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African elephants show high levels of interest in the skulls and ivory of their own species

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An important area of biology involves investigating the origins in animals of traits that are thought of as uniquely human. One way that humans appear unique is in the importance they attach to the dead bodies of other humans, particularly those of their close kin, and the rituals that they have developed for burying them. In contrast, most animals appear to show only limited interest in the carcasses or associated remains of dead individuals of their own species. African elephants (Loxodonta africana) are unusual in that they not only give dramatic reactions to the dead bodies of other elephants, but are also reported to systematically investigate elephant bones and tusks that they encounter, and it has sometimes been suggested that they visit the bones of relatives. Here, we use systematic presentations of object arrays to demonstrate that African elephants show higher levels of interest in elephant skulls and ivory than in natural objects or the skulls of other large terrestrial mammals. However, they do not appear to specifically select the skulls of their own relatives for investigation so that visits to dead relatives probably result from a more general attraction to elephant remains.

Keywords: elephants; skulls; ivory; bones; death

1. INTRODUCTION

In contrast to humans, who attach great importance to the dead bodies of other humans (Tattersall 1998), most mammals show only passing interest in the dead remains of their own or other species. Lions are typical in this respect, briefly sniffing or licking the dead body of a con-specific which, in the case of recently killed individuals, may subsequently be eaten (Schaller 1972; Packer, C. R., personal communication). In chimpanzees (Pan troglodytes), interactions with dead social partners are more prolonged and complex than reported in other species, but here companions tend to leave the carcass when it starts to decompose significantly, and do not appear to interact with the bones once the carcass has rotted (Boesch & Boesch-Achermann 2000). In comparison, African elephants are reported not only to exhibit unusual behaviours

The electronic supplementary material is available at http://dx.doi. org/10.1098/rsbl.2005.0400 or via http://www.journals.royalsoc. ac.uk. on encountering the bodies of dead con-specifics, becoming highly agitated and investigating them with the trunk and feet, but also to pay considerable attention to the skulls, ivory and associated bones of elephants that are long dead (Douglas-Hamilton & Douglas-Hamilton 1975; Moss 1988; Spinage 1994). It has also been suggested that elephants specifically visit the bones of dead relatives (Douglas-Hamilton & Douglas-Hamilton 1975; Moss 1988; Spinage 1994). Despite being widely reported, there have been no attempts to elicit and investigate these unusual behaviours experimentally. Apparent interest in skulls and ivory may simply reflect a strong response to novel objects or a fidelity to certain routes, and the nature and specificity of elephant responses to the remains of other elephants can only be unambiguously determined using controlled experiments. Here, we use experimental presentations of object arrays to test whether elephants are indeed specifically attracted to the skulls and ivory of other elephants, and whether they show particular interest in these remains when they originate from their relatives.

2. MATERIAL AND METHODS

(a) Study population

The research was conducted in Amboseli National Park, Kenya, where long-term data on life histories have been obtained for more than 2200 individual elephants (see McComb *et al.* 2001). The primary social unit in African elephants is the female family unit, composed of adult females that are usually matrilineal relatives and their immature offspring (Moss & Poole 1983).

(b) Procedure for presentations

Between July 1998 and January, 2000, free-ranging African elephants in the study population were presented with animal skulls, ivory and natural objects to investigate: (i) whether they are attracted to elephant skulls and ivory over other objects; (ii) whether they show more interest in elephant skulls than in skulls of other large terrestrial mammals; and (iii) whether they particularly select the skulls of relatives for investigation. Controlled choice tests were achieved by presenting family units with arrays of three objects in which the location of each item in line (left, centre, right with respect to the approaching elephants) was systematically varied between trials to randomize the effects of preferences for particular positions (see figure 1*a* and see electronic supplementary material).

For each presentation a suitable family unit (or section of a family unit) was identified and a set of three objects (details of different choice sets below) was decanted from the research vehicle and placed at a distance of 25-30 m from the nearest individual in the family group. The three objects were placed in a line on the ground with 1 m separating the central object from each of its neighbours. The vehicle was then driven to a position where the trial could be observed and video-recorded.

In the first experiment an elephant skull, a piece of ivory and a piece of wood were presented to 19 different family groups (figure 1a), while in the second, 17 family groups were presented with an elephant skull, a buffalo skull and a rhinoceros skull (see electronic supplementary material). In the third experiment, each of three families that had lost their matriarch in the recent past (last 1-5 years) were presented with the choice between the skull of their own matriarch and those of the matriarchs of the other two families. All three families chose between the same three skulls, with the skull that represented the matriarch for any one family representing a non-matriarch for the other two, and each family received the choice three times, with their own matriarch's skull in each of the three possible positions in the array (see electronic supplementary material). The matriarch is the oldest female in the family unit, and plays an important role in coordinating the group's activities (McComb et al. 2001).

In the first two experiments, two different exemplars of each of the objects were used in the course of the presentations, while in experiment 3, the three objects were skulls from previous matriarchs of the JA/YA family (Jezebel), the TA family (Tuskless) and the AA family (Wartear), who had all died between 1 and 5 years before their skulls were used in choice tests. At least one week was left between different presentations to the same family. All the skulls used in the experiments were completely rotted down,

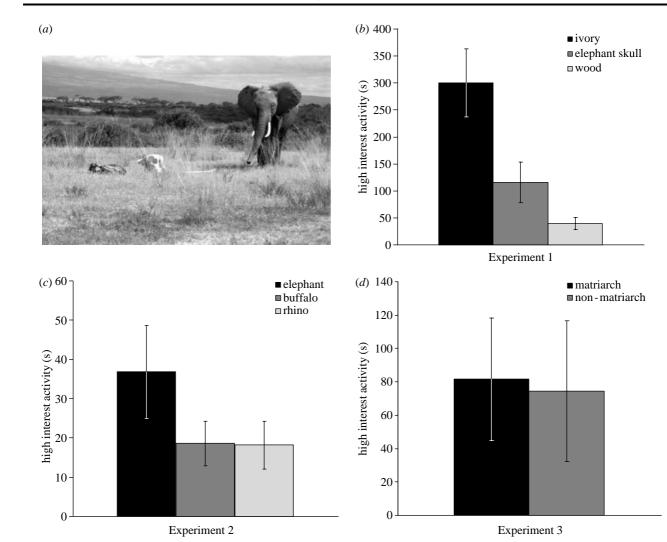


Figure 1. (a) Choice test on array of wood, elephant skull and ivory (left to right) in experiment 1. In this photo, one family member initiates approach to the object array (to be followed by others from right of frame). (b) Distribution of high interest activity in experiment 1, bars show standard errors. (c) Distribution of high interest activity in experiment 2, bars show standard errors. (d) Distribution of high interest activity in experiment 3, bars show pooled standard errors from the three families, where s.e. pooled = $\sqrt{(s.e. fam._1^2 + s.e. fam._2^2 + s.e. fam._3^2)/3}$.

so that there was no remaining flesh and the bone was bleached white by the sun. All items were washed with a solution of Teepol (which has a low number of contaminant volatiles), given two thorough rinses and air dried before and after experiments. This both controlled for any extraneous differences in scent between the objects prior to the experiments, and prevented accumulation of scent (from handling or elephant interest in particular objects) during the experiments.

(c) Behavioural responses

The elephants typically approached the objects and began investigating them by smelling and touching individual objects with their trunks and, more rarely, placing their feet lightly against particular objects and manipulating them (similar behaviours are observed during natural encounters with elephant remains, e.g. Spinage 1994). The responses of subjects to each presentation were recorded using a Sony CCD TR550E video recorder. Trials were terminated when all the individuals had finished investigating the objects and moved on, or if an individual carried an object four or more elephant lengths away from the other items. From video-recordings of their responses. we calculated the cumulative amount of time that adult group members (11 years or older) spent smelling towards an object with the trunk tip less than 1 m from it, or touching the object with the trunk (high interest activity). In addition, in the case of trials involving ivory, where placing of the foot on top of objects occurred fairly regularly, the cumulative time spent by any adult touching an item with its foot was also calculated (Foot on object). Elephants have mechanoreceptors in their feet, and foot placement on objects may enable them to gather tactile information (O'Connell-Rodwell et al. 2000)

3. RESULTS

Subjects directed significantly different amounts of high interest activity towards the three objects in the first experiment, exhibiting a strong preference for ivory over each of the other two objects and for the elephant skull over wood (figure 1b; Friedman test N=19, $\chi^2=22.81$, d.f.=2, p=<0.001; Wilcoxon Signed Ranks Test for ivory versus elephant skull: Z=3.58; p<0.001, for ivory versus wood: Z=3.70; p < 0.001, and for elephant skull versus wood Z = 3.29; p < 0.005.). In the second experiment, interest in the three types of animal skull also differed, subjects exhibiting more interest in the elephant skull than in the buffalo or rhino skulls, but not in the buffalo skull compared with the rhino skull (figure 1c; Friedman Test N=17, $\chi^2=7.12$, d.f.=2, p=<0.05; Wilcoxon Signed Ranks Test for elephant versus buffalo skull: Z=2.27; p<0.05, for elephant versus rhino skull: Z=2.56; p=0.01, and for buffalo skull versus rhino skull Z=0.25; n.s.). In the final experiment, subjects

did not direct significantly more high interest activity towards the skull of their own matriarch than towards the skulls of the two other matriarchs (figure 1*d*; Binomial test on number of trials where skull that received the most attention was own matriarch's skull: N=9, k=4, p=0.35). Due to constraints on the sample size, this experiment would be effective in demonstrating a strong preference for the correct matriarch's skull (for probabilities of success under the alternative hypothesis of 0.7, 0.8 and 0.9, power of tests would be 0.730, 0.914 and 0.992, respectively), but not a weak one (for probabilities of success under the alternative hypothesis of 0.4, 0.5, 0.6, power of tests would be 0.099, 0.254 and 0.483, respectively).

Where touching of objects with the foot was measured (experiment 1—see §2) subjects spent significantly more time with the foot placed on ivory than on the elephant skull or wood, but not on the elephant skull than on wood (Foot on object: Friedman Test N=19, $\chi^2=9.864$, d.f.=2, p=<0.01; Wilcoxon Signed Ranks Test for ivory versus elephant skull: Z=2.511; p<0.05, for ivory versus wood: Z=2.761; p<0.01 and for elephant skull versus wood Z=0.943; n.s.).

4. DISCUSSION

Our experiments cast light on why elephants are often observed interacting with the skulls and ivory of dead social companions-they appear to choose these items for investigation in preference to skulls from other animals or natural objects. Their preference for ivory was very marked, with ivory not only receiving excessive attention in comparison with wood but also being selected significantly more than the elephant skull. Subjects also placed their feet on or against the ivory significantly more often than on other objects. Interest in ivory may be enhanced because of its connection with living elephants, individuals sometimes touching the ivory of others with their trunks during social behaviour. In experiments where no ivory was present, other items in the array appeared to receive less high interest activity overall. Despite this, the elephant skull was clearly selected for attention over the buffalo and rhinoceros skulls and over the wood. It is important to note that our findings cannot be explained by the elephants simply choosing the largest, most complex objects (the object that received the most attention overall was the ivory, which is smallest in size and simplest in shape) or the most novel ones (the rarest object was the rhinoceros skull but this did not receive most attention).

Although there are suggestions in the literature that elephants selectively visit the bones of their relatives (Douglas-Hamilton & Douglas-Hamilton 1975; Moss 1988; Spinage 1994), our matriarch skulls presentations did not reveal a strong preference in experimental subjects for investigating the skull of their matriarch over skulls of unrelated females. While the sample size for this experiment was unavoidably limited to nine (three families presented with their matriarch's skull in each of the three positions in the array), reducing the power of the test, there was no evidence of the marked difference in interest in the three objects that was so clear in the first two experiments.

Reports of elephant graveyards, specific places where old elephants go to die, have been exposed as myths—where large concentrations of elephant bones have been found their occurrence can be adequately explained by hunting practices or mass die-offs during periods of drought (Moss 1988; Spinage 1994). Our results suggest that elephants may not specifically select the skulls of their own relatives for investigation, but their strong interest in the ivory and skulls of their own species means that they would be highly likely to visit the bones of relatives who die within their own home range. This is the most likely explanation for why elephants have sometimes been observed interacting with the bones of particular family members, although it remains possible that where ivory is present alongside skulls, elephants may, through tactile or olfactory cues, recognize tusks from individuals that they have been familiar with in life.

The evolutionary basis for exhibiting such intense interest in the decomposed remains of con-specifics in a non-human mammal remains unclear. While the behaviours described here obviously differ fundamentally from the attention and ritual that surround death in humans, they are unusual and noteworthy. Comparative research is now required to test systematically whether any other species show similar responses and what relationship, if any, they have to particular cognitive abilities or aspects of social behaviour.

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