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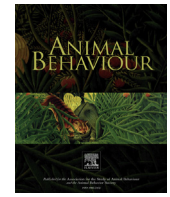

African elephants use plant odours to make foraging decisions across multiple spatial scales

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Mammalian herbivores are known to be extremely selective when foraging, but little is known about the mechanisms governing the selection of patches and, at a finer scale, individual plants. Visual examination and direct sampling of the vegetation have previously been suggested, but olfactory cues have seldom been considered. We examined the use of olfactory cues by foraging African elephants, *Loxodonta africana*, and asked whether they use plant odours to select specific patches or plants when making feeding decisions. Scent-based choice experiments between various preferred and nonpreferred plants were conducted across two spatial scales (between plants and between patches). We used coupled gas chromatography–mass spectrometry (GC–MS) analysis of headspace extracts of volatile organic compounds emitted by the different plant species to explore similarities among the overall odour profiles of each species. We found that elephants selected their preferred plant species across both spatial scales, probably using differences in plant odour profiles. The ability to differentiate between plant odours allowed elephants to reduce their search time by targeting preferred plant species both within a feeding station and between patches. This suggests that olfactory cues probably play an important role in driving herbivore foraging decisions across multiple spatial scales.

Mammalian herbivores make a vast number of foraging decisions across a broad range of spatial scales (Senft et al., 1987). At a small scale, these herbivores can take thousands of bites per day (Illius & Gordon, 1990). At larger scales, they can move across a number of plant communities on a daily basis (Senft et al., 1987), while also strategically moving around their environment on a seasonal basis (Shrader, Bell, Bertolli, & Ward, 2012). Thus, herbivores are faced with a dynamic foraging environment, which they need to navigate effectively. Ultimately, both small- and large-scale movements across the landscape are driven by foraging decisions, with the final goal of maximizing nutritional intake rates (Morgan, Hurly, Martin, & Healy, 2016; Owen-Smith, Fryxell, & Merrill, 2010; Senft et al., 1987; Shipley, 2007). However, a key question that remains unanswered is, what cues do herbivores use to make foraging decisions across these different scales?

Across a landscape, the abundance and distribution of plants vary spatially and, to a lesser extent, temporally (Klaassen, Nolet, van Gils, & Bauer, 2006; Ward, 1992, 2010; Wilmshurst, Fryxell, & Hudson, 1995). Plant species and individuals within a species can vary in nutritional composition and defence investment (Coley, Bryant, & Chapin III, 1985; Harborne, 1991). Nutritional and structural composition can be beneficial (e.g. crude protein, digestibility) and detrimental (e.g. fibre, lignin), while investment in defences can be chemical (e.g. secondary metabolites, such as tannins, terpenes and alkaloids; Freeland & Janzen, 1974; Rhoades, 1979; Bell, 2012) or physical (Kariñho-Betancourt, Agrawal, Halitschke, & Núñez-Farfán, 2015; Ward, Shrestha, & Golan-Goldhirsh, 2012). The differences in nutritional and structural composition are frequently correlated with the dietary preference for a plant species (Barton & Koricheva, 2010; Cooper & Owen-Smith, 1985; Shrader et al., 2012).

While foraging, herbivores must locate preferred food, which can be costly. Moving from patch to patch at random would probably increase search time and energy loss associated with travelling between patches compared to travelling in more directed movements (Charnov, 1976; Owen-Smith et al., 2010; Ward & Saltz, 1994). Thus, herbivores should make informed decisions about how and where to feed. Moreover, they should

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forage in a manner that maximizes their nutritional intake and minimizes travel costs (Houston & McNamara, 2014; Owen-Smith et al., 2010; Pyke, Pulliam, & Charnov, 1977). However, when faced with imperfect knowledge about the abundance and distribution of resources, what mechanisms do herbivores use to reduce search time and thus improve foraging choices and, ultimately, energy gain?

One way herbivores could do this is by continuously sampling forage to update information on nutritional quality (Krebs & McCleery, 1984; Ruedenauer, Spaethe, & Leonhardt, 2016). However, to obtain adequate information on a wide range of plant species, herbivores would need to sample large portions of the landscape throughout the year, which could result in increased travel costs. A second option would be to use visual cues. However, poor visual acuity and colour detection among herbivore species (Entsu, Dohi, & Yamada, 1992; Jacobs, Deegan, & Neitz, 1998; Piggins & Phillips, 1996) probably limits success in making dietary selections (Rutter, Orr, Yarrow, & Champion, 2004). Moreover, visual cues can easily be obstructed by objects in the landscape, such as a preferred plant growing among a number of less preferred plants (Stutz, Banks, Dexter, & McArthur, 2015).

Another option is for herbivores to use odours (volatile organic compounds: VOCs), which are emitted by all plants (Baluska & Ninkovic, 2010; Illius & Gordon, 1993). This has been well studied in insects (see: Bell, 1990; Raguso, 2008). However, the degree to which mammalian herbivores use odours when foraging is largely unknown (Bedoya-Pérez, Isler, Banks, & McArthur, 2014a; Pietrzykowski, McArthur, Fitzgerald, & Goodwin, 2003; Provenza & Balph, 1987).

Green leaves produce a variety of different volatiles including various aliphatics (especially green leaf volatiles) and terpenoids (including both monoterpenes and sesquiterpenes; Peñuelas & Llusià, 2004). These compounds are known to play various roles in plant signalling and defence but their importance for interactions with mammalian herbivores is not well explored (Bedoya-Pérez et al., 2014a). Furthermore, plant odours could be linked to preference for a particular item as a result of a conditioned response to past postingestive consequences (Villalba, Provenza, Catanese, & Distel, 2015). For example, several studies have found that mammalian herbivores have learned to avoid certain plants due to negative postingestive feedback stemming from plant secondary metabolites (Bedoya-Pérez et al., 2014a; Kyriazakis, Anderson, & Duncan, 1998; Provenza & Balph, 1987; Provenza et al., 1990).

Owing to the nature of VOCs that comprise odour profiles, plant odour can probably be detected from much greater distances than visual cues, and can pass through visually obstructing barriers (Bell, 2012; Stutz et al., 2015). While odour has the potential to be directed by the wind, and can be affected by temperature and light (Niinemets, Loreto, & Reichstein, 2004), it can still be a useful tool for herbivores to detect preferred plant species across multiple spatial scales (Bell, 2012). Because odours can be emitted from distant patches, the use of plant odours by herbivores could reduce search time and energy expenditure while foraging (Bell, 2012).

Several recent studies (Finnerty, Stutz, Price, Banks, & McArthur, 2017; Stutz, Banks, Proschogo, & McArthur, 2016; Stutz, Croak, Proschogo, Banks, & McArthur, 2018) have found that swamp wallabies, *Wallabia bicolor*, use a combination of visual and olfactory cues to locate *Eucalyptus* seedlings from which to feed. These studies have focused on seedlings of the same species that have either differing nutritional qualities or varying levels of concealment (both visual and olfactory). Results indicate that leaf odour influences wallaby foraging behaviour, facilitating nonrandom searching for food (Stutz et al., 2016, 2018). Yet, a key question not answered by these studies was whether mammalian herbivores use odour to differentiate between preferred and nonpreferred plant species.

To explore the degree to which mammalian herbivores use plant odours to make foraging decisions across different spatial scales, we focused on the foraging of African elephants, *Loxodonta africana*. Owing to their large body size, elephants have very high absolute nutritional requirements, necessitating a large number of foraging decisions within a day. Although they can tolerate a certain degree of low-quality vegetation, studies have indicated that they are extremely selective foragers (Owen-Smith & Chafota, 2012; Pretorius et al., 2012). Elephants, like many other herbivores, forage in an environment where resources are often clustered in patches (Cohen, Pastor, & Moen, 1999; Crane et al., 2016; De Knegt, Groen, Van De Vijver, Prins, & Van Langevelde, 2008). As a result, they must search and move through areas of low food availability, expending energy without gaining energy, to reach areas of higher resource availability. To forage in a nutritionally maximizing and energetically efficient manner, elephants would need to make foraging decisions that reduce search time for preferred food items within and between these clusters.

Owing to their keen sense of smell (Miller et al., 2015), we predicted that elephants are able to use plant odours to make foraging decisions. Furthermore, we predicted that the combination of plant species presented to elephants, as well as the difference in preference rank between plant species, would influence the elephant's foraging choice. We tested these predictions in choice experiments across two spatial scales. First, we tested whether elephants could use olfactory cues to locate preferred plant species at a fine spatial scale (<0.5 m), mimicking foraging decisions within a feeding station. Second, using a Y-maze to mimic between-patch choices, we determined whether elephants could make between-patch foraging decisions using plant odours at a distance beyond their body length (>7 m).

METHODS

All aspects of this research were approved by the University of KwaZulu-Natal animal ethics committee (reference number: AREC/106/015). To explore the role that odour plays in the foraging decisions of African elephants, we conducted two experiments. The first tested whether elephants used odour to make foraging decisions at the feeding station scale (<0.5 m), and the second tested whether they used it at a larger spatial scale (7 m), which we considered to be equivalent to decisions made between two patches. Both experiments eliminated eyesight and touch as variables driving elephant foraging decisions and focused solely on scent.

All experiments were completed during August 2015 at the *Adventures with Elephants* facility near Bela Bela, Limpopo Province, South Africa. For all trials, professional elephant handlers were used to ensure the comfort and safety of the elephants. We used five semitame, wild foraging, subadult individuals between 15 and 20 years old (three females, two males) for the feeding station experiment, and three of these same individuals (one female, two males) for the between-patches (Y-maze) experiment. We only used three individuals for the between-patch experiment because two of the elephants were unwilling to walk into the Y-maze. For both experiments, we were only interested in whether elephants used odour to make foraging decisions. Thus, we did not include sex as a variable in our analyses.

Plant Species

A total of 12 woody plant species were utilized in our scent-based experiments (see below). Of these 12 species, six