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Behavioural reactions of elephants towards a dying and deceased matriarch☆

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Abstract

The extent to which elephants hold behavioural traits in common with human beings is relevant to the ethics of how we treat them. Observations show that elephants, like humans, are concerned with distressed or deceased individuals, and render assistance to the ailing and show a special interest in dead bodies of their own kind. This paper reports helping and investigative behaviour of different elephants and their families towards a dying and deceased matriarch. We make use of long-term association records, GPS tracking data and direct observations. Records made around the time of death, shows that the helping behaviour and special interest exhibited was not restricted to closely related kin. The case is made that elephants, like human beings, can show compassionate behaviour to others in distress. They have a general awareness and curiosity about death, as these behaviours are directed both towards kin and non-related individuals.

Keywords: Compassion; Recognition; Radio tracking; Association analysis

1. Introduction

Ethics requires us humans to treat animals, especially those who are sentient, as we would like to be treated ourselves, i.e. in a way that meets their needs and aspirations. The Compassion in World Farming Symposium has discussed widely how, and to what extent, animals may be

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sentient and may be conscious. Highly relevant for this discussion is the important question of the extent to which an animal may focus help on a conspecific, i.e. others of its kind that are sick or ailing. This is a trait which is considered deeply human—perhaps uniquely so if triggered by compassion rather than a simple trigger stimulus. The rituals that humans have in their treatment of the dead are a case in point; and the issue of humans recognizing and even identifying a body as an extant individual thus becomes highly interesting. Most animals, by contrast to humans, appear to show little interest in the remains of dead conspecifics (McComb et al., 2005), although some, like chimpanzees (Goodall, 1986), dolphins (Dudzinski et al., 2003) and elephants have been described as concerned with ailing or dead members of their species. African elephants frequently (but not always) exhibit an intense interest in bodies of dead elephants at various stages of decomposition (Douglas-Hamilton, 1972; Douglas-Hamilton and Douglas-Hamilton, 1975; Moss, 1988; Spinage, 1994; Payne, 2003; McComb et al., 2005). The question of whether or not there might be compassion or suffering among surviving elephants who encounter and interact with ailing or dead ones remains so far unanswered. Observations suggest that this may be the case and evolutionary thinking would suggest that it could have a selective advantage, especially if it increases the fitness of surviving kin. To tackle this important issue we need to address also the question of whether an elephant will recognize the identity of a distressed or dead conspecific, and treat a relative differently from a non-relative.

It is rare that we can observe elephants interacting with dying or dead elephants for such events tend to be unpredictable. Records therefore are generally anecdotal, but are nonetheless valuable as they can give insights into important behaviour patterns. For example, Payne and her research team (Payne, 2003) were making continuous quantitative observations of elephants using sound and video recording equipment from a fixed observation platform in a clearing in the Equatorial forest in Bayanga, Congo. Thus, fortuitously they were able to record the death of a calf and many of the interactions that took place with its own family and other elephants right in front of the observers. The dying calf elicited numerous responses both from its own family and from others, and continued to do so for a few days after death.

Recently, McComb et al. (2005) have conducted experiments to test whether elephants show an interest in elephant cadavers. Their findings show elephants spend significantly greater time exploring elephant remains than inanimate objects or the remains of other large herbivores. In this experiment elephants, within the Amboseli area, were presented with ivory skulls and bones of elephants along with the remains of other animals and inanimate objects. These experiments for the first time give a statistical support for the special interest of elephants in the remains of dead elephants. These authors also knew the relationships of the elephants in the experiment to the elephant remains with which they were presented. They found that the elephants' responses were not significantly stronger if the bones happened to be from related individuals.

In Samburu National Reserve in Kenya, 'Save the Elephants' has a research station that monitors the elephant population using the technique of individual recognition (Wittemyer et al., 2005a). Since 1998 there has been extensive radio tracking using GPS technology (Douglas-Hamilton, 1998; Douglas-Hamilton et al., 2005). During the course of this work the research team witnessed the death of a matriarch, Eleanor, within one elephant family unit named the First Ladies. New light was shed on the behaviour towards ailing and dead elephants and on the relationships of those individuals who were involved in these encounters.

This paper looks at the behaviour of several elephants of different degrees of relatedness towards Eleanor, who collapsed on the 10th of October 2003, and died the next day. Although observations of this death and the events that followed are descriptive, the field techniques used

allow strong behavioral inferences to be made. These techniques included long-term monitoring (LTM) of this population based on individual recognition, remote sensing of several of the key players' positions with GPS radio-collars, and the use of digital photography to record time specific behaviour. These methods allowed us to gain information usually unavailable in such rare events and the resulting insights throw up new questions on elephants' behaviour and feelings towards each other.

2. Methods

2.1. Long-term monitoring by individual recognition

In our Samburu study area we have a population of about 900 individually known animals, who since 1997 have been continuously monitored for associations and population dynamics. Research teams have gone out between 10 and 30 days a month, to check which elephant groups are present, current associations of all individuals encountered while monitoring, recent births, and any disappearances since they were last seen (Wittemyer et al., 2005a). Association data presented in this paper have been drawn from between June 1998 to August 1999 and May 2000 to December 2002.

These records were analysed to extract the long-term social relations between family units that were in the vicinity of the dying and dead Eleanor during the week of the 10th–17th October, 2003. Elephants that came near Eleanor were recorded and photographed directly at the times when the LTM team was next to the carcass, or by remote sensing.

2.2. Association analysis

The elephants of Samburu, like those described elsewhere in Africa, have a social organization based on tight-knit cow calf units with mature bulls living independent lives. The females and their offspring most frequently seen together are classically termed ''family units'' (Buss, 1963; Laws, 1970; Douglas-Hamilton, 1972; Moss and Poole, 1983). Our long-term monitoring enables quantitative definition of such social relationships, offering robust definitions of family units in statistical terms. Different social tiers have been defined using cluster analysis, and presented in a cluster tree that distinguishes family units from each other at successive levels (Wittemyer et al., 2005b). In practice immature calves are so strongly bonded with their mothers that the calves' relationships to other animals are identical to their mothers' and they can therefore be considered as one unit in the analysis. In this paper, the association tree in Wittemyer et al. (2005b) serves as the basis for describing the long-term spatial relationships of the animals that showed a short-term active interest in Eleanor over the week when she died. This tree is shown in Fig. 1.

In addition, association indices (AI, Ginsberg and Young, 1992) were calculated for each pair of individuals of those animals that showed the short-term interest, as follows:

$$\mathrm{AI} = \frac{X_{\mathrm{AB}}}{N - D}$$

where X_{AB} is the number of observations during which A and B are together, N the total number of observations, and D the number of observations during which neither A nor B were observed (thus including only observations when A or B were observed). Because association indices are a ratio of the total observations of two individuals together and separate, results are robust against sample size differences between individuals. The AIs between the 12 females on which observations were made during the study period are shown in Table 1. The data used to calculate these AIs were collected over a 5-year period from 1998 through 2002. The members of the same families, as determined from the association analysis by Wittemyer et al. (2005b), show high scores of association of the order of 0.61–0.89 in this period. The other families also scored high values within their own families, but had low values with individuals not identified as their own family members between 0.02 and 0.10. For example

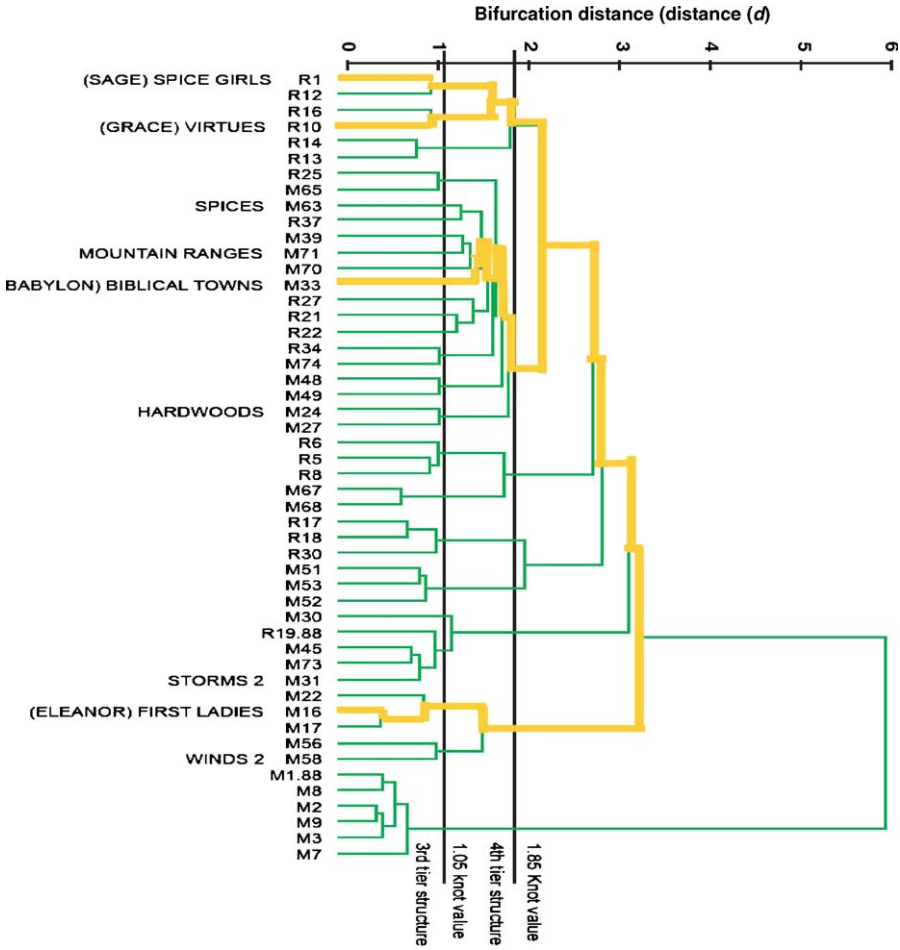

Fig. 1. An association cluster diagram showing putative group relationships between 50 s-tier unit matriarchs (listed with names and letter and number combinations at the left of the cluster tree) using wet season data only. The bifurcation distance (d) is the measure of the strength of association between individuals, where $d = 0$ indicates that two individuals were observed together during 100% of observations (having the same association pattern) and increasing d values represent decreasing degrees of association between individuals. Those matriarchs and their families that exhibited direct interest over the 1-week period in the dying or dead matriarch Eleanor are linked by lines highlighted in yellow.

the AIs of Eleanor with members of her family varied between 0.61 and 0.89, whereas her AI was 0.10 with the Virtues (VR), 0.05 with the Spice Girls (SG), 0.07 with the Hawaiian Islands (HI) and only 0.04 with the Biblical Towns (BT). Yet all of these elephants, related and unrelated showed an exceptional interest in her dead body.

2.3. Radio-tracking

Elephants were tracked using GPS technology as described in Douglas-Hamilton (1998) and Douglas-Hamilton et al. (2005). Three elephants and their family units, Maya (FL), Jerusalem (BT), and Rosemary (SG) all visited the dead or dying animal and their positions were recorded every hour over 1 week. From these hourly coordinates their distances from the carcass and from Maya were calculated (Fig. 2).

Table 1
Association indices (AIs) of all individuals that showed interest in the dying or dead Eleanor during the study period

		M16	M17	M18	M19	M20	S49	R1	R2	R10	R11	M33	M35
Eleanor	M16	1	0.71	0.62	0.88	0.89	0.07	0.05	0.05	0.10	0.09	0.04	0.04
Martha	M17		1	0.71	0.66	0.68	0.07	0.04	0.04	0.10	0.09	0.05	0.04
Cherie	M18			1	0.61	0.64	0.07	0.05	0.05	0.07	0.06	0.05	0.05
Maya	M19				1	0.86	0.09	0.05	0.04	0.09	0.08	0.03	0.03
Mary	M20					1	0.07	0.05	0.05	0.08	0.08	0.04	0.04
Maui	S49						1	0.03	0.04	0.08	0.09	0.06	0.05
Rosemary	R1							1	0.97	0.09	0.10	0.02	0.02
Sage	R2								1	0.09	0.10	0.02	0.02
Grace	R10									1	0.94	0.07	0.07
Generosity	R11										1	0.07	0.07
Babylon	M33											1	0.73
Jerusalem	M35												1

For further explanation see text.

Analysis of G data recorded on the three-collared individuals in relation the location of carcass of Eleanor was conducted in ArcGIS 9.0© (ESRI). The proportions of time spent within 0.5 km, between 0.5 and 2.5 km, and greater than 2.5 km to the carcass by the three-collared individuals were calculated. χ^2 Goodness of Fit statistics were used to determine which individuals spent more or less time than the other individuals within the three categories of spatial proximity to the carcass (Table 2). The expected time spent in each category was calculated as the average time spent by the three females within the distance category of the carcass. Similarly, χ^2 Goodness of Fit statistics were used to determine whether M19 Maya, thought to be Eleanor's daughter, spent more or less time within the three spatial categories of Eleanor's carcass,

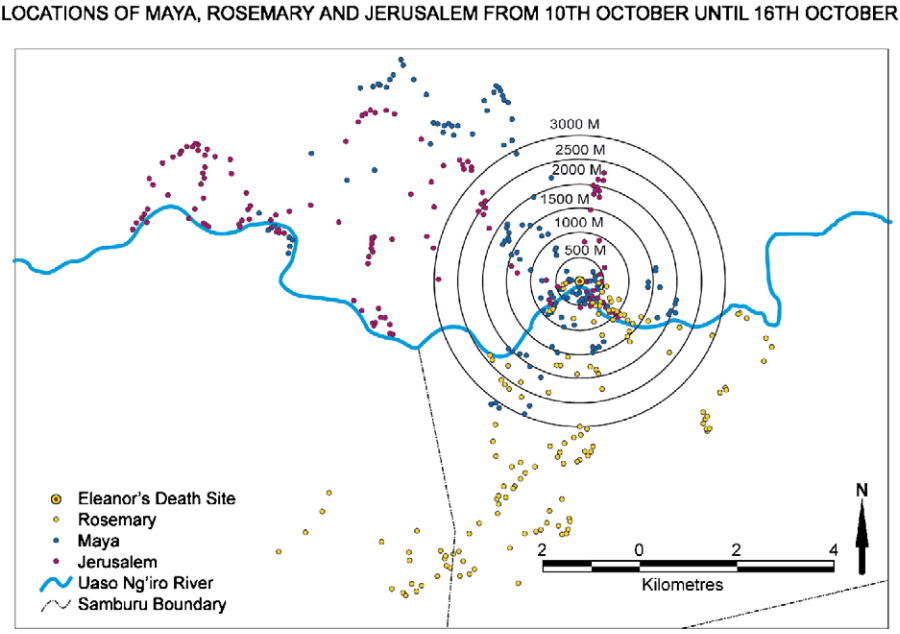

Fig. 2. A record of all GPS fixes, acquired by remote sensing, made of the three tracked elephants that showed an interest in the stricken Eleanor.

Table 2
The number of hours spent by three G radio-collared females within three distance categories from the carcass of Eleanor

Distance (km)	M19 Maya	M35 Jerusalem	R1 Rosemary	Average
0–0.5	**31 (11.53)***	15 (0.24)	**5 (8.47)***	17.00
0.5–2.5	**69 (5.07)***	**35 (5.93)***	54 (0.03)	52.67
>2.5	**63 (9.86)***	**113 (4.14)***	104 (1.22)	93.33

The number of hours and χ^2 values in parentheses. Bold text and * indicates significance $p < 0.05$.

Table 3
The number of hours Maya (M) spent within three distance categories of Eleanor's carcass (C), Rosemary (R), and Jerusalem (J)

Distance (km)	M + C	M + J	M + R	Average
0–0.5	**31 (9.39)***	13 (1.39)	**10 (3.56)***	18.00
0.5–2.5	**69 (6.92)***	43 (1.07)	**39 (2.55)***	50.33
>2.5	**63 (10.59)***	107 (1.61)	**114 (3.95)***	94.67

The number of hours with χ^2 values within parentheses. Bold text and * indicate significance $p < 0.05$.

Rosemary, or Jerusalem (Table 3). The expected time spent in each category was calculated as the average of the time spent by Maya to the three others.

2.4. Digital photography

Shivani Bhalla observed Eleanor when she first collapsed on 10th Oct 03, and revisited the next day and periodically thereafter in the following week. Shivani was able to record interactions on a digital camera automatically dated and timed. This allowed photographic recording of behaviour and subsequent confirmation of identifications of elephants against the photo identification file (Table 4). These photographic data were intermittently collected, but the tracking data were consistently recorded on the hour around the clock.

Table 4
Family responses to the death of the Matriarch, Eleanor

	Observed strong response Number of times behaviour occurs				
Identity of family	VR	SG	HI	FL	BT
Directional sniff towards carcass	3	1		3	2
Raises tail	3				
Rapidly approaches body	3				
Tentatively approaches body	1	1	1	1	
Sniffs body	2	1	1	3	2
Touches body with trunk	3	1	1	2	1
Touches or hovers foot over body	2		2		
Tastes trunk after body touch	1		1		
Screams/rumbles/trumpets	2		1		
Threatens calf's mother away					
Threatens others from nearing/appears to guard body					1
Lifts body with foot			1		
Lifts body with trunk					
Lifts body with tusks	3		1		

3. Results

Eleanor was the matriarch of the family unit called the First Ladies (FL). From January 2000 to June 2004 eight calves were born into this family and three animals died. Eleanor gave birth to a female calf in late April of 2003, approximately 5.5 months before her death. Up until Eleanor's death she was seen 106 times. The associations over 4 years with her own family members and with those individuals who showed special attention to her during her death week are shown in Table 1. The association indices (AIs) between Eleanor and members of her own family range between 0.62 and 0.89, while her AIs with non-family females ranged between 0.04 and 0.10. The AIs of these non-family females to Eleanor are lower than those normally found at the 4th tier or clan level of association (Wittemyer et al., 2005), indicating these females had low spatial ties to Eleanor during the 5 years prior to her death. This weak association is shown diagrammatically in the population association tree (Fig. 1).

Eleanor's closest associate was Maya, seen 101 times up until Eleanor's death and with Eleanor on 91% of those occasions, with an AI of 0.89 (Table 1). She was being radio-tracked during the week of Eleanor's death. Since her ties with the First Ladies were strong both before and after Eleanor's death it is assumed her movements were representative of the whole family.

There were also two other families with radio-collared individuals in the area. These were Jerusalem (BT) and Rosemary (SG). Photographic evidence supplements this data. Other families that were present, which were confirmed by digital photography, included the Virtues and Hawaiian Islands. The following is a chronicle of what interactions were observed, or deduced from remote sensing data over a period of 7 days. Fig. 3 shows the distances of the three radio-tracked elephants from Eleanor's death site over the 7-day period.

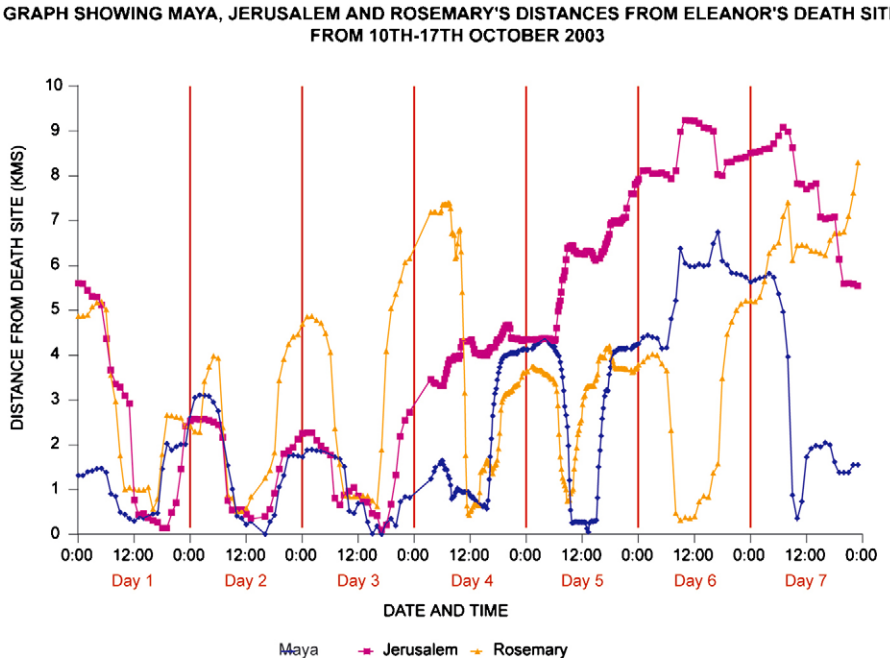

Fig. 3. The distances of three individuals, Maya (FL), Jerusalem (BT) and Rosemary (SG), from the point where Eleanor collapsed and died, over a 1-week period, measured by remote sensing from GPS radio collars.

The sequence of events surrounding Eleanor's death was as follows.

Day 1, 10th October 2003. Eleanor was found at 6:14 pm with a swollen trunk which she was dragging on the ground. She had abrasions to an ear and one leg as well as a broken tusk, probably damaged in a previous fall reported by the rangers. She stood still for a while, then took a few slow small steps before falling heavily to the ground at 6:21 pm. Two minutes later, Grace (AI = 0.10), matriarch of the Virtues rapidly approached her, with tail raised and streaming with temporal gland secretion. She sniffed and touched Eleanor's body with her trunk and foot (Fig. 5). Then she lifted Eleanor with her tusks back on to her feet. Eleanor stood for a short while, but was very shaky. Her back legs began to collapse and she was unable to maintain her upright position (Fig. 6). Grace tried to get Eleanor to walk by pushing her, but Eleanor fell again facing the opposite direction to her first fall. Grace appeared very stressed, vocalizing, and continuing to nudge and push Eleanor with her tusks (Fig. 7). Grace was left by the rest of her family, but continued alone to try and lift Eleanor, with no success. Eleanor was too weak to take advantage of her help. Grace stayed with her for at least another hour as night fell.

During this activity, according to the radio-tracking data, Jerusalem (AI = 0.04) was within 100 m of Eleanor, but Maya (AI = 0.89), probably with the rest Eleanor's family, was already 1.5 km away, moving away from the river, as elephants usually do in the evening. She was probably not aware that her matriarch was down. Temporarily traveling with Maya was Rosemary (AI = 0.05) of the Spice Girls.

Day 2, 11th October 2003. The three tracked animals were still more than 2 km away at 7:00 am. By 10:00 am they were approaching Eleanor, but were still between 400 and 600 m away. Eleanor never got up again and died at about 11:00 am. Maya was now 360 m away, and according to the hourly point data spent the next 7 h in the vicinity of Eleanor, coming as close as 10 m at 4:00 pm. At the same time Maui (AI = 0.07) from the Hawaiian Islands showed a strong behavioural response. She hesitantly approached Eleanor's body, extended her trunk,

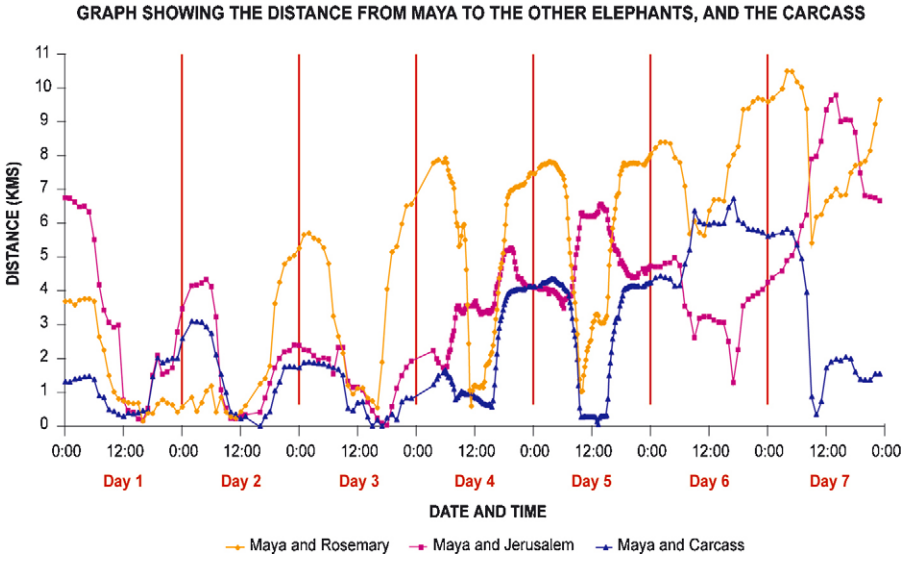

Fig. 4. Graph showing the distance from Maya to the other elephants and to the carcass.

Fig. 5. Day 1, Grace of the Virtues family touches Eleanor of the First Ladies with her trunk and foot, before lifting Eleanor back onto her feet.

Fig. 6. Day 1, within 30 s Grace has Eleanor back on her feet, but Eleanor falls again after a further 8 s.

Fig. 7. Day 1, at 6 min after Eleanor's first fall, Grace continues to try to lift her as night falls.

sniffed the body, touched it, and then tasted her trunk. She hovered her right foot over the body, nudged the body, and then stepped over, pulling the body with her left foot and trunk, before standing over the body and rocking to and fro (Fig. 8). All this attention lasted just under 8 min. By 7:00 pm Maya and the other tracked animals were more than a kilometer away and still moving.

Day 3, 12th October 2003. Overnight Maya had walked nearly 2 km away from Eleanor. In the morning the rangers cut out the tusks, leaving a severed trunk and vacant tusk holes. By 3:00 pm Maya was once again by the side of her dead matriarch. At the same time Grace of the Virtues with her family made an appearance again and was photographed next to the carcass. This time Grace did not appear to be distressed, but just stood around silently. Another member of her family, Generosity (AI = 0.09), sniffed the blood around Eleanor's tusk cavity.

At 5:00 pm Maya and the First Ladies family were right by the carcass. Eleanor's 6-month-old female calf nuzzled her mother's carcass then walked around appearing confused trying to suck from other young calves and returning to her mother.

Twelve minutes later an unrelated family, the Biblical Towns, including the matriarch Babylon (AI = 0.04), approached the carcass and pushed away the First Ladies and then investigated the carcass sniffing it with their trunks. This was witnessed by the long-term monitoring team. However, Eleanor's 6-month-old calf was not pushed from the carcass of her mother (Fig. 9). Maya and the rest of the First Ladies moved from 10 to 200 m from the carcass in 1 h (5:00–6:00 pm) as is shown by the radio-tracking data. Despite the strong interest that the Biblical Towns had shown by ousting Eleanor's family, they left that night and were never recorded again near the carcass site for the rest of the year. Perhaps their interest was some

Fig. 8. Day 2, Maui from the Hawaiian Islands family steps over and pulls at Eleanor's dead body.

Fig. 9. Day 3, Babylon, Jerusalem and Eleanor's 2003 calf with Eleanor's body. The 6-month-old calf remained with Eleanor's body after the rest of her family had been pushed away.

Fig. 10. Day 6, Sage from the Spice Girls family extends her trunk and sniffs Eleanor's body.

curiosity mingled with a dominance interaction to displace a family in possession of something that interested that family.

Day 4, 13th October 2003. Overnight Maya went over 1.5 km away from Eleanor and there is no evidence that she came back any closer than 600 m to the carcass on this day. Radio-tracking data shows that Jerusalem and the rest of the Biblical Towns had departed by over 4.5 km. The carcass was now visited by various scavengers, jackals, hyaenas, vultures and lions.

Day 5, 14th October 2003. Radio-tracking data showed that Maya came within 10 m of the carcass and stayed with Eleanor for 1.5 h, though this was not witnessed by any observers on the ground. The lions were still in possession.

Day 6, 15th October 2003. While the lions were still in close vicinity, R2 Sage (AI = 0.05) from the Spice Girls was observed and photographed visiting Eleanor at 8:27 am. She showed strong behavioural responses towards the carcass. She tentatively approached the body, extended her trunk and sniffed and touched the body for 3 min (Fig. 10). Her matriarch Rosemary was within 500 m of the body at the time that Sage made her close approach. On this day Maya and the First Ladies were more than 4 km away all day.

Day 7, 16th October 2003. Radio-tracking data shows that the First Ladies returned to visit Eleanor's death site. However, this was a very short visit as they spent only about 30 min within 500 m of the death site.

We analyzed the hourly G.P.S data collected continuously on the three females during the study period to determine which individuals spent more time near the carcass. Maya spent significantly more time within 500 m ($\chi^2 = 11.53$, $p < 0.05$) and between 500 m and 2.5 km ($\chi^2 = 5.07$, $p < 0.05$) of Eleanor's carcass during the study period than the average time spent by all three females (Table 2). In contrast, Rosemary spent significantly less time within 500 m

($\chi^2 = 8.47$, $p < 0.05$) and Jerusalem spent significantly less time between 0.5 and 2.5 km ($\chi^2 = 5.93$, $p < 0.05$) than the average. Furthermore, Maya spent significantly less time over 2.5 km from the carcass than the average ($\chi^2 = 9.86$, $p < 0.05$) while the other two females spent more time than the average at this distance (Table 2). Additional analysis of the G data was conducted to determine if Maya spent more time in close proximity to Eleanor, Rosemary, or Jerusalem during the week of Eleanor's death. Maya spent significantly more time within 500 m ($\chi^2 = 9.39$, $p < 0.05$) and between 0.5 and 2.5 km ($\chi^2 = 6.92$, $p < 0.05$) of the carcass than the average time she spent in proximity to all three females at these distances (Table 4). Furthermore, Maya spent less time at distances greater than 2.5 km ($\chi^2 = 10.59$, $p < 0.05$) from Eleanor's carcass than her average to all three females (Table 3). Interestingly, during the 19 h that Maya was within 1 km of Jerusalem, both were within 1 km of the carcass. And of the 28 h Maya was within 1 km of Rosemary, they were within 1 km of the carcass for 14 h. Although the Spice Girls were only observed once physically interacting with Eleanor, when Sage approached her, they had been within 500–600 m on six separate occasions from Day 1 through 6, and other interactions may have occurred that were not witnessed. No bulls were seen visiting Eleanor either while she was dying or when she was dead. Table 4 summarizes the observed behavioural responses for each family.

Eleanor's 6-month-old calf did not survive long, and was recorded as missing presumed dead within 3 months of the death of her mother. Prior to its death in late December of 2003, Eleanor's youngest calf was seen associating with Maya and the rest of Eleanor's calves on seven different occasions. During this period, none of the breeding females normally associated with Eleanor were observed to suckle the youngest calf despite its attempts to suck lactating females. The older calves of Eleanor survived and have been observed associating with Maya as recently as July 2005.

4. Discussion

From radio tracking or direct observations backed up by photo images it is clear that five families visited the dead Eleanor, showing a distinct interest in her body. One of these was the matriarch's own family. We note that, apart from Maya and the First Ladies, the evidence was that these families were not related to Eleanor. From the association tree of Wittemyer et al. (2005b) none of these other than Maya was normally closely associated with Eleanor; and one of them, Maui, S49 of the Hawaiian Islands, was so seldom seen in the park that she was in the category used for sporadic visitors, i.e. those seen less than 3 months of the year, without enough observational data to be a candidate for the association analysis.

The lack of association in the long-term record was backed up by radio-tracking data from Rosemary (SG) and Jerusalem (BT). In the 7 days of the death event these animals were in close proximity to Maya (FL) only when they were near to the carcass. This usually occurred in the afternoon. When the groups moved away from the river, after visiting the carcass, each went its own separate way. This is shown in Fig. 4. There was nothing to suggest a closer order of association with Maya than normal (as defined by the association tree).

The conclusion must be that elephants are interested in the sick, dying or dead elephants irrespective of genetic relationship. There seems to be a generalized response to elephants in distress, rather than help or interest only being restricted to close kin. This conclusion is backed up by earlier observations IDH made in Manyara (Douglas-Hamilton, 1972), where he saw a darted animals guarded and helped by apparently unrelated families, who in two instances replaced the parent family guarding the recumbent animal. Similar guarding of unrelated

individuals has been observed in Samburu during radio-collaring operations (Douglas-Hamilton and Wittemyer, pers. obs.). The non-related Babylon and Jerusalem of the Biblical Towns also drove Maya and the First Ladies away from their dead matriarch, Eleanor. In both Manyara and Samburu several observations were made of unrelated animals showing an interest in the bones of carcasses that were planted in front of them.

In Amboseli IDH also observed a rare interaction around a young female who was found one morning standing over the inert body of her dying calf of a few months old (see supplementary video material submitted to CIWF extracted from Discovery's IMAX picture ''Africa's Elephant Kingdom''). This happened during the drought of 1997; it was the young cow's first baby and she probably had trouble in producing enough milk for it. She tried to raise it to its feet repeatedly, but the calf just flopped from one side to the other without any energy left to stand. Another family, that was totally unrelated, according to the Amboseli monitoring team, came walking towards water and drank. Returning from the waters edge they became aware of the situation and veered from their path towards the mother and the baby. The mother was uneasy at the approach of the larger and strange elephants and turned from side to side and defecated. The matriarch approached her and smelled her faeces, smelt the dying calf and smelt the hind quarters of the mother. She then advanced and extended her trunk up towards the mouth of the mother. This took a few minutes. Just before the strange matriarch left, one of the young bulls within her group made a vicious attack and jabbed his short tusks into the mother. She bellowed and moved round to face him. The strange matriarch left and took her family with her, except for the young bull. As soon as the matriarch had gone away the mother turned on the young bull and chased him away from her calf. The bull's aggressive behaviour was in sharp contrast to his matriarch who showed no aggression, but more what looked like concern.

Hamilton's (1964) discoveries make it easy to explain 'altruistic' behaviour exhibited to kin. After all, when gene sharing relatives benefit, then natural selection tends to encode the beneficial trait in the genome of the family. It is more difficult to explain such generalized responses to non-kin—unless it be reciprocal. Furthermore, examining the remains of another elephant could be potentially dangerous to the investigator if a transmissible disease caused the death; on the other hand, any information gleaned about the dead conspecifics/group member could be important for one's own survival. Although such behaviour is rare and difficult to observe in Nature, the techniques of remote sensing are now enabling us to collect continuous data on position. In this case we were not only lucky to see the death of Eleanor, but also that three tagged animals were being tracked at the same time, so that precise inter-individual distances could be calculated over a time in which elephants probably responded to strong emotions released by the event of the death of a matriarch.

Why should the death of a matriarch matter so much to elephants? In the case of family unit members it means a loss of knowledge or care towards others (McComb et al., 2001). In some cases matriarchal knowledge may prove to be critical to the survival of individuals as was found with the Tarangire elephant population (Foley, 2002). During several years of drought, clans with experienced matriarchs tended to move away from the major river in Foley's study area to find better food, while one clan of several families that had been altered by poaching and were now led by younger less experienced matriarchs, tended to stay near the river where browse was depleted. In consequence the families led by older cows had low calf mortality during this stressful period and those led by young matriarchs suffered significantly greater calf mortality. This suggests that a higher ecological knowledge that accompanied ageing was of direct benefit to group members.

In the case of Eleanor's family unit her orphaned calf did not survive more than 3 months after her death, and apparently died from lack of milk. Deprivation of maternal care, while not

measurable, is also likely to increase emotional stress on calves, with a consequent effect on survival. Furthermore, during the rains of May 2004, another family member, Cherie, was left behind by Martha, and tried several times in vain to cross the flooded Uaso Nyiro river. On a final attempt her 3-month-old female calf was swept away downstream. Cherie pursued the calf through the surging water, caught up with her, and eventually guided her to calmer water on the far bank. However, the calf appeared severely stressed and died shortly after this event. It is possible that Cherie's unfortunate decision was influenced by a lack of matriarchal guidance.

Matriarchs also seem to act as the glue that holds a family together and the loss of the matriarch may also result in a family unit splitting (Douglas-Hamilton and Douglas-Hamilton, 1975; Moss, 1988). In the case of Eleanor's family a splitting tendency was already evident while she was alive and it increased further after her death. Specifically, during the dry season months of July and August 2005 Maya and Mary had not been seen together (in contrast to the relationship shown in Table 1).

To summarize rare but defining events in an elephant's life are important. In the case of Eleanor's death we could use the power of knowledge of elephant identities and family relationships combined with detailed quantitative records of movements. This allowed us to analyse the behaviour surrounding her death. Combined with earlier work and the data of other scientists it leads to the conclusion that elephants have a generalized response to suffering and death of conspecifics and that this is not restricted to kin. It is an example of how elephants and humans may share emotions, such as compassion, and have an awareness and interest about death.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.applanim.2006.04.014.

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