Tusklessness in African elephants: a future trend

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Summary
In the South Luangwa National Park and the adjacent Lupande Game Management Area, located in Zambia’s Eastern Province, the fraction of adult tuskless female elephants increased from 10.5% in 1969 to 38.2% in 1989, apparently as a direct result of selective illegal ivory hunting. From 1989 to 1993, the fraction of adult tuskless females declined from 38.2% to 28.7%, as a result of immigration of a relatively larger fraction of tusked females from adjacent Game Management Areas. Tusklessness appears to run in families and is sex-linked.

Key words: elephants, tusklessness

Résumé
Dans le Parc National de la Luangwa Sud et dans l’Aire de Gestion de la Faune de Lupande voisine, dans la province Orientale de Zambie, la proportion de femelles éléphants sans défenses est passée de 10,5% en 1969 à 38,2% en 1989, suite directe semble-t-il de la chasse sélective pour l’ivoire. De 1989 à 1993, la proportion de femelles adultes sans défenses a baissé de 38,2% à 28,7%, en raison notamment de l’arrivée d’un assez grand nombre de femelles avec défenses en provenance des zones de gestion de la faune adjacentes, mais aussi à cause d’un changement de sex-ratio en faveur des mâles. L’absence de défences semble être un caractère familial et lié au sexe de l’animal.

Introduction
As a result of excessive ivory hunting and probably to a lesser extent habitat loss, the African elephant (Loxodonta africana) has been declining as a species. During the 1970s and 1980s, the age-old lure of ivory has been blamed for the decimation of many local populations. Consequently elephants have become a conservation problem of heroic proportion. This has often resulted in major differences between conservationists over issues like future population trends, culling programmes and the international ivory trade ban. Doom scenarios, resulting from simple linear extrapolations of the overall decline of the African elephant (P. Pfeffer, pers. commun.), and trend analysis of the volume of ivory coming onto the world market (Caughley, Dublin & Parker, 1990), showed the species to be almost extinct or confined to highly secure areas by the turn of the century. Fortunately, the decline of the African elephant is not a straightforward linear equation and its future is most likely not as bleak as is sometimes predicted.
Without offering an opinion on the expected effect of the international ivory trade ban, since the imposition of the ban in 1990, illegal hunting of elephants has declined in a number of range states, simply because of increased levels of law-enforcement effort as a result of a sharp rise in funding by the international donor community (Dublin & Jachmann, 1991).

In countries such as Zimbabwe, Botswana, Namibia and South Africa, elephant populations have been stable or increasing as a result of proper management and the involvement of local communities in decision making and revenue sharing (Martin, Craig & Booth, 1992; Cumming, Du Toit & Stuart, 1990). Large populations of elephants still exist in the rainforests of Gabon, Zaire and the Congo (Barnes, 1989). In addition, simple field observations on the increasing incidence of tusklessness in elephants in the Luangwa Valley, Zambia, showed that in the long term, there may also be hope for relatively large populations of elephants that have been subjected to heavy illegal off-take during the past two decades.

Only scanty information is available in the literature on the incidence of tusklessness in populations of African elephants. Owen-Smith (1966) reported 12.5% tuskless immature and adult elephants in the Mana Pools Game Reserve in 1965, while in 1978, Jachmann (1980) found 8.3% of the adult female population in Kasungu National Park, Malawi, to be tuskless. After some background information on elephant trends in the central Luangwa Valley, this paper reports the incidence of tusklessness in the Luangwa elephants from the early 1960s to 1993.

Elephant population trends in the central Luangwa Valley

The South Luangwa National Park (SLNP) and the Lupande Game Management Area (LGMA) cover approximately 14,000 km² of the central Luangwa Valley in Zambia. From 1970 to 1993, both areas were covered by a series of 14 aerial surveys, specifically designed to count elephants (Bell et al., in press; Jachmann, unpubl. data). Seven of these surveys, covering the period from January 1987 to September 1991, were carried out by more or less the same team, with exactly the same survey design (Bell et al., in press).

In the early 1970s, there were approximately 35,000 elephants in SLNP and LGMA (Bell et al., in press). As a result of the wave of illegal off-take of elephants that spread southwards through Africa starting in the second half of the 1970s, elephant numbers in SLNP and LGMA declined to about 15,000 in 1987 (Fig. 1). In 1988, the population further declined to 2400 (Fig. 1), a decline of approximately 12,500 elephants within a period of one year. Prior to 1979, there was effectively no law-enforcement in the area, and on average 10 elephants were killed by illegal hunters each day (Fig. 1). From 1979 to 1986, the law-enforcement programme of the National Parks and Wildlife Service was supported by 22 scouts of the Save the Rhino Trust (SRT), which operated on a budget of approximately US$15 km⁻² yr⁻¹ (Bell et al., in press). The somewhat improved security situation under SRT resulted in a declining illegal off-take of elephants from 1979 to 1987 (Fig. 1).

The Luangwa Integrated Resource Development Project (LIRDP), operating in SLNP and LGMA and supported by major funding from the Norwegian
The results of a series of 14 aerial surveys, carried out in the central Luangwa Valley between 1973 and 1993, in combination with information from game scout patrol reports, were used in a spreadsheet model to generate numbers of live and dead elephants for each year of the above period (Bell et al., in press). This information was compared with changes in the fraction of tuskless females in the adult female population for the same period.

Fig. 1. The results of a series of 14 aerial surveys, carried out in the central Luangwa Valley between 1973 and 1993, in combination with information from game scout patrol reports, were used in a spreadsheet model to generate numbers of live and dead elephants for each year of the above period (Bell et al., in press). This information was compared with changes in the fraction of tuskless females in the adult female population for the same period.

Elephant mortality; +, elephant numbers; *, % tuskless females.

Agency for Development Cooperation, began its field activities in 1987. Its law-enforcement programme, however, with an operational budget of about US$65 km$^{-2}$ yr$^{-1}$, did not become effective until mid-1988. Between the SRT and LIRDP periods, from 1987 to 1988, the security situation temporarily deteriorated. During this short period, the population of black rhino, the last significant population in Zambia, was annihilated by commercial poachers, who also managed to kill over 1000 elephants during the same period.

The rapid decline of the elephant population between 1987 and 1988, when somewhat less than 12,500 elephants disappeared from the area (Fig. 1), could not have been the result of changes in the aerial survey design, nor the result of a drastically increased mortality (Fig. 1). This sharp decline could have only been the result of movement of large numbers of elephant from the central Luangwa Valley to adjacent Game Management Areas (Lumimba and Munyamadzi GMAs to the north and Chisomo and Sandwe GMAs to the south), most likely due to the relatively low security coverage during this brief period, with the last major influx of commercial illegal hunters, concentrating on black rhino.

With the onset of the effective law-enforcement programme of LIRDP in 1988, illegal hunting declined dramatically to a level of slightly over 20 elephants killed annually from 1989 to 1993 (Fig. 1). As a result of the improved security situation under LIRDP, elephants returned to SLNP and LGMA, starting in 1989. From 1988 to 1989, the population increased by 125%, from 2400 to 5400, and thereafter increased to approximately 6000 in 1993 (Jachmann, unpubl. data), partly due to natural recruitment and partly due to an influx of elephants from adjacent GMAs. However, with the improved security situation under LIRDP and the disappearance of the black rhino from the Luangwa Valley, illegal hunters started to concentrate on the elephant populations in adjacent GMAs, where security levels were low to non-existent. As a result, most of the elephants that moved away from the central Luangwa Valley between 1987 and
Table 1. Tusklessness in adult female elephants in SLNP, Zambia

<table>
<thead>
<tr>
<th>Year</th>
<th>Sample size</th>
<th>Tusked females</th>
<th>Tusless females</th>
<th>% Tusklessness</th>
</tr>
</thead>
<tbody>
<tr>
<td>1969</td>
<td>247</td>
<td>221</td>
<td>26</td>
<td>10.5</td>
</tr>
<tr>
<td>1972</td>
<td>205</td>
<td>180</td>
<td>25</td>
<td>12.2</td>
</tr>
<tr>
<td>1988</td>
<td>132</td>
<td>89</td>
<td>43</td>
<td>32.6</td>
</tr>
<tr>
<td>1989</td>
<td>165</td>
<td>102</td>
<td>63</td>
<td>38.2</td>
</tr>
<tr>
<td>1990</td>
<td>298</td>
<td>194</td>
<td>104</td>
<td>34.9</td>
</tr>
<tr>
<td>1991</td>
<td>171</td>
<td>114</td>
<td>57</td>
<td>33.3</td>
</tr>
<tr>
<td>1992</td>
<td>195</td>
<td>136</td>
<td>59</td>
<td>30.2</td>
</tr>
<tr>
<td>1993</td>
<td>279</td>
<td>199</td>
<td>80</td>
<td>28.7</td>
</tr>
</tbody>
</table>

1988, were killed by illegal hunters operating in the various GMAs bordering on SLNP and LGMA.

**Incidence of tusklessness in the Luangwa elephants**

*Methods*

In 1969 and 1972, samples of 247 and 205 adult female elephants (respectively) were examined for tusklessness (Hanks, 1971; Caughley, 1973). From 1988 to 1993, the population in SLNP was sampled on an annual basis. For each year, the percentage of tuskless adult females (females older than 10 years) was determined.

In 1993, the percentage of tuskless adult males was determined to compare the results with some observations made on tusklessness in adult males in 1969 (Hanks, 1971). Individual recognition of elephants was used wherever possible to avoid counting the same animal twice in a particular year. In addition to the information on tusklessness, from 1992 to 1993, the age and sex composition of 48 elephant groups, mainly family units, was determined, to provide some insight in the genetical mechanism of tusklessness.

**Results**

Apparently, as a direct result of selective illegal ivory hunting, the fraction of adult tuskless females increased from 10.5% in 1969 to 38.2% in 1989 ($\chi^2$, $P<0.001$) (Table 1 and Fig. 1). From 1989 to 1993, however, the fraction of tuskless females declined from 38.2% to 28.7% ($\chi^2$, $P<0.05$) (Table 1 and Fig. 1). Tusklessness in the adult male population appears to have increased from approximately 1% in the early 1970s (Hanks, 1971) to about 10% in 1993. However, this is based on a limited number of observations and should be considered a rough approximation only.

The 48 groups observed in 1992 and 1993, had a mean group size of 6.2 ± 3.1, totalling 296 elephants, of which 145 were adult females (3.0 ± 1.8 per group). Out of 48 groups, 24 groups had one or more adult tuskless female, while 7 of these groups had an additional adult female with a single tusk. There were tuskless sub-adults, which were all females with the exception of two sub-adult males, in all of the 24 groups. Out of the 24 remaining groups without tuskless
adult females, there were only two groups with one adult female with a single tusk, but none of the groups had tuskless sub-adults. Hence, tusklessness appears to run in families, while it is rare in males, but common in females in the Luangwa Valley. As a general rule, a male carrying ivory and a tuskless female appear to have female offspring without tusks and male offspring with tusks. The two tuskless sub-adult males may have been the offspring of a tuskless male and a tuskless female. Both the penetrance and expressivity of the gene complex coding for tusk growth appear to be high, while at least part of the gene complex is sex-linked.

Discussion

The decline in the fraction of tuskless adult females from 1989 to 1993 may be partly explained by the deterioration in the security situation between 1987 and 1988, when the last wave of commercial illegal hunting for rhino and elephant chased a large number of elephants into the GMAs to the north and to the south of SLNP.

Elephants did not move into the Lupande GMA, situated east of SLNP, most likely on account of a small population of black rhino in the Chindeni Hills, that was intensively hunted by commercial gangs. As a direct result of selective hunting pressures (i.e. less pressure on elephant groups carrying insignificant ivory), proportionally more elephants with tusks than without tusks may have moved away from the area. In the late 1980s, this may have temporarily raised the fraction of tuskless females in SLNP. When the surviving elephants started to return to the central Luangwa Valley in 1989, a possibly larger fraction of animals carrying ivory caused relative numbers of tuskless females to drop.

In 1972 there were approximately 35,000 elephants in the central Luangwa Valley (SLNP and LGMA), declining to 15,000 in 1987, after which a large number of elephants moved away from the area. Assuming that the population contained approximately 50% adults with a sex-ratio of 1:2.0 in favour of females (Jachmann, 1980), there would have been approximately 1400 tuskless adult females (12241) in the population in 1972.

Using a density-dependent recruitment rate, increasing from 2% in 1972 to 5% in 1987 and a density-dependent natural mortality rate for tuskless females, decreasing from 4% in 1972 to 2% in 1987, the fraction of adult tuskless females would have been 28.8% in 1987. Although the model is highly simplified, using a constant proportion of adults and a constant sex-ratio for a period of 15 years, the outcome is fairly close to the figure of 32.6% (1988) obtained through field observations with a sample size of only 132 elephants (Table 1).

Maintaining the current low level of illegal off-take, the net influx of elephants into the central Luangwa Valley will eventually stabilize, as well as the sex-ratio, and the fraction of adult tuskless females will probably level out somewhere between 20 and 30% of the adult female population. In the event of another wave of illegal off-take in the future, a large proportion of the current population is more or less guaranteed to survive because of the high percentage of tuskless elephants in the population, while the fraction of tuskless elephants will continue to increase under selective hunting pressures.
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References


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