Evidence for ancestral olfactory sensitivity but not discrimination across two living elephant species

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Abstract:

While African savanna and Asian elephants split between 4.2-9 MYA, they are often regarded as one united group, ‘elephants,’ even in the scientific literature. This is concerning, as while both are keystone species in their respective habitats, each face different environmental pressures and have rarely been compared experimentally. Savanna elephants must locate resources that vary spatially and temporally across patchy savannas, while Asian elephants do so within dense forests containing high biodiversity. Both species use olfaction to guide decision-making, however, considering their ecologies, we hypothesize that their olfactory abilities differ. Thus, we investigated the sensitivity and detection limits of both savanna and Asian elephants’ olfactory systems, as well as changes in these limits in a complex odour environment using two odour-based choice experiments. While both species correctly detected a target odour – savanna elephants detected it at 50 parts per million (ppm) and Asian elephants at 100 ppm – only the savanna elephants’ limit changed (to 1,000 ppm) in the complex odour environment. Our findings suggest that these species have similar olfactory sensitivity, which probably evolved in a shared ancestor, but divergent olfactory discrimination abilities, which are likely a result of variation in both the density and species diversity of their habitats.

Keywords: Cognition, Evolutionary Ecology, Foraging Ecology, Odour, Olfaction, Sensory Abilities, Volatile Organic Compounds

Introduction

Phenotypic comparisons amongst closely-related and relatively recently-diverged species [e.g., chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*): 1] are often made to understand the role that environmental pressures play in shaping differences in behaviour [2, 3]. While these comparisons are prolific in the literature, there has been little attention paid to the behavioural differences between Asian and African elephants, which are morphologically similar, but have a more distant phylogenetic split than chimpanzees and bonobos. African and Asian elephants genetically diverged 4.2-9 MYA [4]. Since then, African populations have split into the extant savanna elephants (*Loxodonta africana*), and forest elephants (*Loxodonta cyclotis*), while Eurasian populations diverged into the extant Asian elephant (*Elephas maximus*), and extinct mammoth (*Mammuthus primigenius*) [4]. Asian elephants and savanna elephants are often considered to be analogous to each other due to their broadly similar morphology, comparable foraging habits, and their roles as ecosystem engineers and keystone species in their respective habitats [5, 6]. However, what is often overlooked is that these species face markedly different physical and social environmental pressures, which may play a key role in shaping differences in their behaviour.

Although both species fill comparable niches in their respective ecosystems [6], there are some key ecological differences between their environments. Savanna elephants live in a range of habitats, but are primarily found in mesic to arid woodlands (i.e., land covered with woody vegetation) and savannas (i.e., areas characterized by a mosaic of trees and grasses) [7]. While Asian elephants also inhabit a variety of habitats, including forests, shrubland, and grassland, they are considered to be forest edge specialists with a preference for a combination of natural forest and secondary vegetation [8-10]. On average, the habitats that savanna elephants live in have lower quality food (Net Primary Production (NPP) <700 g C m^{-2}) compared to the habitats where Asian elephants occur (<1200 g C m^{-2}) [11]. Another key difference among their habitats is the level of floristic diversity. The ecoregions where savanna elephants occur have ~500-3000 species of vascular plants, while the ecoregions where Asian elephants occur include between 1000-5000 species [12], which represent vastly different numbers of potential food options. Thus, Asian elephants need to find key food resources in floristically more complex environments compared to savanna elephants. Moreover, food resources are not evenly distributed across the landscape and are also subject to dramatic changes in availability as a result of seasonality [13, 14]. This is particularly important for savanna elephants that often occur in ecosystems which are characterized by pronounced wet and dry seasons [13, 15]. During the dry season in particular, high-quality food resources are less available than they are in the wet season and are often spread across the landscape mixed in with lower-quality resources [16, 17].

With respect to foraging behaviour, although both species are considered to be generalist herbivores, they do exhibit a degree of selectivity [18-21]. Being megaherbivores (species >1000kg in mass), their large body size results in both species having high absolute intake rate requirements [e.g., >150kg of vegetation per day: 22, 23]. Given this, locating resources that vary in quality and quantity across the landscape has important implications for shaping elephant behaviour. For example, savanna elephants have much larger maximum home range sizes (e.g., 3,700 km^2) than Asian elephants (e.g., 1000 km^2) [24, 25]. This difference is largely a result of differences in resource availability (e.g., plant productivity) and human activity [8, 24, 26, 27]. Ultimately, the two elephant species must locate resources in habitats that differ dramatically in resource availability, quality, and spatial distribution.

To guide their behavioural decision-making within these heterogeneous environments, both elephant species can use cues gathered from their environment. Numerous studies have reported the importance of olfactory cues for social communication and food selection in Asian and savanna elephants, and that their sense of smell may play an important role in physical and social decision-making [28-31]. While olfactory behavioural choice experiments have been performed with both savanna and Asian elephants [32-38], there have been no studies comparing the olfactory abilities of the two species. This is surprising considering the importance of olfaction for both species of elephants. Thus, for the first time, we investigated how shared ancestry and environmental conditions may have shaped the sensitivity of both the African savanna and Asian elephants' olfactory systems and the limit of their capacity for olfactory detection, as well as whether those limits fluctuated in a complex odour environment. To do this, we used two odour-based experiments. The first experiment aimed to determine a limit for olfactory detection under controlled conditions, while the second experiment aimed to determine whether this threshold varied when a masking odour was present, to mimic conditions of wild foraging in a complex odour environment (i.e., floristically diverse environments).

For the ‘detection threshold’ experiment (Experiment 1), we hypothesized that savanna elephants would perform better than Asian elephants because savanna elephants must locate resources that are more patchily distributed across their habitats than those in which Asian elephants live. However, it is possible that both species have similar overall detection abilities, which is likely rooted in their shared evolutionary history. For the ‘detection in complex environments’ experiment (Experiment 2), we hypothesized that Asian elephants may out-perform savanna elephants because they must locate target food resources that are mixed into a high diversity of other plants in structurally dense habitats. This would result in more complex odour environments, compared to those in which savanna elephants live. Alternatively, the ability to detect target food items in complex odour environments may be similar for both species due to their shared ancestry. Any differences in olfactory discrimination between the two species are likely the result of the different ecological and socio-environmental factors each species faces in their respective habitat.

Methods

Using similar procedures conducted in previous research on elephant olfaction [e.g., 31, 32, 33, 36-39], we aimed to compare the olfactory capabilities of savanna and Asian elephants with respect to their abilities to detect differing emissions of *cis-3-Hexenyl acetate* (Sigma-Aldrich, natural ≥95% FG, CAS 3681-71-8), a common green leaf volatile found in the elephants’ food items [21, 33]. To do this, we conducted two odour-based object choice experiments. In the first experiment, we aimed to test the threshold detection ability of Asian and savanna elephants using serial dilutions of *cis-3-Hexenyl acetate* (Table 1). In the second experiment, we aimed to understand how this threshold detection varied when a masking odour was present, to mimic conditions of foraging in a complex odour environment. The range of concentrations of *cis-3-Hexenyl acetate* was based on previous research that has shown Asian elephants can successfully detect and discriminate a target odour from 1,000,000 ppm down to 10,000 ppm [30, 40]. Both of our experiments were run in the same manner; however, an additional odour was added to each bucket in a separate vial to act as a masking odour to increase the complexity (noise) of the background odour for the second experiment (see below).

The experiments were conducted with savanna elephants in September, 2019 at the Adventures with Elephants facility near Bela Bela, Limpopo Province, South Africa. For all trials, professional elephant handlers were present to ensure the comfort and safety of the elephants. We used five semi-tame, wild foraging, adult individuals between 20 and 25 years old (three females, two males). The experiments with Asian elephants were conducted between October 2020 and July 2021 at the Rosamond Gifford Zoo in Syracuse, NY, USA. We studied five resident elephants between 24 and 53 years old (five females). Both experiments for the savanna elephants were conducted in a free-contact environment (as pictured in Figure 1), with handlers holding buckets on a stationary table. However, a protected-contact testing procedure was used when testing the Asian elephants, following the zoo's elephant husbandry and handling guidelines (Figure 1). This protected-contact procedure followed Plotnik et al. [32], which used a sliding table to present the elephants with the buckets.

Ethics Statement

This research was reviewed and approved by both elephant facilities (Adventures with Elephants in South Africa, and the Rosamond Gifford Zoo in New York, USA) and approved by the following ethics committees prior to data collection: Duke IACUC (#A248-18-10) for the savanna elephants, and the Hunter College IACUC (JP-Categorization Elephants 3/22) for the Asian elephants.

Table 1. Serial dilutions of *cis-3-Hexenyl acetate* used in both experiments represented by ppm of *cis-3-Hexenyl acetate* suspended in liquid paraffin.

Treatment	Ppm
A	100,000
B	50,000
C	10,000
D	5,000
E	1,000
F	500
G	100
H	50
I	10
J	5

The Asian and savanna elephants in our study were tested using the same basic experimental setup for both experiments. Similar to prior studies [e.g., 31, 32, 33, 36, 38, 39], we presented the elephants with a binary choice using buckets in which either the target odour or control odour were hidden (as well as the addition of the masking odour in the case of Experiment 2). The buckets were clear 6.15 L plastic totes, measuring 29.2 cm X 21.5 cm X 16.5 cm with latching lids. The lids had 18 holes drilled into the top to allow airflow. Holes were drilled in a rectangular grid fashion across a 120 cm^2 portion of the lid. In the savanna elephant tests, handlers held the buckets on a stationary table, while in the Asian elephant tests, the buckets were secured to the table by nesting them inside a second bucket that was bolted to the rolling table (Figure 1). The bucket bolted to the table acted simply as a brace and there was no hindrance to air flow for the buckets nested within them in which the odorants were placed. To avoid any selection bias based on the handlers holding the buckets in place for the savanna elephant experiments, handlers were rotated randomly. To ensure that each elephant did not observe the experimental set-up before each trial began, a professional handler instructed the elephants to face away (180°) from the testing arena before buckets were presented; in this position, it was impossible for the elephants to see the placement of the bins. Once the vials holding the target and control odours (and masking odour in the case of Experiment 2) were placed inside each bin, the bins were arranged side-by-side on a table. The elephant was then instructed to turn, face forward, and to "smell" the bins. At this point, the elephant stepped up to the bins and placed its trunk on each holey lid and inhaled the odours from each bucket. As per a number of previous studies [31-33, 36, 37, 39], each elephant was able to smell or touch each bucket when presented, but could not open or reach inside them. The elephants had 10 seconds to touch and smell both buckets on the table. If the elephants smelled both buckets in 10 seconds, the elephants and the buckets were separated at the 10 s mark and then buckets were re-presented after 3 s so that the elephants could make a choice. In the case of the savanna elephants, we instructed them to remove their trunks from the buckets at the 10-second mark, however, due to the protected-contact requirements associated with the Asian elephants' environment, we rolled the table with the buckets away from the elephants instead of instructing them to remove their trunks. Each elephant indicated which bucket contained the target odour by touching or tapping on it. After the elephant made its choice, it was rewarded with a food reward if correct. As per

[37], the lids and buckets were cleaned with a wet cloth in between each trial to ensure that the elephants could not use mucus deposited during previous trials.

For our second experiment, we investigated the use of olfaction during foraging in a complex odour environment, and used 1-Nonanol Sigma-Aldrich, purum ≥98%, CAS 143-08-8, as a masking odour. Nonanol is commonly found in the environment, but is not something that has a known positive or negative association for either species of elephants. The concentration of this odour remained constant throughout the experiment. Its concentration was set to 100,000 ppm, which is relatively high [41], to determine how well each species can detect weaker odours when there are potentially highly concentrated odorants in the environment.

Training

Prior to running the experiments, both Asian and savanna elephants were trained to select a high concentration of *cis-3-Hexenyl acetate* hidden inside a bucket. To teach the elephants the nuances of a behavioural choice experiment, they were initially trained to detect a food item in one of the buckets. When the elephants chose the bucket containing the food item ≥8/10 times in two consecutive sessions of ten trials, they moved on to training to detect *cis-3-Hexenyl acetate*. Chemical detection training consisted of the same setup as testing, although the buckets were transparent, visually identical, and contained either a vial of 150,000 ppm *cis-3-Hexenyl acetate*, or the same suspension fluid (i.e., liquid paraffin) with no target odor. Once the elephants successfully chose the bucket containing the target odour ≥8/10 times in three consecutive sessions of ten trials each, they moved onto experimental trials. This rigorous training regime ensured that the elephants were motivated to participate and delivered consistent results in detecting olfactory information. The training also allowed the elephants to learn a) the task procedure to select one of two buckets after first being presented with two options and then having to make a choice, and b) to locate a 150,000 ppm concentrated solution before we started testing them on more diluted solutions.

Fig. 1. Panel (A) depicts the testing setup conducted with free-contact savanna elephants while (B) shows the testing setup conducted with Asian elephants in protected contact. Free contact allows for direct interaction with the elephants; protected contact means a barrier exists between humans and the elephants. Panel (C) shows an example of the testing bucket in which a vial of either the target odour or control odour is hidden and (D) illustrates an Asian elephant smelling through the holes in the lid during the experimental procedure.

Testing

For both experiments, each elephant was tested six times per session, covering the 10 different concentrations of the target odour over the course of the study, totalling 20 sessions per elephant. Only one concentration was presented per session, but the concentrations were presented in a random order over the course of the study. For both groups of elephants, no more than two concentrations were tested per day (i.e., two sessions). We used two testing times per day: one at 9 am and the other at 12 pm. Each elephant had a minimum gap of 3 h between testing sessions. The two experiments were conducted with the savanna elephants over a 10-day period and over the course of 30 days for the Asian elephants. For the savanna elephants, one individual (elephant #2) refused to participate in two sets of trials for experiment 1 (i.e., 100,000 ppm and 5,000 ppm), and two sets of trials for experiment 2 (i.e., 100,000 ppm and 10,000 ppm). To ensure hunger levels did not influence diet selection, the elephants were able to forage for one hour prior to testing.

Statistical Models

For both experiments, the elephants were tested against 10 different concentrations of the target odour six times. The results from all trials from both experiments were analysed using generalized estimating equations (GEEs). We treated individual elephants as the subjects for repeated measures in GEEs because of potential non-independence of our data, which could stem from an individual's growing experience over repeated trials. Furthermore, GEEs use a population-level approach based on a quasi-likelihood function, which delivers population-averaged estimates of the parameters. In addition, the coefficients of GEE regressions are marginal effects (i.e., the effects average across all the subjects in the data [42]). Thus, in our case, GEEs modelled the number of times the elephants made the correct choice (i.e., selected the bucket with the target odour) compared to an expected 50% distribution expected under random selection for a given choice. Our model used an exchangeable correlation matrix and a binomial error distribution with a logit link function. We ran separate models for each species and each experiment. To explore whether detection varied across treatments, we considered the chemical concentration (treatment) as the independent variable, and the successful detection of the target odour as the dependent variable.

Results

Experiment 1

The concentration of *cis-3-Hexenyl acetate* presented to both savanna and Asian elephants significantly influenced their choice (savanna: GEE: $\chi 2$= 53.291, P<0.0001, Asian: GEE: $\chi 2$=101.558, P<0.000). Across 7 of the 10 concentrations, both savanna and Asian elephants correctly detected *cis-3-Hexenyl acetate* (Figure 2a and b). Both savanna and Asian elephants were unable to detect the target odour in the treatments with the weakest concentrations of the target odour—10 ppm and 5 ppm respectively. However, the two species differed with respect to the third treatment in which they were unable to discern the target odour. Savanna elephants were unable to significantly identify the target odour at 100 ppm, but were able to detect the target odour at 50 ppm, which is one treatment level more diluted than 100 ppm. By contrast, Asian elephants were unable to locate the target odour at 50 ppm. While the significant detection for this third treatment differed between the two species, the threshold drop-off points in detection occurred in treatments that were within the same magnitude of concentration (i.e., 50 ppm is half the concentration of 100 ppm).

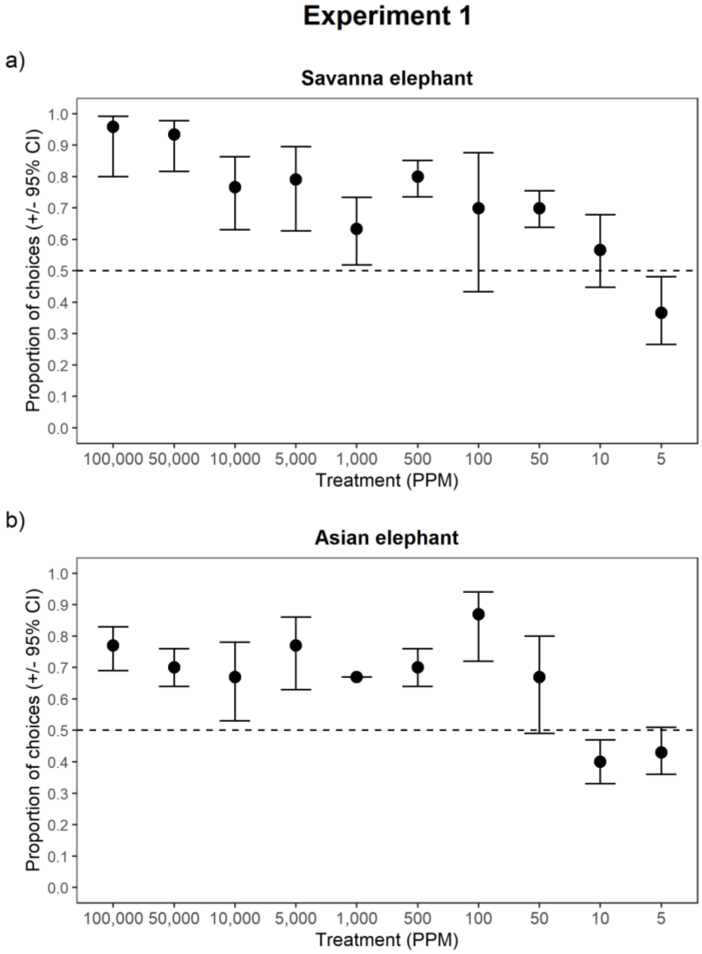

Fig. 2. Proportion of choices in which the target odour was selected as a function of diminishing concentration (ppm) of the target odour. Panel (a) reflects savanna elephant detection abilities while panel (b) reflects Asian elephant detection abilities. Marginal means (±95% Confidence Intervals) of the proportion of selection of a given treatment are plotted. If there is no overlap of the 95% CI with the 0.5 expectation (i.e., random selection), this indicates significant selection

for the target odour. If there is overlap with the 0.5 expectation (i.e., random selection), this indicates no significant selection for the target odour.

Experiment 2

The concentration of *cis-3-Hexenyl acetate* presented to both savanna and Asian elephants when in the presence of a masking odour significantly influenced detection (savanna: GEE: χ^2= 50.273, *P*<0.0001, Asian: GEE: χ^2 910.313, *P*<0.0001). Savanna elephants were able to detect the target odour in 5/10 treatments, while Asian elephants maintained their ability to detect the target odour in 7/10 treatments (Figure 3a and b). The detection threshold for savanna elephants was 1000 ppm, while for Asian elephants it remained 100 ppm.

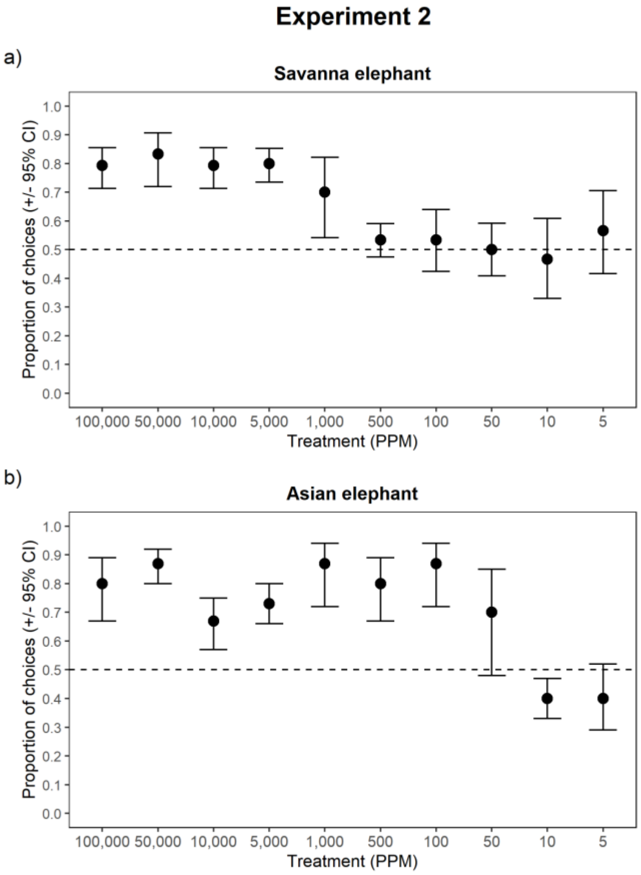

Fig. 3. Proportion of choices in which the target odour was selected as a function of diminishing concentration (ppm) of the target odour in the presence of a masking odour. Panel (a) reflects savanna elephant detection abilities while panel (b) reflects Asian elephant detection abilities. Marginal means (±95% Confidence Intervals) of the proportion of selection of a given treatment

are plotted. If there is no overlap of the 95% CI with the 0.5 expectation (i.e., random selection), this indicates significant selection for the target odour. If there is overlap with the 0.5 expectation (i.e., random selection), this indicates no significant selection for the target odour.

Discussion

While savanna and Asian elephants have historically been categorized as similar species both morphologically and behaviourally, our study is the first, to our knowledge, to make a direct comparison between their olfactory sensory abilities. We have shown that elephants have an olfactory sensitivity limit lower than previously determined, $\geq$50 ppm for savanna elephants and $\geq$100 ppm for Asian elephants. When analysed in a complex odour environment, these limits have disparate fluctuations for each species. The addition of a complex odour environment decreased savanna elephant's sensitivity and discrimination ability for odour detection by an order of magnitude (from $\geq$50 ppm up to $\geq$1,000 ppm). The addition of a complex odour environment for Asian elephants did not impact their ability to discriminate the target odour. The similar initial sensitivity of 50 ppm and 100 ppm could be due to savanna and Asian elephant's shared ancestry. The differential results in experiment 2 could reflect their different ecological and socio-environmental situations.

Our results suggest that both savanna and Asian elephants have a sensitivity limit to their olfactory capabilities $\geq$100 ppm, which extends the lower limit for both species further than previously determined [30, 40]. This highlights the importance of olfaction as a key sense that both savanna and Asian elephants use to locate resources that vary both spatially and temporally. For all herbivores, the ability to detect a salient cue in their environment can be integral to their foraging success [43-45]. Each bite a herbivore takes represents a decision about what plant or plant part to eat [46]. Thus, olfactory cues can be a key indicator that herbivores use to inform their decisions. For species such as savanna and Asian elephants that forage for a majority of a 24-hour cycle [47], live in ecosystems containing hundreds or thousands of different species of plants (Kier et al. 2005), and consume vast quantities of vegetation [22, 23], enhanced localization can have a multiplicative benefit on the animal's time budget.

The greater the level of sensory evidence available to an animal, the faster they can decide whether to ingest a food item or not [48, 49]. Thus, enhanced detection down to 100 ppm of a target odour could provide elephants with additional olfactory evidence on which to base their foraging decisions. Plant species vary not only in their abundance, but also in their nutritional quality, and both of these factors can vary across a seasonal cycle [21, 50, 51]. Thus, for herbivorous mammals, olfaction can be a useful tool to locate and assess variable resources [33, 37, 52-57]. For example, reindeer (*Rangifer tarandus*) were able to distinguish good and poor lichen sources via olfactory cues below 90 cm of snow [43], and savanna elephants can detect differences in sugar content of fruits from marula trees, *Sclerocarya birra* [34]. Moreover, Bester et al. [37] demonstrated that savanna elephants show varied responses (i.e., neutral vs. deterrent) to differing concentrations of volatile monoterpenes that are found in the plants in their environment, indicating the importance of olfactory sensitivity for foraging decision-making. Beyond making decisions at a patch scale, herbivores also make foraging decisions at larger spatial scales [58]. For example, both swamp wallabies (*Wallabia bicolor*) and greater sage-grouse (*Centrocercus urophasianus*) use olfactory cues emitted from target plant species to locate resources across the landscape [55, 56, 59, 60]. Consequently, being able to detect 100 ppm of a target odour could help an herbivore identify important Volatile Organic Compounds (VOCs) that are further away [61, 62], particularly in seasonal environments, such as African savannas, where resource quality and quantity varies dramatically.

Target plant species can also be hidden among an array of other plant structures or within an environment with a diversity of species, making desired items difficult to locate visually. However, herbivores can use olfactory cues emitted from target species to locate them in complex odour environments [33, 55, 56]. Interestingly, when we tested whether the threshold of detection for both Asian and savanna elephants varied when a masking odour was present, we found disparate results between the two species. The presence of a masking odour did not impact the ability of Asian elephants to detect the target odour, however, its presence shifted the detection threshold for savanna elephants by an order of magnitude, whereby they could only now detect the target odour when it was 1,000 ppm instead of 100 ppm. Our results suggest that a complex odour environment does not affect the ability of Asian elephants to discriminate, while it does appear to influence the discrimination abilities of savanna elephants, which may be a result of differences in their natural history and foraging environment. Dense forests with covered canopies, where Asian elephants are naturally found [63], have between 1000 - >5000 species of vascular plants [12]. Several studies have demonstrated that forest canopies have reduced VOC diffusion [64, 65] and trap odours below the canopy [66]. This incubator effect, coupled with high vegetation cover and high species diversity that characterize the habitats where Asian elephants occur [67-69], could result in habitats with highly complex odour environments. Therefore, Asian elephants may need to be able to distinguish trace amounts of a target odour among many other odours while foraging, explaining their performance in the discrimination experiment. While both savanna and Asian elephants forage selectively [i.e., they do not eat everything that is available to them – 18, 70], it is likely that Asian elephants perform better with complex background odours compared to savanna elephants as a result of their high biodiversity, high odour complexity environment. Thus, each species' performance is likely indicative of a more adaptive fit to their environments.

Our experimental setup for both groups of elephants had two slight differences resulting from the free-contact vs. protected-contact environments in which the savanna and Asian elephants were kept, but were unlikely to have influenced our findings. The first difference in experimental procedures was the fact that the buckets presented to the Asian elephants were nested inside a bucket of the same size that was bolted to the table, while the buckets were held in place on the table by handlers when presented to the savanna elephants. This difference is unlikely to have influenced our results for a few reasons. First, airflow and accessibility to the buckets were not impacted by either method. The bucket bolted to the table in the Asian elephant experiments acted simply as a brace and did not hinder airflow to the top of the bucket in which the odorants were placed. In the case of the savanna elephants where handlers held the buckets in place, handlers never touched the target odours, could not contaminate the buckets and were rotated randomly to ensure that the elephants could not cue off of them. Moreover, all buckets in both settings were wiped down in between trials to limit differences in external odours that potentially could influence the elephants' choices. The second difference was the manner in which the elephants were presented with the buckets. The savanna elephants were instructed to walk up to the table, while the Asian elephants were presented the buckets on a table that rolled up to them. It is unlikely that this minor difference in procedure would influence the elephant's abilities to identify the target odours because they were both able to touch and interact with the buckets with their trunks for the same amount of time and in the same way.

Both experiments were run with a single group of savanna elephants (n=5) and a single group of Asian elephants (n=5). Our work is the first step towards comparing the olfactory capabilities of two distantly related elephant species. However, it is possible that some of the variability seen at 50 ppm for Asian elephants and 100 ppm for savanna elephants is a result of our relatively small sample size. This variation in individual abilities highlights the effect of an individual's choices and behaviours in shaping the pattern we see across a system. Olfactory sensitivity and discrimination accuracy can fluctuate within a subject [71], and subjects can have different baseline sensitivities, leading to a single subject's choices impacting the overall results when sample sizes are small. While cognitive studies with elephants typically have a small sample size, we recognize that more research is needed here. For example, studies that investigate a direct comparison between extant species of elephants can provide further evidence about the degree to which the species differ. In addition, future work should explore the olfactory abilities of forest elephants, which are more closely related to savanna elephants but live in environments more similar to Asian elephants.

Our findings highlight the fact that these species have similar olfactory sensitivity, which likely evolved in a shared ancestor and persisted due to both species' social and foraging needs for olfactory detection. However, our results suggest that they have divergent olfactory discrimination abilities, which are potentially a result of variation in both the woody density and the vegetation species diversity of the habitats in which the two species live. These data suggest that millions of years of independent evolution may have shaped yet unknown behavioural and physiological variation within the elephant taxon.

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