice with simple background plant odour

In Trial 3 we tested whether elephants could detect the signal from a high preference plant species despite the presence of sensory noise comprising a simple, single, low preference species as background odour. Each elephant was presented with the low preference species in both bins but the high preference species (placed on top) in only one of the bins, with the perforated lids then closed.

For the bin with both low and high preference species, we used various ratios of the two species to explore the elephants' olfactory sensitivity to a quantitative increase in background odour from the low preference species. For *G. coloratum*, the three ratios with Bana grass differed slightly from those with *P. rotundifolius* because we thought (incorrectly) elephants would find the odour chemistry of Bana grass (the fodder crop) easier to differentiate than *P. rotundifolius* (native species) would be from the other two native species. So for *G. coloratum* & Bana grass, we used 2, 10 or 25 pieces of *G. coloratum* with one piece of Bana grass (ratios 2:1, 10:1 or 25:1) tested against 2, 10 or 25 pieces of *G. coloratum* alone. For *G. coloratum* & *P. rotundifolius*, we used 2, 2 or 10 pieces of *G. coloratum* with 4, 1 or 1 piece of *P. rotundifolius* respectively (ratios 1:2, 2:1 or 10:1) tested against 6, 2 or 10 pieces of *G. coloratum* alone. For *E. natalensis* & Bana grass and for *E. natalensis* & *P. rotundifolius*, we used 2 or 10 pieces of *E. natalensis* with one piece of Bana grass, or one piece of *P. rotundifolius* (ratios 2:1 or 10:1) tested against 2 or 10 pieces of *E. natalensis* alone. The procedure for choice and reward was the same as for Trial 2 except the reward was either the single piece of the high preference species if that bin was chosen, otherwise a single piece of the low preference species.

Choice with complex background plant odour

In Trial 4 we tested whether elephants could detect the signal of a high preference plant species, despite the presence of odour background comprising both of the low preference species representing even more complex sensory noise. We used a single ratio (10:1) but the low preference background was 5 pieces of each of the two low preference species in each bin. The procedure for choice and reward was similar to Trial 3, with the reward of the single piece of the high preference species if that bin was chosen, otherwise a single piece of either of the two low preference species (i.e. pulled haphazardly from the bin by the handler).

Choice with green leaf volatile background odour

In Trial 5 we tested whether elephants could detect and choose high preference *P. rotundifolius* over low preference *G. coloratum* despite a strong background plant odour of the green leaf volatile (GLV), synthetic (Z)-hex-3-en-1-yl acetate, which we thought may act both as a mask and attractant. This is a common GLV involved in communication and ecological interactions among plants and invertebrates (Scala, Allmann, Mirabella, Haring, & Schuurink, 2013), and therefore, conceivably, mammalian herbivores. It was also one of the major VOCs in the four plant species we used (see results).

Each elephant was presented with the background GLV odour in both bin, and one piece of either *P. rotundifolius* or *G. coloratum*, with the lids then closed. For the background odour, we placed 2 ml of a (Z)-hex-3-en-1-yl acetate solution (10% in liquid paraffin (white mineral oil)) in a 3 ml Perspex vial plugged loosely with cotton

wool, taped inside each bin 15 mins before running a set. The procedure for choice and reward was the same as for Trial 3, with the reward of either the high or low preference species based on the chosen bin.

If elephants did not discriminate between bins, we hypothesised this was because either (a) the strong GLV odour masked the odour of the plant pieces, or (b) elephants considered the reward to be a plant with GLV, irrespective of the bin chosen. We teased apart these alternatives by running three sets, allowing elephants time to learn about the reward and respond differently over time. We ran Sets 1 and 2 three hours apart on the same day, then Set 3 three days later with no other trials in between.

Chemical analysis of volatile organic compounds

We analysed the volatile organic compounds forming the headspace odour profiles of the four plant species used in the odour choice trials, as both single species (Trial 2) and as mixed species samples (Trials 3 and 4) or plant plus artificial green leaf volatile (Trial 5) as presented to the elephants. Our methods followed Melissa H. Schmitt et al. (2018), collecting volatiles in the headspace of each sample then analysing them with gas chromatography-mass spectrometry (GC-MS) (for details of replicates and GC-MS methods, see Appendix A2). Leaf areas were measured using ImageJ (Schneider, Rasband, & Eliceiri, 2012), to estimate total emissions per cm^2 leaf surface area per hour.

Statistical analyses

For the choice trials, we modelled the probability of one of the two plant samples being chosen (1, 0), focusing on the preferred plant sample. We used generalised linear mixed models using PROC GLIMMIX in SAS® version 9.3, with a binomial distribution and logit link function, and individual elephant as a random factor (for details see Appendix S3). We tested whether the choice of the focal plant sample was significant by testing whether the probability was significantly different from 50% (specifically, whether the log of the odds ratio was significantly different from zero), with fixed effects of Pair, Set Number, Ratio (Trial 3) and relevant interactions. Where Pair was significant, we performed multiple pairwise comparisons with the Tukey-Kramer adjustment.

To quantify how the odour profiles differed between treatments (plant species or their combinations) — indicating cues that elephants could use to discriminate and select particular species — we used ANOSIM followed by post-hoc pairwise comparisons and SIMPER using Primer v6 (Anderson, Gorley, & Clarke, 2008; Clarke & Gorley, 2006). These analyses were based on relative amounts (%) of the different compounds detected in headspace samples, and we initially 4^{th} root transformed the data before generating the resemblance matrix (based on Bray-Curtis similarity). Results were visualised with non-metric multi-dimensional (nMDS) plots in two dimensions. For the three native species, we also compared odour profiles of detached samples (as offered to elephants) with those sampled on the intact plant using PERMANOVA with two crossed factors, species and sample type, in Primer v6 (Table A2).

RESULTS

Defining high and low preference plants

In Trial 1, the probability that elephants chose Bana grass and *P. rotundifolius* (hereafter high preference species) over *G. coloratum* or *E. natalensis* (hereafter low preference species) were all significant ($P \leq 0.02$; Figure 2a). There was a significant effect of Pair but not Set (Table A3), with the probabilities greater for the two Bana grass pairs than the two *P. rotundifolius* pairs.

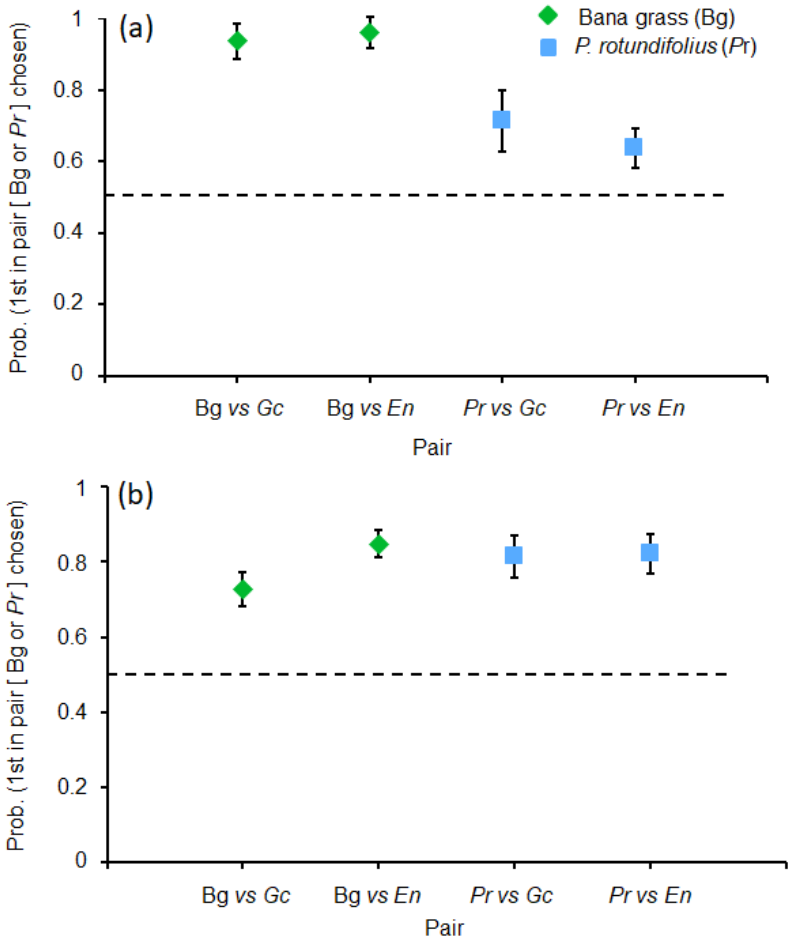

Figure 2. Probability of a particular choice by the elephants, with one plant species per bin. For (a) Preference Trial 1 and (b) Odour Trial 2, probability of the plant listed first in pair, i.e., Bana grass (Bg) ◆ or *P. rotundifolius* (*Pr*) ■, being chosen over the plant listed second in pair, i.e., *G. coloratum* (*Gc*) or *E. natalensis* (*En*). Values are means ± SEM. Dashed line represents random choice.

Simple choice using plant odour cues

In Trial 2, the probabilities that elephants chose the high preference species over the low preference species based on odour alone were all significant (Table A3, all $P < 0.0001$, Figure 2b). There was no significant effect of Pair ($P = 0.140$) or Set ($P = 0.922$).

Choice with simple background plant odour

In Trial 3 with simple background odour in both bins, the probability that elephants chose the bin containing the high preference species was always significant (Table A3, Figure 3). There was a significant effect of Pair (all $P < 0.02$); and the probabilities were significantly greater for pairs with Bana grass than with *P. rotundifolius*. There was no significant effect of Ratio (all $P > 0.11$), Set (all $P > 0.23$) or the interactions ($P > 0.30$).

Choice with complex background plant odour

In Trial 4 with the complex background odour in both bins, the probability that elephants chose the bin with the high preference species was always significant (Table A3, Figure 4a). The effect of Pair was not significant ($P = 0.294$), but Set was significant ($P = 0.027$) with probabilities increasing from Set 1 to 3 (Figure 4b).

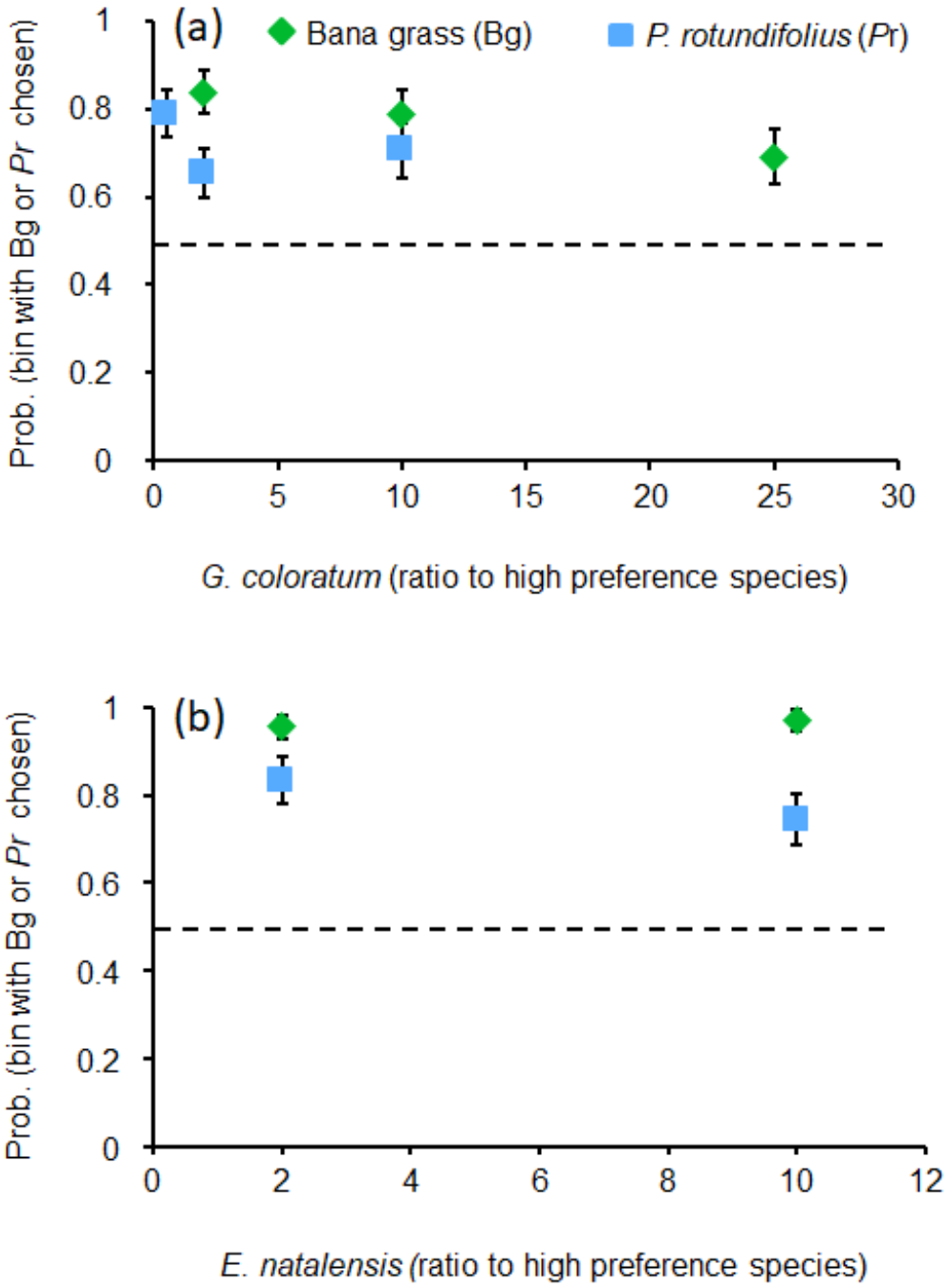

Figure 3. Trial 3 choice with simple background plant odour. Probability of the bin with the high preference species, i.e. bana grass (Bg) ◆ or *P. rotundifolius* (*Pr*) ■, and the simple background of either (a) *G. coloratum* (*Gc*) or (b) *E. natalensis* (*En*), being chosen over the bin with just the simple background. The x-axis shows the number of pieces of the background, low preference species in the bin, as a ratio to high preference species, Bg or *Pr*, when either of these were present. Values are means ± SEM. Dashed line represents random choice.

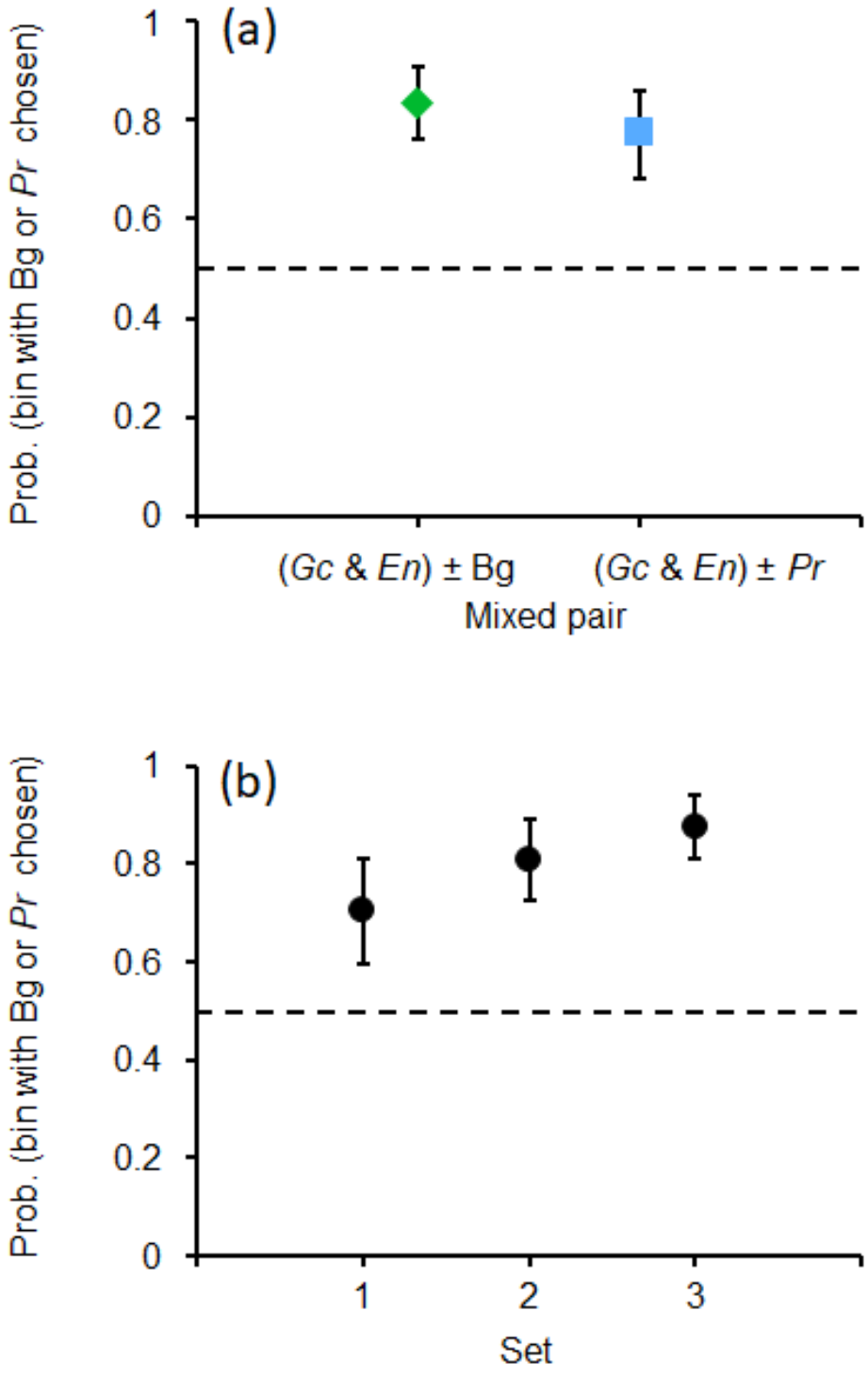

Figure 4. Trial 4 choice with complex background plant odour. (a) Probability of the bin with the high preference species, i.e. bana grass (Bg) ◆ or *P. rotundifolius* (*Pr*) ■, and the complex background of *G. coloratum* (*Gc*) and *E. natalensis* (*En*), being chosen over the bin with just the complex background; (b) Probability of the bin with Bg or *Pr* being chosen as a function of set number. Values are means ± SEM. Dashed line represents random choice.

Choice with artificial green leaf volatile background odour

In Trial 5 when artificial green leaf volatile background odour was in both bins, there was a significant effect of Set (Table A3, $P = 0.026$) on the probability of the bin containing the high preference species being chosen over the low preference species. In Set 1, elephants chose randomly ($P = 1.000$) but in Sets 2 and 3, they were significantly more likely to choose the bin with the high preference species ($P \leq 0.030$, Figure 5). The effect of Position was also significant (Table A3) with a higher probability of choosing the bin on the right.

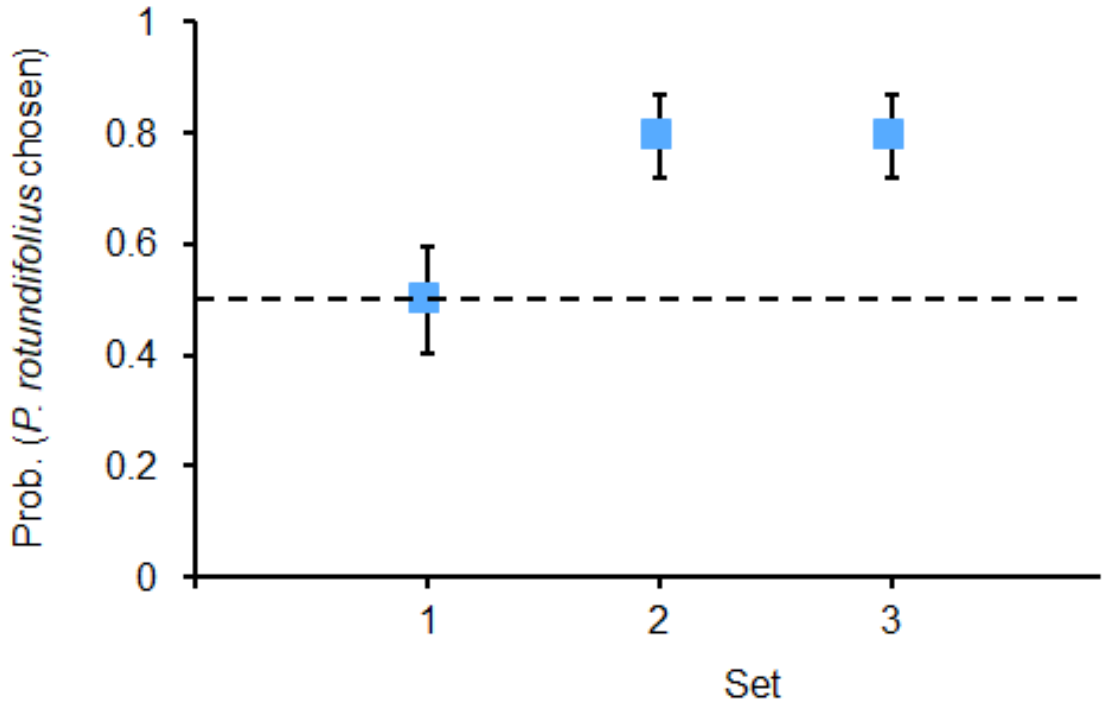

Figure 5. Trial 5 choice with green leaf volatile background odour. Probability of the bin with the high preference species, *P. rotundifolius*, being chosen over the bin with the low preference species, *G. coloratum*, when both bins have the green leaf volatile, (Z)-hex-3-en-1-yl acetate, as the background odour; and as a function of set number (1 to 3) and overall (All). Values are means ± SEM. Dashed line represents random choice.

Distinguishing odour profiles among plants and test combinations

We detected 49 volatile organic compounds (VOCs) among the four plant species (Table A3), with 5-26 compounds per species, mainly aliphatics and terpenoids. VOC profiles differed significantly among species (ANOSIM R = 0.735, *P* = 0.001, all post-hoc pairwise comparisons P ≤0.002; Figure 6). No single VOC distinguished each plant species (Tables A4 and A5). Instead, 6-8 compounds formed 50% of the cumulative difference among the species. (Z)-hex-3-en-1-yl acetate then (E)-4,8-dimethylnona-1,3,7-triene [DMNT] were consistently dominant. The monoterpenes, (E)-β-ocimene and linalool, were also dominant in the native species but minor in Bana grass. Indole was dominant in Bana grass, but minor in the native species. 1-methylpyrrole, an uncommon heterocyclic nitrogen-containing compound, was detected in *P. rotundifolius* but not in *G. coloratum* or *E. natalensis*. Several aliphatic esters in *P. rotundifolius* and *E. natalensis* were undetected in Bana grass and *G. coloratum*. The sesquiterpene, β-caryophyllene, was the major compound differentiating *E. natalensis* from G*. coloratum* species (higher in *E. natalensis*), but its contribution to the overall difference was still minor (8%).

ANOSIM results were significant for tests associated with Trial 3 at the global level (all *P* = 0.001; Table A6). Bana grass with a simple background odour (either *G. coloratum* or *E. natalensis*) did not differ significantly from either of the latter alone (Figure A1a, b; although elephants could distinguish these). In contrast, *P. rotundifolius* with *G. coloratum* differed significantly from pure *G. coloratum*, but not from pure *P. rotundifolius* (Figure A1c, although again, elephants could distinguish these). *Pterocarpus rotundifolius* mixed with *E. natalensis* differed significantly from pure *E. natalensis* and pure *P. rotundifolius* (Figure A1d).

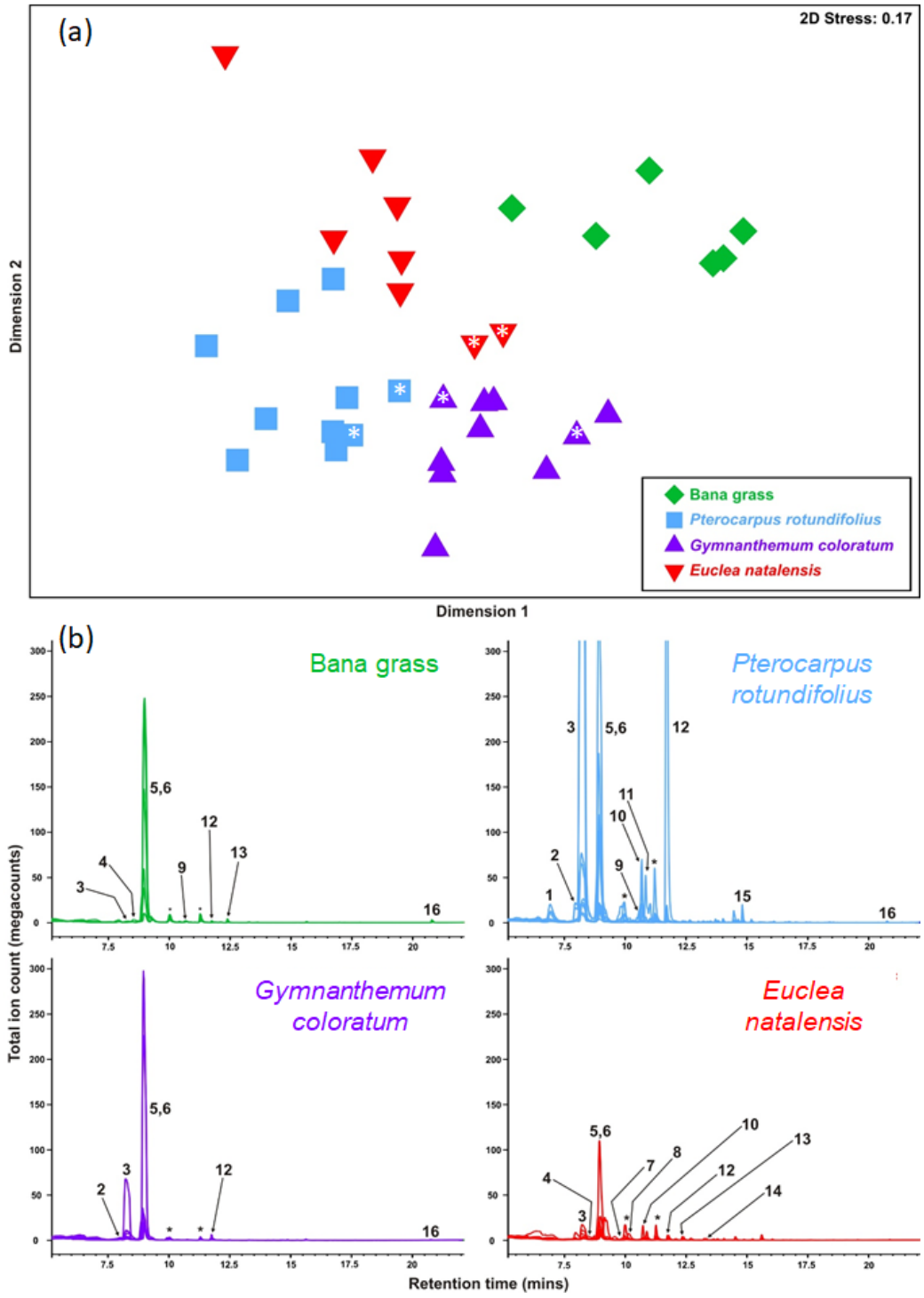

Figure 6. Odour profiles of the four plant species used in Preference and Odour Trials 1-5. (a) Individual replicates plotted in two-dimensional odour space based on nMDS. * indicates intact sample, otherwise samples were detached pieces as offered to the elephants. (b) Total ion chromatograms (TIC) for each species (all replicates per species plotted on the same axes). Compounds that best distinguish total odour profiles of each species (based on a SIMPER analysis) are labelled. Note that some peaks for *P. rotundifolius* are truncated at this scale, and many of the

minor peaks for all species are not visible. **1,** 1-methylpyrrole; **2,** (Z)-β-ocimene; **3,** (E)-β-ocimene; **4,** hexyl acetate; **5,** (E)-4,8-dimethylnona-1,3,7-triene; **6,** (Z)-hex-3-en-1-yl acetate; **7,** unidentified compound with mass fragments 67,82,71,43,55,81 (listed in decreasing order of abundance); **8,** (E)-hex-2-en-1-ol; **9,** oct-1-en-3-ol; **10,** (Z)-hex-en-1-yl butyrate; **11,** (Z)-hex-3-en-1-yl isovalerate; **12,** linalool; **13,** β-caryophyllene; **14,** unidentified compound with mass fragments 117,91,90,65,89 (listed in decreasing order of abundance); **15,** (E,E)-2,6-dimethylocta-3,5,7-triene-2-ol; **16,** indole; * represent nonanal and decanal, which were both environmental contaminants in all samples.

ANOSIM results were significant for tests associated with Trial 4 at the global level (both $P = 0.001$; Table A7). The odour profile of pure Bana grass or pure *P. rotundifolius* differed significantly from the complex background odour with Bana grass or *P. rotundifolius* (Table A7 and Figure A2).

ANOSIM results were significant for tests associated with Trial 5 at the global level but did not distinguish the paired samples actually offered to elephants: background green leaf volatile with *P. rotundifolius vs G. coloratum* (Table A7 pairwise comparison not significant, and Figure A3). As expected, the overwhelming contribution to both these samples was (Z)-hex-3-en-1-yl acetate. SIMPER identified (E)-β-ocimene, (E)-4,8-dimethylnona-1,3,7-triene, (Z)-hex-3-en-1-ol and β-caryophyllene as together contributing to 43.4% of the odour difference between the two samples, thus providing a means for elephants to distinguish the two.

DISCUSSION

We found that elephants were able to detect, discriminate and select preferred plants based on odour signals despite increasingly complex background noise from odours

of non-preferred plants, and despite attempting to mask the odour signal. Our findings support the hypothesis that plant odour provides a salient cue for mammalian herbivores even in the presence of sensory noise from background odour. By demonstrating the role of plant odours as cues in complex odour backgrounds mimicking multi-species food patches, our results show that plant odour provides an efficient mechanism for selective foraging. They also indicate that the capacity of mammalian herbivores to use plant odour as a cue can equal if not exceed that of insect herbivores, since background odour can confound the latter (Schröder & Hilker, 2008).

For mammalian herbivores to use odour to choose food plants, the odour profiles of the plants must differ. GC-MS analysis confirmed this difference. Important components differentiating the three native species were the monoterpenes β-ocimene (both E and Z isomers) and linalool, the sesquiterpene β-caryophyllene, and 1-methylpyrrole. Indole was an important differentiating component of Bana grass. Whether elephants use the ratios (i.e. relative concentrations) of a subset of odour compounds to differentiate plant species, as do insects (Bruce, Wadhams, & Woodcock, 2005), rather than honing in on particular compounds or particular combinations of compounds awaits future research.

Elephants non-randomly selected the odour signal of their preferred plants in both simple and complex odour backgrounds. In the odour trials of a single species (Trial 2) and with simple background odour (Trial 3), their preference did not improve over time. But they did improve when the background odour was complex (Trial 4, Fig.

4b). Background sensory noise, created by odourants from non-host plants, alters the ratio of volatile compounds and so obscures cues (Riffell et al., 2014), making it hard for insects to detect and track preferred odours (Kerr, Kelly, Bader, & Brockerhoff, 2017; Riffell et al., 2014; Xu et al., 2017). Similarly, the complex background odour may have initially obscured the signal for elephants.

From a cognitive perspective, elephants may have improved over time when the background odour was complex (Trial 4) by exerting greater selective attention to the task of discriminating the odour profiles — effectively creating an odour search image (Bernays & Wcislo, 1994; Zentall, 2005). This enabled quick effective foraging decisions for the high preference plants in later sets. Consistent with this interpretation, mice improve their foraging performance for olfactorily cryptic food over time, particularly if it is preferred (Price & Banks, 2017). We do not think the elephants were initially unclear as to their reward in Trial 4, because it was identical in form to Trial 3 with simple background odour.

Elephants also strengthened their preference over time when we attempted to mask the differentiating odours (Trial 5, Fig. 5); choosing randomly in Set 1 for the first time in all our trials but selecting the preferred plant option in Sets 2 and 3. There are two possible explanations for this improvement. First, the artificial green leaf volatile masked the other odours. Second, we inadvertently confused the elephants about their reward. The “masking” compound, (Z)-hex-3-en-1-yl acetate, smells like cut grass, and is often the dominant volatile of nutritious plants (Arey et al., 1991). Indeed, it was the major VOC from the fodder crop we used, Bana grass, although it

was also in the native plants. Elephants may therefore have chosen randomly at first, expecting the same nutritious reward irrespective of their choice. Yet, depending on their choice, they received either the high or low preference plant species. Given that from Set 2 the elephants chose the bin with the high preference plant (Fig. 5), it is clear that the second explanation is correct and the odours from the plants had not been masked. At least four VOCs contributed to the difference between the samples, and the biggest contributor, (E)-β-ocimene, was also one of the top five compounds differentiating *P. rotundifolius* from *G. coloratum* (higher in the former) in the simple single species comparison. Ocimene attracts insect pollinators, insect herbivores and their natural enemies (Farre-Armengol, Filella, Llusia, & Penuelas, 2017; Fors, Mozuraitis, Blazyte-Cereskiene, Verschut, & Hamback, 2018; Knauer, Bakhtiari, & Schiestl, 2018), and was likely a key component of the signal for elephants.

Selection of foods within patches is one of the key foraging decisions animals make (Senft et al., 1987). Plant odour allows elephants to detect preferred plants (Melissa H. Schmitt et al., 2018), and critically, as we show here, allows them to do so in complex odour backgrounds. Such foraging decisions can therefore be made quickly and efficiently, improving foraging performance. By affecting foraging performance, plant odour — and the capacity to use it — should ultimately affect fitness, particularly because mammalian herbivores devote a large part (both absolute and proportional) of their daily time budget to foraging (Owen-Smith, 1994; Wyatt & Eltringham, 1974), and this includes foraging at night when visual cues are diminished (Ramesh, Kalle, Sankar, & Qureshi, 2015; Wyatt & Eltringham, 1974).

We used plants that were familiar to elephants. Yet how effectively they can use or learn to detect, discriminate and use novel odours while foraging remains an open question with important ecological implications. Newly invading plant species, translocation of animals to new regions with unfamiliar plants, and even the chemical degradation and change in odours of familiar plants from air pollution, could all impinge on the capacity to recognise and make effective use of odour cues for efficient foraging, at least in the short term. There has been a massive increase in atmospheric VOC levels globally, fuelled in part by increasing urbanisation (Karl, Striednig, Graus, Hammerle, & Wohlfahrt, 2018). This air pollution, including raised CO_2 levels associated with climate change, alters the volatile organic compounds emitted by plants (Block, Vaughan, Christensen, Alborn, & Tumlinson, 2017), degrades them differentially and drastically contracts the area over which they spread (McFrederick, Fuentes, Roulston, Kathilankal, & Lerdau, 2009; McFrederick, Kathilankal, & Fuentes, 2008). The impact of these changes has been considered for insects and the ecosystem services they provide (Blande, Holopainen, & Niinemets, 2014; McFrederick et al., 2009), but not for mammalian herbivores.

Given the ecological and morphological similarities among mammalian herbivores, and the evidence that plant odour is important for eutherian elephants and marsupial wallabies and possums, we predict that plant odour cues play a key role enabling selective foraging by other ecologically-influential mammalian herbivores in other ecosystems, such as ungulates in America, Europe and Asia, and antelope in Africa. Accounting for the capacity to use plant odour cues will improve models of both the foraging behaviour of mammalian herbivores and the ecosystem impacts of their foraging.

Author contributions

CMcA, PBF, MHS and AMS conceived and designed the experiments. CMcA and PBF performed the experiments, AS analysed the odour chemistry, CMcA analysed the data. All authors contributed to the manuscript, led by CMcA.

Conflict of interest

We have no competing interests.

Data availability

The supporting data for this paper is deposited in the Figshare Digital Repository (McArthur, Finnerty, Schmitt, Shuttleworth, & Shrader, 2019).

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References

Anderson, M. C., Gorley, R. N., & Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. Plymouth, UK.: PRIMER-E.

Arey, J., Winer, A. M., Atkinson, R., Aschmann, S. M., Long, W. D., & Morrison, C. L. (1991). The emission in (Z)-3-hexen-1-ol, (Z)-3-hexenylacetate and other oxygenated hydrocarbons from agricultural plant species. *Atmospheric Environment Part a-General Topics, 25*(5-6), 1063-1075. doi: 10.1016/0960-1686(91)90148-z

Bates, L. A., Sayialel, K. N., Njiraini, N. W., Moss, C. J., Poole, J. H., & Byrne, R. W. (2007). Elephants classify human ethnic groups by odor and garment color. *Current Biology, 17*(22), 1938-1942. doi: 10.1016/j.cub.2007.09.060

Bayani, A., Tiwade, D., Dongre, A., Dongre, A. P., Phatak, R., & Watve, M. (2016). Assessment of Crop Damage by Protected Wild Mammalian Herbivores on the Western Boundary of Tadoba-Andhari Tiger Reserve (TATR), Central India. *Plos One, 11*(4). doi: 10.1371/journal.pone.0153854

Bedoya-Perez, M., Issa, D., Isler, I., Banks, P. B., & McArthur, C. (2014). Roles of the volatile terpene, 1,8-cineole, in plant-herbivore interactions: a foraging odor cue as well as a toxin? *Oecologia, 174*(3), 827-837.

Bernays, E. A., & Wcislo, W. T. (1994). Sensory capabilities, information-processing, and resource specialization. *Quarterly Review of Biology, 69*(2), 187-204. doi: 10.1086/418539

Beuchner, H. K., & Dawkins, H. C. (1961). Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology, 42*, 752-766.

Blande, J. D., Holopainen, J. K., & Niinemets, U. (2014). Plant volatiles in polluted atmospheres: stress responses and signal degradation. *Plant Cell and Environment, 37*(8), 1892-1904. doi: 10.1111/pce.12352

Block, A., Vaughan, M. M., Christensen, S. A., Alborn, H. T., & Tumlinson, J. H. (2017). Elevated carbon dioxide reduces emission of herbivore-induced volatiles in Zea mays. *Plant Cell and Environment, 40*(9), 1725-1734. doi: 10.1111/pce.12976

Bruce, T. J. A., Wadhams, L. J., & Woodcock, C. M. (2005). Insect host location: a volatile situation. *Trends in Plant Science, 10*(6), 269-274. doi: http://dx.doi.org/10.1016/j.tplants.2005.04.003

Bulinski, J., & McArthur, C. (1999). An experimental field study of the effects of mammalian herbivore damage on *Eucalyptus nitens* seedlings. *Forest Ecology and Management, 113*, 241-249.

Cai, X. M., Bian, L., Xu, X. X., Luo, Z. X., Li, Z. Q., & Chen, Z. M. (2017). Field background odour should be taken into account when formulating a pest attractant based on plant volatiles. *Scientific Reports, 7*. doi: 10.1038/srep41818

Clarke, K. R., & Gorley, R. N. (2006). *PRIMER v6: User Manual/Tutorial*: PRIMER-E Ltd.

Codron, J., Lee-Thorp, J. A., Sponheimer, M., Codron, D., Grant, R. C., & De Ruiter, D. J. (2006). Elephant (*Loxodonta africana*) diets in Kruger National Park, South Africa: spatial and landscape differences. *Journal of Mammalogy, 87*(1), 27-34. doi: 10.1644/05-mamm-a-017r1.1

Coppes, J., Burghardt, F., Hagen, R., Suchant, R., & Braunisch, V. (2017). Human recreation affects spatio-temporal habitat use patterns in red deer (*Cervus elaphus*). *Plos One, 12*(5). doi: 10.1371/journal.pone.0175134

Cote, S. D., Rooney, T. P., Tremblay, J. P., Dussault, C., & Waller, D. M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics, 35*, 113-147. doi: 10.1146/annurev.ecolsys.35.021103.105725

Daskin, J. H., Stalmans, M., & Pringle, R. M. (2016). Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. *Journal of Ecology, 104*(1), 79-89. doi: 10.1111/1365-2745.12483

Dexter, N., Hudson, M., James, S., MacGregor, C., & Lindenmayer, D. B. (2013). Unintended Consequences of Invasive Predator Control in an Australian Forest: Overabundant Wallabies and Vegetation Change. *PLoS ONE, 8*(8), e96087. doi: 10.1371/journal.pone.0069087

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., . . . Wardle, D. A. (2011). Trophic Downgrading of Planet Earth. *Science, 333*(6040), 301-306. doi: 10.1126/science.1205106

Farre-Armengol, G., Filella, I., Llusia, J., & Penuelas, J. (2017). beta-Ocimene, a Key Floral and Foliar Volatile Involved in Multiple Interactions between Plants and Other Organisms. *Molecules, 22*(7). doi: 10.3390/molecules22071148

Finnerty, P. B., Stutz, R. S., Price, C. J., Banks, P. B., & McArthur, C. (2017). Leaf odour cues enable non-random foraging by mammalian herbivores. *Journal of Animal Ecology, 86*, 1317-1328. doi: 10.1111/1365-2656.12748

Firestein, S. (2001). How the olfactory system makes sense of scents. *Nature, 413*(6852), 211-218.

Fleischer, J., Pregitzer, P., Breer, H., & Krieger, J. (2018). Access to the odor world: olfactory receptors and their role for signal transduction in insects. *Cellular and Molecular Life Sciences, 75*(3), 485-508. doi: 10.1007/s00018-017-2627-5

Fors, L., Mozuraitis, R., Blazyte-Cereskiene, L., Verschut, T. A., & Hamback, P. A. (2018). Selection by parasitoid females among closely related hosts based on volatiles: Identifying relevant chemical cues. *Ecology and Evolution, 8*(6), 3219-3228. doi: 10.1002/ece3.3877

Foster, C. N., Barton, P. S., & Lindenmayer, D. B. (2014). Effects of large native herbivores on other animals. *Journal of Applied Ecology, 51*(4), 929-938. doi: 10.1111/1365-2664.12268

Gupta, S. C., & Mhere, O. (1997). Identification of superior pearl millet by napier hybrids and napiers in Zimbabwe. *African Crop Science Journal, 5*(3), 229-237.

Hein, A. M., & McKinley, S. A. (2012). Sensing and decision-making in random search. *Proceedings of the National Academy of Sciences of the United States of America, 109*(30), 12070-12074. doi: 10.1073/pnas.1202686109

Horsley, S. B., Stout, S. L., & DeCalesta, D. S. (2003). White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications, 13*(1), 98-118. doi: 10.1890/1051-0761(2003)013[0098:Wtdiot]2.0.Co;2

Johnston, R. E. (2003). Chemical communication in rodents: From pheromones to individual recognition. [Review]. *Journal of Mammalogy, 84*(4), 1141-1162.

Karl, T., Striednig, M., Graus, M., Hammerle, A., & Wohlfahrt, G. (2018). Urban flux measurements reveal a large pool of oxygenated volatile organic compound emissions. *Proceedings of the National Academy of Sciences of the United States of America, 115*(6), 1186-1191. doi: 10.1073/pnas.1714715115

Kerr, J. L., Kelly, D., Bader, M. K. F., & Brockerhoff, E. G. (2017). Olfactory Cues, Visual Cues, and Semiochemical Diversity Interact During Host Location by Invasive Forest Beetles. *Journal of Chemical Ecology, 43*(1), 17-25. doi: 10.1007/s10886-016-0792-x

Knauer, A. C., Bakhtiari, M., & Schiestl, F. P. (2018). Crab spiders impact floral-signal evolution indirectly through removal of florivores. *Nature Communications, 9*. doi: 10.1038/s41467-018-03792-x

Marneweck, C., Jurgens, A., & Shrader, A. M. (2017). Dung odours signal sex, age, territorial and oestrous state in white rhinos. *Proceedings of the Royal Society B-Biological Sciences, 284*, 20162376. doi: http://dx.doi.org/10.1098/rspb.2016.2376

McArthur, C., Finnerty, P. B., Schmitt, M. H., Shuttleworth, A., & Shrader, A. M. (2019). Data from: Elephants target preferred plants despite background plant odour. Figshare Digital Repository DOI: 10.6084/m9.figshare.7610276.

McFrederick, Q. S., Fuentes, J. D., Roulston, T., Kathilankal, J. C., & Lerdau, M. (2009). Effects of air pollution on biogenic volatiles and ecological interactions. *Oecologia, 160*(3), 411-420. doi: 10.1007/s00442-009-1318-9

McFrederick, Q. S., Kathilankal, J. C., & Fuentes, J. D. (2008). Air pollution modifies floral scent trails. *Atmospheric Environment, 42*(10), 2336-2348. doi: 10.1016/j.atmosenv.2007.12.033

McInnes, P. F., Naiman, R. J., Pastor, J., & Cohen, Y. (1992). Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology, 73*(6), 2059-2075. doi: 10.2307/1941455

Mella, V. S. A., Possell, M., Troxell-Smith, S. M., & McArthur, C. (2018). Visit, consume and quit: patch quality affects the three stages of foraging. *Journal of Animal Ecology, 87*, 1615-1626. doi: DOI: 10.1111/1365-2656.12882

Miller, A. K., Hensman, M. C., Hensman, S., Schultz, K., Reid, P., Shore, M., . . . Lee, S. (2015). African elephants (*Loxodonta africana*) can detect TNT using olfaction: Implications for biosensor application. *Applied Animal Behaviour Science, 171*, 177-183. doi: 10.1016/j.applanim.2015.08.003

Nevitt, G. A., Veit, R. R., & Kareiva, P. (1995). Dimethyl sulfide as a foraging cue for Antarctic Procellariiform seabirds. *Nature, 376*(6542), 680-682. doi: 10.1038/376680ao

Owen-Smith, N. (1994). Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology, 75*(4), 1050-1062. doi: 10.2307/1939429

Owen-Smith, N., & Chafota, J. (2012). Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*). *Journal of Mammalogy, 93*(3), 698-705. doi: 10.1644/11-mamm-a-350.1

Parsons, M. H., Apfelbach, R., Banks, P. B., Cameron, E. Z., Dickman, C. R., Frank, A. S. K., . . . Blumstein, D. T. (2018). Biologically meaningful scents: a framework for understanding predator-prey research across disciplines. *Biological Reviews, 93*(1), 98-114. doi: 10.1111/brv.12334

Plotnik, J. M., Lair, R., Suphachoksahakun, W., & de Waal, F. B. M. (2011). Elephants know when they need a helping trunk in a cooperative task. *Proceedings of the National Academy of Sciences of the United States of America, 108*(12), 5116-5121. doi: 10.1073/pnas.1101765108

Plotnik, J. M., Shaw, R. C., Brubaker, D. L., Tiller, L. N., & Clayton, N. S. (2014). Thinking with their trunks: elephants use smell but not sound to locate food and exclude nonrewarding alternatives. *Animal Behaviour, 88*, 91-98. doi: 10.1016/j.anbehav.2013.11.011

Price, C. J., & Banks, P. B. (2012). Exploiting olfactory learning in alien rats to protect birds' eggs. *Proceedings of the National Academy of Sciences of the United States of America, 109*(47), 19304-19309. doi: 10.1073/pnas.1210981109

Price, C. J., & Banks, P. B. (2017). Food quality and conspicuousness shape improvements in olfactory discrimination by mice. *Proceedings of the Royal Society B-Biological Sciences, 284*(1847). doi: 10.1098/rspb.2016.2629

Pudyatmoko, S. (2017). Free-ranging livestock influence species richness, occupancy, and daily behaviour of wild mammalian species in Baluran National Park, Indonesia. *Mammalian Biology, 86*, 33-41. doi: 10.1016/j.mambio.2017.04.001

Ramesh, T., Kalle, R., Sankar, K., & Qureshi, Q. (2015). Role of body size in activity budgets of mammals in the Western Ghats of India. *Journal of Tropical Ecology, 31*, 315-323. doi: 10.1017/s0266467415000188

Riffell, J. A., Shlizerman, E., Sanders, E., Abrell, L., Medina, B., Hinterwirth, A. J., & Kutz, J. N. (2014). Flower discrimination by pollinators in a dynamic chemical environment. *Science, 344*(6191), 1515-1518. doi: 10.1126/science.1251041

Rizvanovic, A., Amundin, M., & Laska, M. (2013). Olfactory Discrimination Ability of Asian Elephants (*Elephas maximus*) for Structurally Related Odorants. *Chemical Senses, 38*(2), 107-118. doi: 10.1093/chemse/bjs097

Scala, A., Allmann, S., Mirabella, R., Haring, M. A., & Schuurink, R. C. (2013). Green Leaf Volatiles: A Plant's Multifunctional Weapon against Herbivores and Pathogens. *International Journal of Molecular Sciences, 14*(9), 17781-17811. doi: 10.3390/ijms140917781

Schmitt, M. H., Shuttleworth, A., Ward, D., & Shrader, A. M. (2018). African elephants use plant odours to make foraging decisions across multiple spatial scales. *Animal Behaviour, 141*, 17-27. doi: DOI: 10.1016/j.anbehav.2018.04.016

Schmitt, M. H., Ward, D., & Shrader, A. M. (2016). Incorporating secondary metabolites, tannin-binding proteins, and diet breadth into carrying-capacity models for African elephants. *Ecological Modelling, 332*, 8-18. doi: 10.1016/j.ecolmodel.2016.03.016

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods, 9*, 671. doi: 10.1038/nmeth.2089

Schoonhoven, L. M., Van Loon, J. J. A., & Dicke, M. (2005). *Insect-Plant Biology* (2nd Edition ed.). Oxford, U.K.: Oxford University Press.

Schröder, R., & Hilker, M. (2008). The Relevance of Background Odor in Resource Location by Insects: A Behavioral Approach. *BioScience, 58*(4), 308-316. doi: 10.1641/B580406

Seidler, R. G., Long, R. A., Berger, J., Bergen, S., & Beckmann, J. P. (2015). Identifying impediments to long-distance mammal migrations. *Conservation Biology, 29*(1), 99-109. doi: 10.1111/cobi.12376

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., & Swift, D. M. (1987). Large herbivore foraging and ecological hierachies. *BioScience, 37*(11), 789-799.

Shrader, A. M., Bell, C., Bertolli, L., & Ward, D. (2012). Forest or the trees: At what scale do elephants make foraging decisions? *Acta Oecologica-International Journal of Ecology, 42*, 3-10. doi: 10.1016/j.actao.2011.09.009

Stutz, R. S., Banks, P. B., Proschogo, N., & McArthur, C. (2016). Follow your nose: leaf odour as an important foraging cue for mammalian herbivores. *Oecologia, 182*(3), 643-651. doi: DOI 10.1007/s00442-016-3678-2

Stutz, R. S., Croak, B., Banks, P. B., Proschogo, N., & McArthur, C. (2017). Olfactory and visual plant cues as drivers of selective herbivory. *Oikos, 126*, 259-268. doi: 10.1111/oik.03422

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2017). Learning from the mistakes of others: How female elk (Cervus elaphus) adjust behaviour with age to avoid hunters. *Plos One, 12*(6). doi: 10.1371/journal.pone.0178082

Western, D., & Maitumo, D. (2004). Woodland loss and restoration in a savanna park: a 20-year experiment. *African Journal of Ecology, 42*(2), 111-121. doi: 10.1111/j.1365-2028.2004.00506.x

Wilson, J. K., Kessler, A. P., & Woods, H. A. (2015). Noisy communication via airborne infochemicals. [Review]. *BioScience, 65*(7), 667-677. doi: 10.1093/biosci/biv062

Wyatt, J. R., & Eltringham, S. K. (1974). The daily activity of the elephant in the Rwenzori National Park, Uganda. *African Journal of Ecology, 12*(4), 273-289. doi: doi:10.1111/j.1365-2028.1974.tb01037.x

Xu, X. X., Cai, X. M., Bian, L., Luo, Z. X., Li, Z. Q., & Chen, Z. M. (2017). Does background odor in tea gardens mask attractants? Screening and application of attractants for *Empoasca onukii* Matsuda. *Journal of Economic Entomology, 110*(6), 2357-2363. doi: 10.1093/jee/tox269

Zentall, T. R. (2005). Selective and divided attention in animals. *Behavioural Processes, 69*(1), 1-15. doi: 10.1016/j.beproc.2005.01.004

Appendix 1.

In the pilot study we tested 10 plant species. Nine were native tree/shrub species that grew in the reserves in which the elephants foraged daily: bushveld hairy guarri, *E. natalensis angustifolia* (Family Ebenaceae), camphor bush, *Tarchonanthus camphoratus* (Family Asteraceae), Cape Holly *Ilex mitis* (Family Aquifoliaceae), jackalberry, *Diospyros mespiliformis* (Family Ebenaceae), large-fruited bushwillow, *Combretum zeyheri* (Family Combretaceae), lowveld bittertea, *G. coloratum* (Family Asteraceae), red bauhinia, *Bauhinia galpinii* (Family Fabaceae), round-leafed teak, *P. rotundifolius rotundifolius* (Family Fabaceae) and silver clusterleaf, *Terminalia sericea* (Family Combretaceae); and the 10th was a fodder crop, which the elephants ate regularly: bana grass, a hybrid of pearl millet, *P. glaucum*, and napier grass, *P. purpureum*.

Appendix 2. **Methods Used to Determine Odour Profiles**

We placed a small sample of a single plant type or combination (mean ± s.d.: 16.3 ± 13.2 g wet weight, 7.7 ± 5.7 g leaf wet weight, 335 ± 177 cm^2 leaf area) into a polyacetate bag (NaloPhan®, Kalle, Germany). Volatiles in the headspace were then collected by sucking air from the bag for 3 h through a small cartridge filled with 1.5 mg each of Tenax® TA (60/80) (SupelcoTM; Bellefonte, PA, USA) and Carbotrap® B (20-40 mesh) (Sigma-Aldrich Co.; St. Louis, MO, USA) using a PAS500 Personal Air Sampler (Spectrex, Redwood City, CA, USA). Control samples were collected in the same way from empty bags and used to identify environmental contaminants. Cartridges were stored at -18 °C until further analysis.

Volatiles were analysed by gas chromatography-mass spectrometry (GC-MS) using a Varian CP 3800 gas chromatograph (fitted with a Varian 1079 PTV injector port modified with a ChromatoProbe thermal desorption device into which sample cartridges were placed) coupled to a Varian 1200 quadrupole mass spectrometer or a Bruker 300 quadrupole mass spectrometer. The latter was used for nine of the samples taken from mixed species (two replicates of Bg & Gc, two replicates of Pr & Gc, one replicate of Bg & En, three replicates of Bg, Gc & En and one replicate of Pr, GC & En)).

Both mass spectrometers were operated in electron-impact ionization mode at 70 eV with the detector voltage set by Extended Dynamic Range (EDR). Helium was used a carrier gas (1ml/min column flow) and all samples were analysed using a polar capillary column (Bruker BR-Swax, 30m long, 0.25 mm I.D., 0.25µm film thickness).

For each run, the injector and column oven were programmed as follows. Injector: 40 °C for 2 min with a 20:1 split, then increased to 200 °C at 200 ◦C min^{-1} in splitless mode and held at 200 °C for 2 min for thermal desorption. Oven: 40 °C for 3 min, then ramped up to 240 ◦C at 10 °C min−1 and held at 240 °C for 12 min. Compounds were identified using the NIST 2011 mass spectral library. Library identifications were confirmed using injections of synthetic standards or published *n*-alkane retention indices (Kovats). Absolute emissions were estimated by injecting known amounts of synthetic standards (injected under identical conditions to samples) and comparing peak areas with those from samples. The following standards were used to estimate emissions of particular compounds or compound classes: (Z)-3-hexen-1-yl actetate (98% purity, SAFC Supply Solutions, St Louis, MO) for aliphatics; β-ocimene (mixture of Z and E isomers, 90% purity, Sigma-Aldrich, St Louis, MO) and linalool (95% purity, Sigma-Aldrich Chemie, GmbH, Buchs, Switzerland) and a mean of these two for the remaining terpenoids; and, methyl benzoate (98% purity, Merck Schuchardt OHG, Hohenbrunn, Germany) for aromatics. Unknowns were quantified using the mean for all standards.

For Trial 2, replication for the single plant type was n = 6 (Bana grass), n = 10 (*P. rotundifolius*), n = 10 (*G. coloratum*), n = 8 (*E. natalensis*). For the three native plant species, two of these replicates were sampled on the intact plant to compare with odour profiles of detached samples, as offered to the elephants. This intact sampling was not possible for Bana grass because we offered both the dense tiller close to the ground as well as part of the upper leaf blade from these 1-2 m plants. For Trial 3, we had 3-4 replicates for each of the simple background plant odour combinations. For Trial 4, we had four replicates for the two complex background plant odour

combinations. For Trial 5, we had two replicates for each of the two plant types with green leaf volatile background odour.

Appendix 3. Statistical Analyses

We initially explored the fixed effects of Test Number (1 – 5), Position (left, right) and Carryover (Position from the preceding test) for each of the paired combinations in separate models. Carryover was never significant, Test Number was rarely significant, and Position was never significant in Trials 1 – 4, and so these were removed from the final models. Within each trial, we then tested the fixed effects of Pair, Set Number (as a continuous variable, to test whether elephants changed their decision between sets, with increased experience of the pair and its reward) and their interaction, and with individual elephant as a random factor. In Trial 4, we included Ratio in the model, and because only two of the three Ratios were the same for Bana grass and *P. rotundifolius* against *G. coloratum*, we tested two models, one using data across all ratios (unbalanced), and one with just the ratios of 1:2 and 1:10 (hence balanced). The statistical results for the fixed effects were similar. For Trial 5, Position was significant and so it was retained in the final model.

Table A1. PERMANOVA results testing the effect of species and sample type (intact (i.e., on plant) versus detached (i.e., as offered to elephants) on odour profiles of the three native plant species.

Factor	ndf, ddf	Pseudo-F value	*P* value
Species	2, 22	5.19	0.001
Sample type	1, 22	2.58	0.025
Species * Sample type	2, 22	1.13	0.322

Note that when tested by ANOSIM the Species effect was significant (Global R = 0.734, *P* = 0.001) but the Sample Type effect was not significant (Global R = 0.072, *P* = 0.305). SIMPER showed that intact samples had greater (E)- and (Z)-4,8-dimethylnona-1,3,7-triene and (Z)-hex-3-en-1-yl acetate but less linalool and (E)-β-ocimene than detached samples, together contributing to over a third (35 %) of the difference.

Table A2. Results of the generalised linear mixed models showing the effect of factors on the probability of Bana grass or *P. rotundifolius* each being chosen over *G. coloratum* or *E. natalensis*.

Trial	Factor	ndf, ddf	F value	*P* value
1	Pair	3, 246	7.78	**< 0.001**
	Set	1, 246	0.47	0.493
2	Pair	3, 338	1.84	0.140
	Set	1, 338	0.01	0.922
3Ai	Pair	1, 378	5.83	**0.016**
	Ratio	3, 378	1.96	0.120
	Set	1, 378	0.76	0.384
	Pair*Ratio	1, 378	0.89	0.347
3Aii	Pair	1, 260	6.13	**0.014**
	Ratio	1, 260	0.01	0.942
	Set	1, 260	1.73	0.232
	Pair*Ratio	1, 260	1.03	0.312
3B	Pair	1, 260	14.3	**0.002**
	Ratio	1, 260	0.01	0.910
	Set	1, 260	1.74	0.188
	Pair*Ratio	1, 260	0.88	0.349
4	Pair	1, 167	1.11	0.294
	Set	1, 167	4.96	**0.027**

5	Set	1, 82	5.15	**0.026**
	Position	1, 82	8.49	**0.005**

ndf = numerator degrees of freedom, ddf = denominator degrees of freedom. 3A = Bana grass or *P. rotundifolius* with *G. coloratum* background odour (i) using all ratios, (ii) using just balanced ratios; 3B = Bana grass or *P. rotundifolius* with *E. natalensis* background odour.

Table A3. Summary of the mean (± SEM) relative amounts (%) of volatile organic compounds detected in headspace samples from the four plant species used in all odour trials (Bg Bana grass (*Pennisetum* hybrid), *Pr Pterocarpus rotundifolius*, *Gc Gymnanthemum coloratum*, and *En Euclea natalensis angustifolia)*.

Volatile organic compound	Kovats Index	ID criteria	Bg (n = 6)	SEM	*Pr* (n = 10)	SEM	*Gc* (n = 10)	SEM	*En* (n = 8)	SEM
Aliphatics										
Aldehydes										
(E)-Hex-2-enal	1222	A	0.00	0.00	0.00	0.00	0.00	0.00	1.43	1.43
(E,E)-Hepta-2,4-dienal	1502	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(E)-Non-2-enal	1538	A	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.35
(E,Z)-Nona-2,6-dienal	1584	A	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.22
Alcohols										
Hexan-1-ol	1354	B	0.00	0.00	0.00	0.00	0.00	0.00	0.62	0.62
(Z)-Hex-3-en-1-ol	1377	A	0.19	0.10	0.14	0.07	0.12	0.08	0.00	0.00
Octan-3-ol	1393	A	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.00
(E)-Hex-2-en-1-ol [a]	1402	A	0.61	0.42	0.00	0.00	0.00	0.00	1.64	1.05
Oct-1-en-3-ol	1441	B	0.67	0.12	0.70	0.32	0.00	0.00	0.42	0.20
(E)-Oct-2-en-1-ol	1611	A	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
Esters										
Hexyl acetate	1267	B	0.25	0.10	0.07	0.05	0.09	0.06	0.78	0.78
(Z)-Hex-3-en-1-yl acetate	1307	B	85.52	7.90	27.22	8.36	60.59	9.31	46.17	9.07
(E)-Hex-2-en-1-yl acetate	1324	A	0.00	0.00	0.00	0.00	0.00	0.00	4.01	4.01
(Z)-Hex-en-1-yl butyrate [b]	1448	A	0.00	0.00	1.50	0.88	0.00	0.00	2.23	0.82
(Z)-Hex-3-en-1-yl isovalerate	1458	A	0.00	0.00	0.31	0.16	0.00	0.00	1.11	0.59
(E)-2-Hexen-1-yl butyrate [a]	1462	A	0.00	0.00	0.00	0.00	0.00	0.00	0.72	0.72
(Z)-3-Hexenyl caproate	1641	A	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00

Terpenoids										
Monoterpenes										
β-Pinene	1182	B	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Limonene	1211	B	0.00	0.00	0.00	0.00	0.32	0.26	0.00	0.00
(Z)-β-Ocimene	1232	B	0.00	0.00	1.66	0.39	0.36	0.28	0.05	0.05
(E)-β-Ocimene	1256	B	0.75	0.45	47.84	7.90	23.48	5.08	22.99	4.05
Linalool [c]	1534	B	0.21	0.21	4.93	3.41	0.42	0.19	2.02	0.53
Terpinen-4-ol	1597	A	0.00	0.00	0.00	0.00	0.10	0.07	0.00	0.00
α-Terpineol	1687	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(E)-Linalool oxide (pyranoid)	1738	A	0.00	0.00	0.00	0.00	0.07	0.07	0.29	0.29
(Z)-Linalool oxide (pyranoid)	1757	A	0.00	0.00	0.00	0.00	0.08	0.08	0.00	0.00
(E,E)-2,6-Dimethylocta-3,5,7-triene-2-ol	1811	A	0.00	0.00	0.27	0.10	0.15	0.11	0.00	0.00
2,6-Dimethylocta-3,7-diene-2,6-diol	1930	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sesquiterpenes										
β-Caryophyllene	1588	B	1.14	0.52	0.10	0.05	0.00	0.00	3.01	1.34
Humulene	1663	A	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.17
α-Farnesene	1732	A	0.00	0.00	0.13	0.12	0.00	0.00	0.12	0.12
Irregular terpenes										
(Z)-4,8-Dimethylnona-1,3,7-triene	1274	A	0.77	0.77	0.39	0.36	0.37	0.27	0.04	0.02
(E)-4,8-dimethylnona-1,3,7-triene	1306	A	8.16	5.88	7.13	3.41	13.73	6.18	11.96	3.88
Aromatics										
Methyl salicylate	1783	B	0.02	0.02	0.18	0.10	0.02	0.01	0.33	0.33
Phenylethyl alcohol	1921	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nitrogen-containing compounds										
1-Methylpyrrole	1152	A	0.00	0.00	7.16	4.44	0.00	0.00	0.00	0.00

Indole	2431	B	1.34	0.54	0.01	0.00	0.08	0.08	0.00	0.00
Unknowns										
m/z: 67,82,71,43,55,81	1378		0.00	0.00	0.00	0.00	0.00	0.00	0.48	0.20
m/z: 103,57,43,85,56,41	1418		0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
m/z: 43,80,79,39,41,77,81	1425		0.06	0.05	0.02	0.02	0.00	0.00	0.00	0.00
m/z: 81,110,39,53,41,57	1468		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
m/z: 82,67,57,85,79,41,55	1475		0.00	0.00	0.11	0.08	0.00	0.00	0.09	0.05
m/z: 57,70,55,41,69,42	1476		0.03	0.02	0.00	0.00	0.00	0.00	0.00	0.00
m/z: 57,85,86,43,55,42,41	1538		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
m/z: 117,91,90,65,89	1670		0.00	0.00	0.00	0.00	0.00	0.00	0.58	0.29
m/z: 82,67,69,55,41,83	1705		0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00
m/z: 150*,59,79,94,91,77,93	1715		0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
m/z: 152*,71,43,109,81,79,67	1789		0.00	0.00	0.04	0.02	0.00	0.00	0.00	0.00
m/z: 196*,68,67,81,55,54,82	2018		0.27	0.16	0.00	0.00	0.00	0.00	0.00	0.00
Aliphatics			87.25	7.81	29.98	9.30	60.80	9.37	59.70	8.52
Terpenoids			11.03	7.62	62.46	9.23	39.11	9.35	40.82	8.06
Aromatics			0.02	0.02	0.18	0.10	0.02	0.01	0.33	0.33
Nitrogen-containing compounds			1.34	0.54	7.17	4.43	0.08	0.08	0.00	0.00
Unknowns			0.37	0.14	0.22	0.11	0.00	0.00	1.15	0.46
Number of compounds			14.17	0.40	17.60	1.48	12.20	0.70	14.13	1.64
Total emissions ($ng.cm^{-2}$ leaf surface.$hour^{-1}$)			0.34	0.11	0.77	0.33	0.20	0.07	0.10	0.03

Unknowns are listed with the molecular mass first (tentatively identified from the mass spectrum), if known, indicated by * followed by the base peak and remaining fragments in decreasing order of abundance. For the ID (identification) criteria: A, library match confirmed with comparison of *n*-alkane relative retention index (Kovats) to published values; B, library match confirmed with synthetic standard.

[a] May be the cis (Z) isomer as these could not be distinguished using our apparatus.

[b] May be the trans (E) isomer as these could not be distinguished using our apparatus.

[c] Present in small amounts in some control samples but included as they were in significantly higher amounts in plant samples

Table A4. SIMPER results showing the volatile organic compounds contributing to each of the four plant species used in all odour trials (Bg Bana grass (*Pennisetum* hybrid), *Pr Pterocarpus rotundifolius*, *Gc Gymnanthemum coloratum*, and *En Euclea natalensis angustifolia)*.

Species (ave. similarity)	**Volatile organic compound**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Bana grass Bg (71.09)	(Z)-Hex-3-en-1-yl acetate	3.03	27.06	4.96	38.06	38.06
	Oct-1-en-3-ol	0.89	7.53	8.55	10.59	48.66
	Indole	0.97	6.94	5.08	9.76	58.41
	β-Caryophyllene	0.86	5.62	3.48	7.90	66.32
	(E)-4,8-dimethylnona-1,3,7-triene	1.09	4.48	1.14	6.30	72.62
	(Z)-Hex-3-en-1-ol	0.49	2.90	1.01	4.08	76.70
	Hexyl acetate	0.51	2.88	0.78	4.05	80.75
	(E)-β-Ocimene	0.59	2.63	1.24	3.70	84.45
	(E)-Hex-2-en-1-ol	0.58	2.60	1.38	3.65	88.10
	m/z: 196*,68,67,81,55,54,82	0.47	1.88	0.91	2.65	90.75
P. rotundifolius Pr (67.59)	(E)-β-Ocimene	2.56	15.93	4.66	23.57	23.57
	(Z)-Hex-3-en-1-yl acetate	2.09	12.04	3.40	17.81	41.38
	(Z)-β-Ocimene	1.09	6.72	5.10	9.95	51.33
	(E)-4,8-dimethylnona-1,3,7-triene	1.31	6.45	1.78	9.55	60.87
	Linalool	1.18	6.35	6.31	9.39	70.27
	Oct-1-en-3-ol	0.79	4.27	2.38	6.31	76.58
	1-Methylpyrrole	1.04	3.91	1.12	5.79	82.37
	(E,E)-2,6-Dimethylocta-3,5,7-triene-2-ol	0.53	2.09	1.10	3.09	85.46
	β-Caryophyllene	0.38	1.59	1.57	2.35	87.82
	m/z: 152*,71,43,109,81,79,67	0.33	1.47	2.26	2.18	90.00
	(Z)-Hex-en-1-yl butyrate	0.54	0.98	0.49	1.45	91.44

G. coloratum Gc (69.23)	(Z)-Hex-3-en-1-yl acetate	2.71	25.35	4.23	36.62	36.62
	(E)-β-Ocimene	2.06	17.81	3.97	25.72	62.34
	(E)-4,8-dimethylnona-1,3,7-triene	1.50	10.78	2.49	15.57	77.91
	Linalool	0.62	4.08	1.59	5.90	83.81
	Terpinen-4-ol	0.37	2.24	2.04	3.24	87.05
	(Z)-β-Ocimene	0.40	2.10	1.95	3.03	90.08
E. natalensis En (64.83)	(Z)-Hex-3-en-1-yl acetate	2.49	15.27	2.48	23.56	23.56
	(E)-β-Ocimene	2.14	13.53	3.52	20.87	44.43
	(E)-4,8-dimethylnona-1,3,7-triene	1.73	10.08	2.71	15.55	59.98
	Linalool	1.07	5.59	1.95	8.62	68.60
	β-Caryophyllene	1.06	4.67	1.81	7.20	75.81
	(Z)-Hex-en-1-yl butyrate	0.91	3.30	1.15	5.09	80.90
	Oct-1-en-3-ol	0.65	2.86	1.90	4.41	85.32
	(E)-Hex-2-en-1-ol	0.72	2.16	0.80	3.33	88.64
	(Z)-Hex-3-en-1-yl isovalerate	0.68	1.96	0.71	3.03	91.67

Table A5. SIMPER results showing the volatile organic compounds contributing to the differences in odour profile in each pairwise comparison of the four plant species used in all odour trials (Bg Bana grass (*Pennisetum* hybrid), *Pr Pterocarpus rotundifolius*, *Gc Gymnanthemum coloratum*, and *En Euclea natalensis angustifolia)*.

Comparison [ave. dissimilarity] **Volatile organic compound**	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
***P. rotundifolius* Pr *vs.* Bana grass Bg *(Pr & Bg)* [59.47]**	Group Pr	Group Bg				
(E)-β-Ocimene	2.56	0.59	7.84	2.67	13.18	13.18
(Z)-β-Ocimene	1.09	0	4.31	4.21	7.24	20.42
1-Methylpyrrole	1.04	0	4.16	1.22	6.99	27.41
Linalool	1.18	0.18	4.01	2.11	6.74	34.15
(Z)-Hex-3-en-1-yl acetate	2.09	3.03	3.77	1.7	6.34	40.49
(E)-4,8-dimethylnona-1,3,7-triene	1.31	1.09	3.49	1.35	5.86	46.36
Indole	0.18	0.97	3.03	2.56	5.1	51.45
(E)-Hex-2-en-1-ol	0	0.58	2.16	1.37	3.63	55.08
β-Caryophyllene	0.38	0.86	2.07	1.69	3.48	58.56
(E,E)-2,6-Dimethylocta-3,5,7-triene-2-ol	0.53	0	2.03	1.5	3.41	61.97
(Z)-Hex-en-1-yl butyrate	0.54	0	1.92	0.83	3.24	65.2
Hexyl acetate	0.2	0.51	1.86	1.36	3.12	68.32
m/z: 196*,68,67,81,55,54,82	0	0.47	1.75	1.28	2.95	71.27
(Z)-4,8-Dimethylnona-1,3,7-triene	0.32	0.24	1.68	0.89	2.82	74.1
(Z)-Hex-3-en-1-ol	0.32	0.49	1.67	1.35	2.8	76.9
(Z)-Hex-3-en-1-yl isovalerate	0.41	0	1.46	1	2.45	79.35
Methyl salicylate	0.35	0.1	1.3	0.96	2.19	81.53
m/z: 152*,71,43,109,81,79,67	0.33	0	1.25	1.79	2.1	83.64
m/z: 57,70,55,41,69,42	0	0.29	1.22	1.4	2.05	85.69
m/z: 43,80,79,39,41,77,81	0.07	0.28	1.18	0.99	1.98	87.67
Oct-1-en-3-ol	0.79	0.89	0.92	1.07	1.55	89.22

m/z: 82,67,57,85,79,41,55	0.24	0	0.82	0.73	1.39	90.61
***G. coloratum* Gc vs. Bana grass Bg *(Gc & Bg)* [52.71]**	Group Gc	Group Bg				
(E)-β-Ocimene	2.06	0.59	7.25	2.12	13.76	13.76
(E)-4,8-dimethylnona-1,3,7-triene	1.5	1.09	4.71	1.38	8.93	22.69
Indole	0.18	0.97	3.85	2.53	7.29	29.99
β-Caryophyllene	0.09	0.86	3.61	2.35	6.84	36.83
Oct-1-en-3-ol	0.18	0.89	3.42	7.22	6.48	43.31
Linalool	0.62	0.18	2.84	1.79	5.4	48.71
(E)-Hex-2-en-1-ol	0	0.58	2.63	1.39	5	53.7
Hexyl acetate	0.23	0.51	2.24	1.44	4.26	57.96
(Z)-Hex-3-en-1-ol	0.23	0.49	2.17	1.49	4.11	62.07
m/z: 196*,68,67,81,55,54,82	0	0.47	2.14	1.29	4.05	66.12
(Z)-Hex-3-en-1-yl acetate	2.71	3.03	1.9	1.04	3.6	69.72
(Z)-β-Ocimene	0.4	0	1.85	1.13	3.51	73.23
(Z)-4,8-Dimethylnona-1,3,7-triene	0.27	0.24	1.82	0.74	3.46	76.68
Terpinen-4-ol	0.37	0	1.74	1.43	3.31	79.99
m/z: 57,70,55,41,69,42	0	0.29	1.52	1.39	2.89	82.89
Limonene	0.31	0	1.46	0.71	2.77	85.65
m/z: 43,80,79,39,41,77,81	0.04	0.28	1.37	0.94	2.6	88.25
(E,E)-2,6-Dimethylocta-3,5,7-triene-2-ol	0.26	0	1.16	0.75	2.2	90.45
***P. rotundifolius* Pr vs. *G. coloratum* Gc *(Pr & Gc)* [43.82]**	Group Pr	Group Gc				
1-Methylpyrrole	1.04	0	4.34	1.22	9.91	9.91
(E)-4,8-dimethylnona-1,3,7-triene	1.31	1.5	3.11	1.28	7.1	17.01
(Z)-Hex-3-en-1-yl acetate	2.09	2.71	3.1	1.42	7.07	24.08
(Z)-β-Ocimene	1.09	0.4	3.09	2.01	7.05	31.13
(E)-β-Ocimene	2.56	2.06	2.6	1.21	5.93	37.06
Oct-1-en-3-ol	0.79	0.18	2.51	1.94	5.74	42.79

Linalool	1.18	0.62	2.36	1.28	5.39	48.18
(Z)-Hex-en-1-yl butyrate	0.54	0	2	0.83	4.57	52.75
(E,E)-2,6-Dimethylocta-3,5,7-triene-2-ol	0.53	0.26	1.85	1.35	4.23	56.98
(Z)-4,8-Dimethylnona-1,3,7-triene	0.32	0.27	1.61	0.88	3.67	60.65
(Z)-Hex-3-en-1-yl isovalerate	0.41	0	1.51	1.01	3.46	64.11
Terpinen-4-ol	0	0.37	1.48	1.43	3.38	67.49
(Z)-Hex-3-en-1-ol	0.32	0.23	1.42	1.05	3.25	70.74
Methyl salicylate	0.35	0.21	1.39	1.29	3.16	73.9
m/z: 152*,71,43,109,81,79,67	0.33	0	1.3	1.8	2.97	76.87
β-Caryophyllene	0.38	0.09	1.28	1.16	2.93	79.8
Limonene	0	0.31	1.24	0.71	2.82	82.62
Hexyl acetate	0.2	0.23	1.09	0.97	2.5	85.12
m/z: 82,67,57,85,79,41,55	0.24	0	0.86	0.73	1.95	87.07
Indole	0.18	0.18	0.72	0.84	1.64	88.71
α-Farnesene	0.17	0	0.68	0.48	1.55	90.26
***E. natalensis* En vs. Bana grass Bg *(En & Bg)* [54.64]**	Group En	Group Bg				
(E)-β-Ocimene	2.14	0.59	6.28	2.2	11.49	11.49
(E)-4,8-dimethylnona-1,3,7-triene	1.73	1.09	3.91	1.32	7.16	18.66
Indole	0	0.97	3.72	3.24	6.81	25.46
Linalool	1.07	0.18	3.67	1.85	6.72	32.18
(Z)-Hex-en-1-yl butyrate	0.91	0	3.27	1.55	5.98	38.17
(Z)-Hex-3-en-1-yl isovalerate	0.68	0	2.4	1.18	4.39	42.56
(E)-Hex-2-en-1-ol	0.72	0.58	2.25	1.36	4.11	46.67
Hexyl acetate	0.24	0.51	2.2	1.5	4.02	50.69
β-Caryophyllene	1.06	0.86	2.13	1.43	3.91	54.6
(Z)-Hex-3-en-1-yl acetate	2.49	3.03	2.12	1.17	3.88	58.48
(Z)-Hex-3-en-1-ol	0	0.49	2.01	1.49	3.69	62.16
m/z: 117,91,90,65,89	0.54	0	1.95	1.09	3.58	65.74

m/z: 67,82,71,43,55,81	0.56	0	1.95	1.19	3.57	69.3
m/z: 196*,68,67,81,55,54,82	0	0.47	1.76	1.24	3.22	72.52
(Z)-4,8-Dimethylnona-1,3,7-triene	0.28	0.24	1.53	1.05	2.81	75.33
Oct-1-en-3-ol	0.65	0.89	1.37	1.05	2.5	77.83
Humulene	0.41	0	1.33	0.93	2.43	80.26
m/z: 57,70,55,41,69,42	0	0.29	1.23	1.34	2.24	82.51
m/z: 43,80,79,39,41,77,81	0	0.28	1.15	0.92	2.11	84.61
m/z: 82,67,57,85,79,41,55	0.25	0	0.81	0.73	1.48	86.09
(E)-Linalool oxide (pyranoid)	0.2	0	0.78	0.48	1.43	87.52
(E)-Hex-2-en-1-yl acetate	0.3	0	0.73	0.37	1.34	88.85
(E,E)-Hepta-2,4-dienal	0	0.18	0.7	4.62	1.28	90.13
***E. natalensis* En vs. *P. rotundifolius* Pr *(En & Pr)* [45.78]**	Group En	Group Pr				
1-Methylpyrrole	0	1.04	3.61	1.2	7.89	7.89
(Z)-β-Ocimene	0.16	1.09	3.19	2.5	6.97	14.86
(Z)-Hex-en-1-yl butyrate	0.91	0.54	2.52	1.31	5.51	20.37
β-Caryophyllene	1.06	0.38	2.44	1.51	5.33	25.7
(Z)-Hex-3-en-1-yl acetate	2.49	2.09	2.43	1.46	5.3	31
(E)-4,8-dimethylnona-1,3,7-triene	1.73	1.31	2.34	1.27	5.1	36.1
(E)-Hex-2-en-1-ol	0.72	0	2.29	1.29	5.01	41.11
(Z)-Hex-3-en-1-yl isovalerate	0.68	0.41	1.96	1.27	4.28	45.39
(E,E)-2,6-Dimethylocta-3,5,7-triene-2-ol	0	0.53	1.77	1.46	3.86	49.26
(E)-β-Ocimene	2.14	2.56	1.74	1.57	3.8	53.06
m/z: 67,82,71,43,55,81	0.56	0	1.72	1.2	3.75	56.81
m/z: 117,91,90,65,89	0.54	0	1.71	1.1	3.74	60.55
Linalool	1.07	1.18	1.49	1.08	3.26	63.81
Methyl salicylate	0.16	0.35	1.28	1	2.8	66.61
Oct-1-en-3-ol	0.65	0.79	1.23	1.02	2.68	69.3
Humulene	0.41	0	1.18	0.94	2.58	71.88

m/z: 152*,71,43,109,81,79,67	0	0.33	1.09	1.71	2.39	74.26
(Z)-4,8-Dimethylnona-1,3,7-triene	0.28	0.32	1.06	0.87	2.31	76.58
m/z: 82,67,57,85,79,41,55	0.25	0.24	1.04	1	2.28	78.85
(Z)-Hex-3-en-1-ol	0	0.32	0.99	0.85	2.17	81.02
Hexyl acetate	0.24	0.2	0.95	0.84	2.08	83.1
α-Farnesene	0.15	0.17	0.8	0.65	1.75	84.85
(E)-Linalool oxide (pyranoid)	0.2	0	0.68	0.48	1.48	86.33
(E)-Hex-2-en-1-yl acetate	0.3	0	0.67	0.37	1.46	87.79
Indole	0	0.18	0.6	1.6	1.3	89.1
Hexan-1-ol	0.23	0	0.56	0.51	1.22	90.31
***E. natalensis* En vs. *G. coloratum* Gc *(En & Gc)* [45.93]**	Group En	Group Gc				
β-Caryophyllene	1.06	0.09	3.84	1.87	8.36	8.36
(Z)-Hex-en-1-yl butyrate	0.91	0	3.4	1.56	7.41	15.77
(E)-4,8-dimethylnona-1,3,7-triene	1.73	1.5	3.07	1.54	6.68	22.44
(E)-Hex-2-en-1-ol	0.72	0	2.73	1.29	5.95	28.4
(Z)-Hex-3-en-1-yl isovalerate	0.68	0	2.49	1.18	5.43	33.83
Linalool	1.07	0.62	2.38	1.52	5.18	39.01
(Z)-Hex-3-en-1-yl acetate	2.49	2.71	2.04	1.17	4.44	43.44
m/z: 117,91,90,65,89	0.54	0	2.04	1.09	4.43	47.88
m/z: 67,82,71,43,55,81	0.56	0	2.02	1.2	4.41	52.28
(E)-β-Ocimene	2.14	2.06	1.79	1.13	3.91	56.19
Oct-1-en-3-ol	0.65	0.18	1.79	1.4	3.89	60.08
Terpinen-4-ol	0	0.37	1.49	1.37	3.24	63.31
(Z)-4,8-Dimethylnona-1,3,7-triene	0.28	0.27	1.46	1.08	3.18	66.49
Humulene	0.41	0	1.38	0.94	3	69.49
(Z)-β-Ocimene	0.16	0.4	1.33	0.92	2.9	72.39
Hexyl acetate	0.24	0.23	1.26	0.88	2.74	75.14
Limonene	0	0.31	1.24	0.7	2.7	77.84

Methyl salicylate	0.16	0.21	1.1	1.15	2.39	80.23
(E)-Linalool oxide (pyranoid)	0.2	0.13	1.09	0.63	2.37	82.61
(E,E)-2,6-Dimethylocta-3,5,7-triene-2-ol	0	0.26	1	0.74	2.17	84.78
(Z)-Hex-3-en-1-ol	0	0.23	0.92	0.67	1.99	86.77
m/z: 82,67,57,85,79,41,55	0.25	0	0.84	0.74	1.82	88.59
(E)-Hex-2-en-1-yl acetate	0.3	0	0.75	0.38	1.63	90.22

Table A6. ANOSIM results for Trial 3 comparing odour profiles from single species versus dual samples (Bana grass Bg, *P. rotundifolius* Pr, *G. coloratum* Gc, and *E. natalensis* En) used in testing the effect of simple background odour and illustrated as nMDS plots in Figure A1.

Figure A1	Global R	*P*	Post-hoc pairwise comparison
(a)	0.639	0.001	Bg[a] *vs* **Gc**[b] *vs* (**Bg & Gc**)[b]
(b)	0.608	0.001	Bg[a] *vs* **En**[b] *vs* (**Bg & En**)[b]
(c)	0.493	0.001	Pr[a] *vs* **Gc**[b] *vs* (**Pr & Gc**)[a]
(d)	0.532	0.001	Pr[a] *vs* **En**[b] *vs* (**Pr & En**)[c]

For the post-hoc pairwise comparisons, different superscripts (a, b, c) indicate significant differences between pairs, and samples in bold were those offered as pairs to the elephants.

Table A7. ANOSIM results comparing odour profiles from single species versus complex (Trial 4) or strong green leaf volatile (Trial 5) background odour samples (Bana grass Bg, *P. rotundifolius* Pr, *G. coloratum* Gc, *E. natalensis* En, and (Z)-hex-3-en-1-yl acetate green leaf volatile GLV), illustrated as nMDS plots in Figures A2 and A3.

Trial	Figure	Global R	*P*	Post-hoc pairwise comparison
4	A2a	0.677	0.001	Bg^{a} *vs* Gc^{b} *vs* En^{c} vs (Bg & Gc & En)^{d}
4	A2b	0.566	0.001	Pr^{a} *vs* Gc^{b} *vs* En^{c} vs (Pr & Gc & En)^{bd}
5	A3	0.656	0.001	Pr^{a} *vs* Gc^{b} *vs* (Pr & GLV)^{c} *vs* (Gc & GLV)^{bc}

For the post-hoc pairwise comparisons, different superscripts (a, b, c) indicate significant differences between pairs.

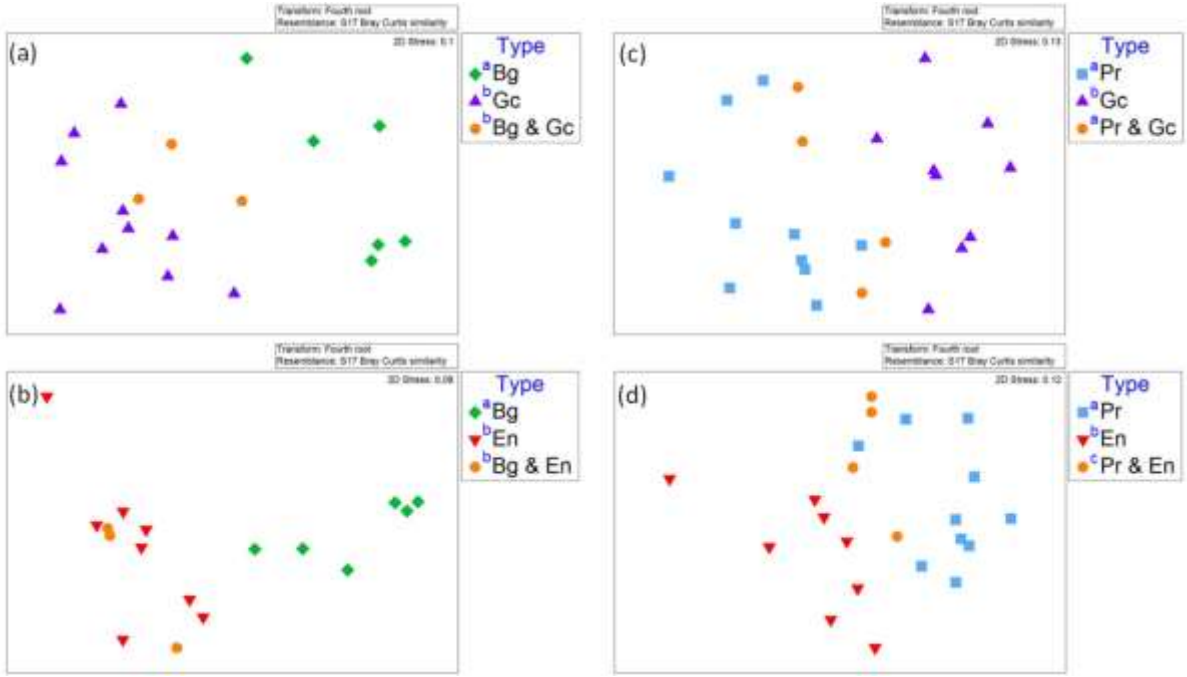

Figure A1. Trial 3 nMDS plot of the odour profile of (a) Bana grass (Bg) alone, *G. coloratum* (Gc) alone, and both species together (Bg & Gc); (b) Bana grass (Bg) alone, *E. natalensis* (En) alone, and both species together (Bg & En); (c) *P. rotundifolius* (Pr) alone, *G. coloratum* (Gc) alone, and of both species together (Pr & Gc); *P. rotundifolius* (Pr) alone, *E. natalensis* (En) alone, and of both species together (Pr & En). Different superscripts are significantly different.

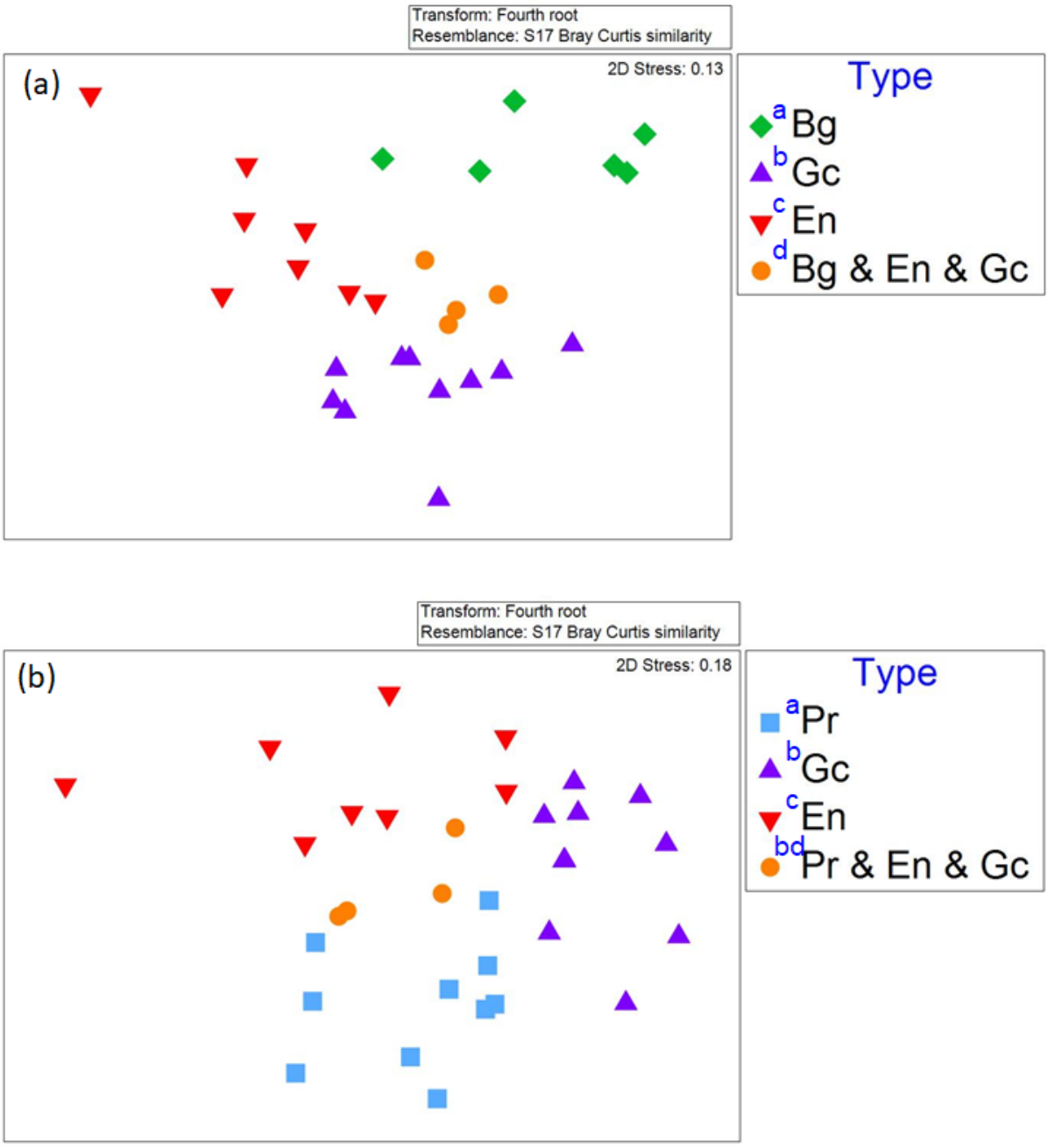

Figure A2. Trial 4 nMDS plot of the odour profile of (a) Bana grass (Bg) alone, *G. coloratum* (Gc) alone, *E. natalensis* (En) alone, and of all three species together (Bg & En & Gc); (b) *P. rotundifolius* (Pr) alone, *G. coloratum* (Gc) alone, *E. natalensis* (En) alone, and of all three species together (Pr & En & Gc). Different superscripts are significantly different.

Figure A3. Trial 5 nMDS plot of the odour profile of *P. rotundifolius* (Pr) alone, *G. coloratum* (Gc) alone, *P. rotundifolius* with background odour of the green leaf volatile (Pr & GLV), and *G. coloratum* with background odour of the green leaf volatile (Gc & GLV). Different superscripts are significantly different.