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Tusklessness and tusk fractures in free-ranging African savanna elephants (*Loxodonta africana*)

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ABSTRACT

The incidence of tusklessness varies between free-ranging African elephant populations. Sex-linked genetic drift predicts 2 outcomes – the condition becomes fixed and sex-specific incidences diverge when populations are small and/or heavily poached. By contrast, for large and intact populations, tusklessness diminishes and there is no variation between sexes. We tested these predictions by comparing sex-specific incidences between 15 populations: a small one with a skewed founder effect towards tusklessness; 5 that had experienced intense levels of poaching; 2 that had been subjected to non-selective culling and 7 that are relatively pristine. Patterns of rainfall were studied of tusk fractures amongst these populations to correct for any effect that acquired tusklessness may have on our predictions. The incidence of tusk fractures was related to annual rainfall, but the mechanism that leads to an increase of the condition in drier areas was not clear. Incidences of tusk fractures in free-ranging populations implied that the frequency of acquired bilateral tusklessness is low and should not affect our results. All males had tusks. Tusklessness in females was high in the small skewed founder population and some of those where there was a history of poaching. The incidence is expected to decline if the residual population is large.

Key words: African savanna elephant, free-ranging populations, tusk fractures, tusklessness.

Steenkamp G, Ferreira S M, Bester M N **Tusklessness and tusk fractures in free-ranging African savanna elephants (*Loxodonta africana*)**. *Journal of the South African Veterinary Association* (2007) 78(2): 75–80 (En.). Mammal Research Institute, University of Pretoria, Pretoria, 0002 South Africa.

INTRODUCTION

Tusklessness is common in some African elephant (*Loxodonta africana*) populations. The condition can be inherited (usually bilateral) or acquired (usually unilateral)[20]. Incidences vary between populations[1,8,20], and over time, within populations[4,13]. Elephants that are bilaterally tuskless may act as an early warning sign of genetic drift in a population[24]. Tusklessness also increases in heavily poached populations[8]. Moreover, tusklessness appears to be sex-linked to females[13,20,24].

These observations evoke 2 outcomes that may both result from genetic drift if the condition has a genetic basis. In the 1st instance, small populations often created by intense poaching, are prone to genetic drift[25]. It may then be expect that tusklessness increases over time, *i.e.* the 'tuskless-gene' becomes fixed in the population through drift. If the condition is sex-linked, then it can be expected that sex-specific relative frequencies to diverge. Tuskless males should not be found.

Secondly, for populations recovering from selective poaching where the residual numbers were relatively high, tusklessness should decrease over time. The 'tuskless gene' is presumably lost from the population also through genetic drift. Here we expect that sex-specific relative frequencies converge onto zero if the condition is sex-linked.

The above expected outcomes evoke a 3rd expectation – small founder populations skewed towards tusklessness or poached populations will have higher incidences of tusklessness than non-disturbed populations. To test these predictions 15 populations were observed. One of these is a small population with a skewed founder effect; 5 experienced intense levels of poaching; 2 had culling for varying periods which removed elephants non-selectively; and 7 were relatively natural.

Acquired tusklessness is the result of a fracture of a tusk below the skin fold surrounding the tusk (labio-dental fold) or avulsion of a tusk. This may inflate the number of elephants that appear to be tuskless. The frequency of tusk fractures was thus 1st considered in wild populations, because dental disorders are common in captive elephants. Most dental disorders are fractures of the exposed incisors (tusks) – 31 % (n = 350) of the elephants in captivity in 60 North American zoos, had tusk fractures. African elephants comprised 48 % (n = 182) of this sample[16]. In the only study on tusk fractures of African elephants in the wild, the incidence was only 5 % of all tusks in an unidentified population[14]. The incidence of tusk fractures may conceivably be linked to nutritient levels of major food items, humidity or some other factors. How tusk fractures and rainfall correlate were therefore explored as rain is likely to influence these factors.

In the present study the incidence of tusk fractures was 1st quantified in the 15 African elephant populations and a correction factor calculated for 'apparent bilateral tusklessness'. The predictions for tusklessness were then evaluated by comparing the incidences in the 15 populations of free-ranging African elephants.

MATERIALS AND METHODS

Digital images of approximately 10 000 African elephants from 15 populations across the African continent (Fig. 1, Table 1) in the photographic library of the Conservation Ecology Research Unit at the University of Pretoria were scrutinised. These images were taken to define demographic variables of selected populations in a separate study by randomly sampling breeding herds and male groups. Several images of the same group provided a number of views for individual elephants. Elephants for which either the tusks or the skin covering the tusks at its alveolus were clearly visible were selected. For each individual, the sex (male, female, unknown), age, presence and fractures of tusks were recorded. A number of criteria were employed to sex elephants. Cows were distinguished from bulls by the more angular shape of their forehead[11]. In addition, observations of sexual organs, genital folds and mammary glands clari-

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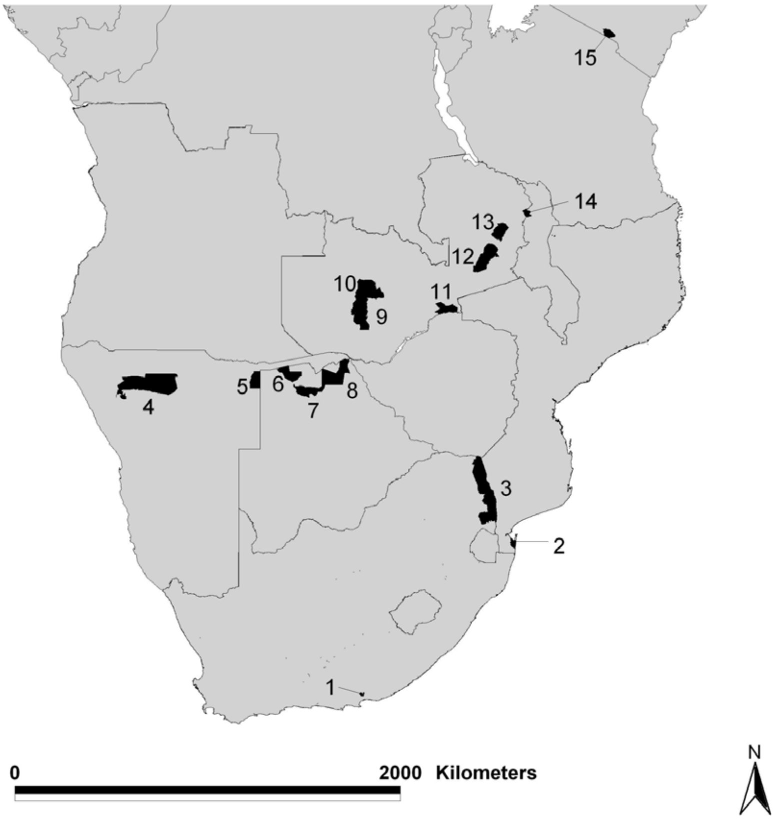

Fig. 1: **Locations of populations sampled in our study. 1, Addo Elephant National Park; 2, Maputo Elephant Reserve; 3, Kruger National Park; 4, Etosha National Park; 5, Kaudom Game Reserve; 6, Ngamiland 11; 7, Moremi Wildlife Reserve; 8, Chobe National Park; 9, southern section of the Kafue National Park; 10, northern section of the Kafue National Park; 11, Lower Zambezi National Park; 12, South Luangwa National Park; 13, North Luangwa National Park; 14, Vwaza Marsh Game Reserve; 15, Amboseli National Park.**

fied uncertainties with regard to the sex of an individual. Age classes were broadly defined as either subadult or adult[11]. Tusks were classified as left or right tusk fractures only when a sharp, clear break was visible. Tusklessness was recorded for left or right tusks, or both.

The incidence of tusk fractures and tusklessness and was calculated using a log-linear model[3] to test for population and sex-specific differences in these. To explore how incidences of fractures vary between populations with different rainfall, rainfall statistics were collated for each population. It was assumed that rainfall might serve as an index to some important variable such as nutrient levels of vegetation or as a crude estimate of humidity, that conceivably affect the incidence of tusk fractures. Finally, incidences of left and right tusk fractures were used to calculate the probability that we a fractured left ($P_{f,l}$) or right ($P_{f,r}$) tusk may be observed. The probability of observing an elephant with both tusks fractured ($P_{f,l+r}$) is thus the product of these 2 probabilities.

Incidences of tusklessness were used in a log-linear model (see above) to test for population-, sex- and age-specific differences. The probability of observing an elephant with no tusk on the left ($P_{t0,l}$) and right ($P_{t0,r}$) was first calculated from incidences of tusklessness on the left and right side. As unilateral tusklessness is usually acquired[20], the probability of acquired bilateral tusklessness ($P_{t0,l+r}$) is thus the product of these 2 probabilities and that of observing 2 fractured tusks ($P_{f,l+r}$). This was used to correct the frequencies of tusklessness if needed.

RESULTS

Tusk fractures

The incidences of tusk fractures were variable (Table 2) and associated with populations, sex and age (log-linear model goodness-of-fit, maximum likelihood $\chi^2_{28} = 19.39$, $P = 0.89$). The incidence of tusk fractures depended mostly on the population where the data were collected (partial association $\chi^2_{14} = 1519.61$, $P < 0.01$). The populations in the western parts of the range of study areas had higher incidences of tusk fractures. In

Table 1: **Summary of the number of African elephants sampled in 15 populations across 7 countries. The years for which rainfall statistics are available and the mean and standard deviation of annual rainfall at each location are noted.**

Country	Population	Individuals sampled			Rainfall	
		Male	Female	Unknown	Years	Annual
South Africa	Addo Elephant National Park	30	44	23	1960–2004	407.9 ± 118.7
	Kruger National Park	29	112	12	1970–2003	478.6 ± 178.0
Namibia	Khaudum Game Reserve	43	81	31	1965–2004	451.0 ± 191.4
	Etosha National Park	11	43	17	1939–2005	368.7 ± 118.7
Botswana	Ngamiland 11	0	12	2	1983–2003	448.2 ± 147.4
	Moremi Wildlife Reserve	24	36	17	1983–2003	449.4 ± 145.5
	Chobe National Park	30	67	5	1983–2003	457.9 ± 137.9
Mozambique	Maputo Elephant Reserve	1	11	2	1980–2003	753.3 ± 230.0
Zambia	Lower Zambezi National Park	1	52	8	1976–2001	798.6 ± 272.2
	Southern Kafue National Park	5	87	1	1983–2003	696.7 ± 185.7
	Northern Kafue National Park	25	95	3	1982–2003	729.1 ± 230.5
	South Luangwa National Park	1	76	4	1983–2003	768.8 ± 186.8
	North Luangwa National Park	7	90	9	1993–2003	816.3 ± 142.2
Malawi	Vwaza Marsh Game Reserve	0	19	3	1983–2001	865.7 ± 278.3
Kenya	Amboseli National Park	40	223	47	1976–2000	346.5 ± 120.0
Total		247	1048	184	–	–

Table 2: **Frequencies of tusk fractures in samples of elephants taken from 15 populations.**

Population	Females				Males				Unknown				Total number of tusks	
	Adults		Subadults		Adults		Subadults		Adults		Subadults			
	t_f	n	t_f	n	t_f	n	t_f	n	t_f	n	t_f	n	t_f	n
Etosha[a]	41	75	2	8	5	10	3	10	9	12	0	20	60	135
Kaudom[b]	29	142	0	14	20	74	1	10	–	–	1	60	51	300
NG11[b]	0	18	0	5	–	–	–	–	–	–	0	4	0	27
Moremi[b]	21	55	2	14	2	30	3	18	–	–	1	34	29	151
Chobe[b]	23	131	0	2	6	40	0	20	0	2	0	8	29	203
S-Kafue[c]	1	164	0	2	0	6	0	4	–	–	0	2	1	178
N-Kafue[c]	2	177	0	8	0	38	0	10	–	–	0	6	2	239
L-Zambezi[b]	0	88	0	2	0	2	–	–	–	–	0	14	0	106
S-Luangwa[c]	0	104	0	12	–	–	0	2	–	–	0	8	2	126
N-Luangwa[c]	2	125	0	8	0	14	–	–	–	–	0	12	2	159
Vwaza[c]	4	30	–	–	–	–	–	–	–	–	0	6	4	36
Kruger[a]	5	206	0	16	0	48	0	10	–	–	0	24	5	304
Maputo[b]	0	21	–	–	0	2	–	–	–	–	0	4	0	27
Amboseli[b]	5	384	0	52	2	40	0	40	0	6	1	88	8	610
Addo[d]	0	7	–	–	0	30	0	29	0	6	0	22	0	94

t_f denotes the number of fractured tusks in a total sample of n tusks.
[a]Populations where controlled culling took place.
[b]Populations with no intensive management of numbers.
[c]Populations that had high levels of poaching.
[d]Population with a small founder effect.

Etosha National Park, 44.4 % of all tusks had fractures irrespective of sex or age. For the Khaudum Game Reserve, Moremi Game Reserve and Chobe National Park, these values were 17.0 %, 19.2 % and 14.2 %, respectively. Populations in the eastern parts of the study area had low incidences of tusk fractures, ranging from 0 % to 1.6 % (Table 2).

The sex of an individual was less important than the population from which samples came, but it also influenced the incidence of tusk fractures (partial association $\chi^2_2 = 1463.85$, $P < 0.01$). The incidence of tusk fractures was usually higher in males (14.9 %) than in females (11.0 %). The role of age was the least important factor determining incidences once the effects of populations and sex were accounted for (partial association $\chi^2_1 = 815.63$, $P < 0.01$). Incidences of tusk fractures were higher in adults (13.0 %) than in subadults (8.8 %) (Table 2).

The various populations experience different rainfall each year (Table 1). The incidences of tusk fractures in adult males and females decrease when annual rainfall increases (males: $y = 15790e^{-0.016(x+1)}$, $r^2 = 0.88$, $F_{1,10} = 55.88$, $P < 0.01$; females: $y = 4205e^{-0.012(x+1)}$, $r^2 = 0.84$, $F_{1,10} = 74.25$, $P < 0.01$). Similar associations were recorded for subadults (males: $y = 13000e^{-0.016(x+1)}$, $r^2 = 0.84$, $F_{1,10} = 39.38$, $P < 0.01$; females: $y = 65640e^{-0.021(x+1)}$, $r^2 = 0.81$, $F_{1,10} = 35.93$, $P < 0.01$) (Fig. 2).

The median incidence of tusk fractures

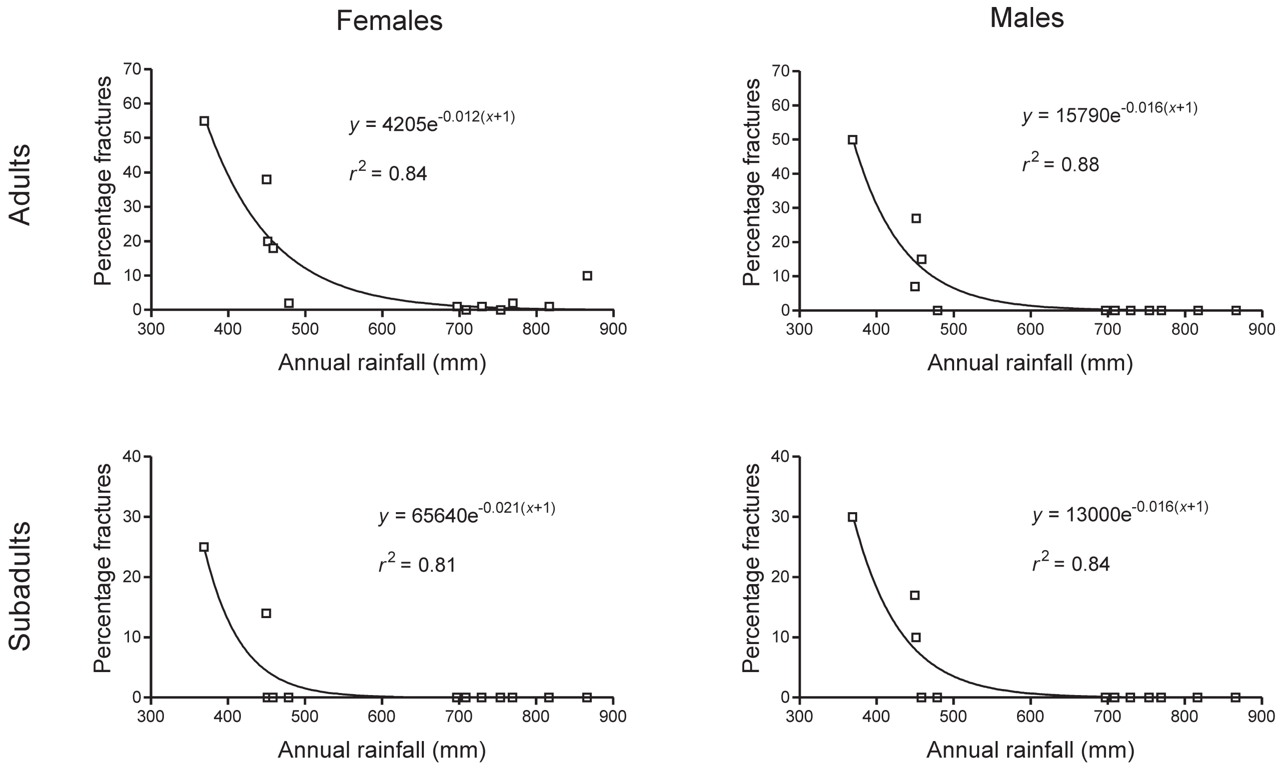

Fig. 2: **Change in the percentage tusks fractured recorded for populations with different annual rainfall. The incidence of male and female tusk fractures in a population was associated with rainfall and decreased as annual rainfall increased.**

Table 3: **Frequencies of tusklessness recorded for elephants in 15 populations across Africa.**

Population	Females				Males				Unknown				Total number of animals	
	Adults		Subadults		Adults		Subadults		Adults		Subadults			
	T_0	*n*	T_0	*n*	T_0	*n*	T_0	*n*	T_0	*n*	T_0	*n*	T_0	*n*
Etosha[a]	1	39	0	4	0	6	0	5	0	6	1	11	2	71
Kaudom[b]	0	73	0	8	0	38	0	5	–	–	0	31	0	155
NG11[b]	0	9	0	3	–	–	–	–	–	–	0	2	0	14
Moremi[b]	1	29	0	7	0	15	0	9	–	–	0	17	1	77
Chobe[b]	0	66	0	1	0	20	0	10	0	1	0	4	0	102
S-Kafue[c]	2	86	0	1	0	3	0	2	–	–	0	1	2	93
N-Kafue[c]	0	91	0	4	0	20	0	5	–	–	0	3	0	123
L-Zambezi[b]	2	51	0	1	0	1	–	–	–	–	1	8	3	61
S-Luangwa[c]	17	70	0	6	–	–	0	1	–	–	0	4	17	81
N-Luangwa[c]	23	86	0	4	0	8	–	–	1	1	2	8	26	106
Vwaza[c]	3	19	–	–	–	–	–	–	–	–	0	3	3	22
Kruger[a]	0	104	0	8	0	24	0	5	–	–	0	12	0	153
Maputo[b]	0	11	–	–	0	1	–	–	–	–	0	2	0	14
Amboseli[b]	3	197	0	26	0	20	0	20	0	3	0	44	3	310
Addo[d]	40	44	–	–	0	15	0	15	1	4	8	19	53	97

T_0 denotes the number of tuskless animals in a total sample of *n*.
[a]Populations where controlled culling took place.
[b]Populations with no intensive management of numbers.
[c]Populations that had high levels of poaching.
[d]Population with a small founder effect.

was 1.31 %, considerably lower than that recorded in captive populations (31 %). Only the elephants living in Etosha National Park had higher incidences of tusk fractures (44.4 %) than that of captive elephants.

Tusklessness

The greatest probability of observing acquired bilateral tusklessness was negligibly small at 0.0001 for the elephants in Etosha National Park. No corrections were thus made to the observed tuskless frequencies (Table 3). The incidence of tusklessness depended on the population sampled as well as the sex of individuals (log-linear model goodness-of-fit, maximum likelihood $\chi^2_{98} = 81.61$, $P = 0.88$). The origin of samples contributed most to the variation in frequencies of tusklessness (partial association $\chi^2_{14} = 639.89$, $P < 0.01$). In the Addo Elephant National Park (small founder population) 91.0 % of the adult females were tuskless. Tusklessness amongst adult females ranged from 21.1 % to 26.7 % in populations that experienced poaching. The incidence of tusklessness in populations that experienced non-selective culling and those that were relatively free from major disturbances were similar and ranged from 0.0 % to 3.9 % (Fig. 3).

Incidences of tusklessness also differed with sex (partial association $\chi^2_2 = 770.66$, $P < 0.01$) as no males were tuskless. Age was not included in our log-linear model, but more adult females than subadult females were tuskless in Addo Elephant National Park and South Luangwa National Park (Fig. 4).

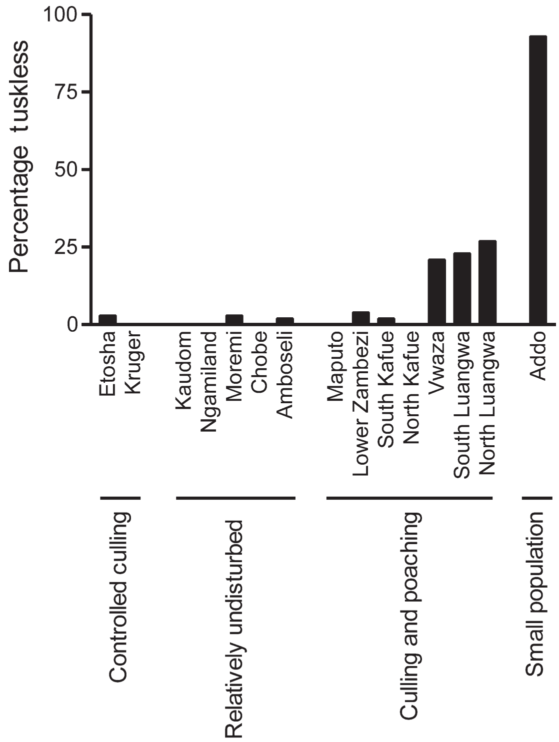

Fig. 3: **Association between population features and the incidence of tusklessness recorded amongst adult females. Small populations with a founder effect and some of the populations that experienced intense poaching had higher incidences of tusklessness.**

DISCUSSION

The incidence of tusklessness varied considerably amongst populations. The population with a small founder size in Addo Elephant National Park had the highest incidence. Three additional populations, all with a poaching history, had relatively elevated incidences. These trends lend support to the prediction that small populations with founder effects and/or poached populations tend to have higher incidences of tusklessness than other populations. In addition, the incidence of tusk fractures varied amongst the 15 populations along an East–West gradient and correlated with annual rainfall. Only the elephants in Etosha National Park (this study) had higher incidences of fractures than captive ones[16].

Fractures of elephant tusks appear to be more common in drier areas – it exponentially increased as mean annual rainfall decreased. The mechanism responsible for this observation may be complex.

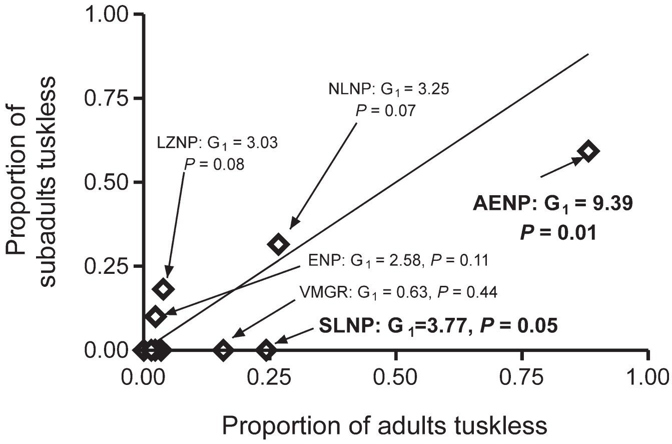

Fig. 4: **Proportion of tuskless subadult females in relation to adult females recorded in 15 populations. Only 2 populations had age-specific differences in tusklessness, with fewer subadults tuskless than adults** (marked in bold)**. LZNP, Lower Zambezi National Park. NLNP, North Luangwa National Park. ENP, Etosha National Park. VMGR, Vwaza Marsh Game Reserve. SLNP, South Luangwa National Park, AENP, Addo Elephant National Park.**

Stored elephant tusks lose weight due to desiccation[22] and become more brittle[21]. It is, however, unsure whether innervated healthy tusks withstand desiccation, particularly at their periphery. It is likely that some level of dehydration could stress such tusks in areas of low annual rainfall/humidity. When used by the bearers for defense, debarking of trees or digging in soil, these weakened tusks may have a higher risk of fracturing.

Social constraints as a result of the distribution of resources may add to incidences of fractures, as elephant range patterns centre on water[5], particularly in the dry season[23] With larger aggregations at permanent water in the dry season, hostile social interactions may increase the risk of fracturing tusks. In dryer areas permanent water often comes in the form of small springs or waterholes, sometimes artificially provided, that access for only a few individuals be given at a time. Certainly, such interactions in confined space lead to tusk fractures in captivity[16].

Rainfall may well affect important environmental factors such as certain microelements directly or indirectly through vegetation. For instance, various waterholes in the Etosha National Park have high concentrations of fluoride[2]. Fluorosis may increase the incidence of tusk fractures due to the fact that it causes brittle teeth; however there are no reports on the effect of fluorosis affecting other species in the Etosha National Park, or molar teeth of elephants. Nonetheless, it is likely that rainfall affects some key micro- or macroelement which may influence the chance that a tusk would fracture. On the other hand, warthogs (*Phacochoerus africanus*), a possible surrogate for elephants, have tusks that are exposed and used to dig and forage[6]. It is not known whether warthogs have suffered from increased tusk fractures in the Etosha National Park. This species furthermore spend some time of day underground, in disused aardvark burrows, which will have a higher humidity than the exposed environment[6].

The frequency of tusk fractures that may reflect on bilateral acquired tusklessness was negligibly small (this study). The incidence of tusklessness is thus unrelated to tusk fractures. However, tusklessness is more common among females than males; all males had tusks (this study). This is in stark contrast to that of the Asian elephant (*Elephas maximus*): females are tuskless, while the incidence in males varies between populations[15]. Tusklessness amongst African elephant males is indeed rare[1,19] and may diminish with time. One reason is that tuskless males may not mate successfully in the presence of younger, but larger-tusked males. Some tuskless males in 3 Kenyan populations are reproductively active where there are no tusked males left[1]. In addition, tuskless females in Amboseli National Park have both tusked and tuskless male and female calves[17]. Furthermore, no tuskless males were born from tuskless females in Addo Elephant National Park[24]. Our data may thus suggest a strong female sex-linked trait of tusklessness, but historical observations noted above suggest that the condition must be passed on through both males and females.

Such genetic linking suggests that history may play a role in the incidence of tusklessness. This was strong when events in the past selected against elephants that had large tusks. The population in Addo Elephant National Park started with at least 50 % of the breeding females without tusks[24]. We recorded 90 % of all females (91 % adults and 84.5 % subadults) without tusks, lower than the 98 % noted in 2001. Non-selective genetic changes, the small size of the population and its isolation lead to the high levels of tusklessness here[24].

Three of the populations in this present study had incidences of tusklessness higher than 20 % and all of these have a strong poaching history. Population sizes in the Vwaza Game Reserve, South Luangwa National Park and North Luangwa National Park declined during the 1970s and 1980s[9,18]. In this study, up to 21.1 %, 22.9 % and 26.7 %, respectively, of the females in these populations had no tusks. In South Luangwa the incidence increased from 10.5 % in 1969 to 38.2 % in 1989[13]. This change most likely resulted from selective poaching[1]. From 1989 to 1993, the incidence declined to 28.7 %, possibly as a result of the migration of tusked females from adjacent Game Management Areas[13]. However, no subadult females were found here that were tuskless. The reduction of tusklessness may in this case also result from random genetic processes.

Published data on high incidences of tusklessness was found for 3 other populations – all with a history of poaching. In the Queen Elizabeth National Park, 1.0 % of the elephants living there in 1930 had no tusks. By 1988, 10.5 % of the females and 9.5 % of the males were without tusks[1]. At Kasungu National Park, close to the 3 populations, we noted high frequencies of tusklessness; 8.3 % of the females living here in 1978 had no tusks[12]. Finally, 10.0–15.0 % of the elephants at Mana Pools in Zimbabwe were tuskless in 1966. At that time 23.0 % of the subadults had the condition[19] suggesting that the incidence was on the increase then. Incidences of 3.9 % and 12.5 % were recorded for adult and subadult females living in the Lower Zambezi National Park close to Mana Pools, incidences of tusklessness may be on the decline, following high frequencies earlier that most likely resulted from selective removal of tuskers.

The other populations that were studied had low numbers of elephants without tusks. Some of these also had poaching histories *e.g.* Maputo Elephant Reserve[7] and the Kafue National Park[10]. However, selective removal of large tuskers from these areas was most likely not as strong as in the other poached populations. Places that had non-selective culling such as Etosha National Park and Kruger National Park had low frequencies of tusklessness. Although it was recorded that all adult females had tusks in Kruger, Raubenheimer[20] reported a 4.2 % incidence of tusklessness previously. Overall the incidence of tusklessness was low for those relatively undisturbed populations in this study. The highest value was 3.4 % for adult females in the Moremi Game Reserve, and that for females of Amboseli National Park was 2.0 % in 1988[17], similar to a value of 1.5 % that we recorded in 2004.

It is concluded that the incidence of tusklessness is often the result of disruptive human selection for tusk-bearing elephants in a population and/or genetic drift. Selective removal of tusked elephants appears to play a role in determining how frequent tuskless animals occur in populations. The later dynamics of tusklessness then depends on the residual or founder population – if this is small, non-selective genetic change may easily lead to rising frequencies of the condition. However, if the residual population is large, those same genetic changes may lead to a decline in the incidence of tusklessness. Conservation managers may thus only need to consider actions when the incidence of the condition is on the increase. Such a change may serve as an indicator of genetic drift that could later lead to inbreeding depression[24].

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