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Population ecology

Severe drought and calf survival in elephants

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Climate change in Africa is expected to lead to a higher occurrence of severe droughts in semi-arid and arid ecosystems. Understanding how animal populations react to such events is thus crucial for addressing future challenges for wildlife management and conservation. We explored how gender, age, mother's experience and family group characteristics determined calf survival in an elephant population during a severe drought in Tanzania in 1993. Young males were particularly sensitive to the drought and calf loss was higher among young mothers than among more experienced mothers. We also report high variability in calf mortality between different family groups, with family groups that remained in the National Park suffering heavy calf loss, compared with the ones that left the Park. This study highlights how severe droughts can dramatically affect early survival of large herbivores and suggests that extreme climatic events might act as a selection force on vertebrate populations, allowing only individuals with the appropriate behaviour and/or knowledge to survive.

Keywords: *Loxodonta africana*; drought; Tanzania; matriarchs

1. INTRODUCTION

Droughts are of regular occurrence and are expected to become more frequent in most arid and semi-arid ecosystems (Easterling *et al.* 2000). Understanding how animal populations react to such hydric stress is thus crucial to address future challenges in wildlife management and conservation (Garel *et al.* 2004), especially in these drought-sensitive areas (Saltz *et al.* 2006). In such ecosystems, however, drought can vary in severity: rainfall records from Tsavo National Park, Kenya, showed, for example, that poor rainfall leading to food stress for wildlife occurs in every five years on average (Phillipson 1975). Extended periods of severe droughts are rarer, with previous projections suggesting that droughts leading to famine would occur, on average, every 43–50 years (Phillipson 1975). Such a drought was experienced by elephants (*Loxodonta africana*) in Tarangire National Park (TNP), Tanzania, in 1993. As a consequence normal patterns of wet and dry season movements and range use were disrupted, with some groups moving to unknown areas outside the normal dry season refugia of the Park, while others remained within the Park during the drought period.

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This study aims to examine mortality patterns among elephant calves during this extreme climatic event. Among large mammals, early survival is most sensitive to variations in density and climatic conditions (Gaillard *et al.* 2000). Most of the deaths during the 1993 drought occurred among calves, so our analyses focused on mortality patterns among calves. We addressed the following questions: (i) was there any between-sex difference in calf mortality? (ii) Did the age of the mother influence the calf's likelihood to survive? (iii) Was there any advantage for calves to belong to family groups that moved out of the National Park during the drought?

2. MATERIAL AND METHODS

(a) *Study area*

The study area is in TNP in Northern Tanzania (latitude 3°40′ E—4°35′ S, longitude 35°45′—37′ E, elevation 1100 m). Mean annual rainfall is 656 ± 239 mm ($n=26$ years), and annual rainfall is bimodal with rains mostly falling from November to May (figure 1). In 1993, a severe drought occurred, with only 57 mm of rain falling between June 1993 and February 1994 (Foley, C. A. H. 2002).

(b) *Elephant data*

The monitoring of the TNP elephants is an ongoing long-term project that started in 1993 (Foley, C. A. H. 2002; appendix in the electronic supplementary material). By June 1993, 21 family groups and 3 clans were identified (table 1). The three clans form the northern sub-population of elephants that share the same wet season dispersal range (Foley, C. A. H. 2002). A combination of body size, and tusk length and circumference was used to estimate the ages of elephants (Moss 1988). From 22 November 1993 to 11 February 1994 when the first rains fell, a second survey was performed and a total of 56 full days were spent in the Park locating elephant groups.

(c) *Statistical analyses*

We used generalized linear models to assess the factors affecting the survival of 81 calves (under age 8) belonging to 21 family groups, from June 1993 (start of the dry season) to February 1994. Death was considered to have occurred (i) if the carcass of the calf was found during the period considered or (ii) if the calf was never seen alive again after February 1994, although the calf mother and the family group were regularly observed (appendix in the electronic supplementary material).

Factors considered included the sex of the calf, the age of the mother and whether the calf's family group left the Park during the 1993 drought. Family groups that were recorded in the Park for less than 10 per cent of observation days during the drought were considered to have migrated outside the Park boundary (table 1). All the statistical analyses were performed in the statistical package R (www.r-project.org).

3. RESULTS

Sixteen of 81 elephant calves died within a 9-month period: 11 out of 27 belonged to clan B, 4 out of 39 to clan A and 1 out of 15 to clan C (table 1). Mother's age was a significant predictor of calf survival, with younger mothers having a lower chance of their calf surviving the drought (slope$=0.22 \pm 0.10$, $z=2.23$, $p=0.03$). The sex and age of the calf were also found to significantly influence survival probability: young males had the lowest chance of surviving the 1993 drought (table 2). Finally, calves belonging to family groups that migrated out of the National Park suffered lower mortality than calves whose family group remained in the Park (table 2).

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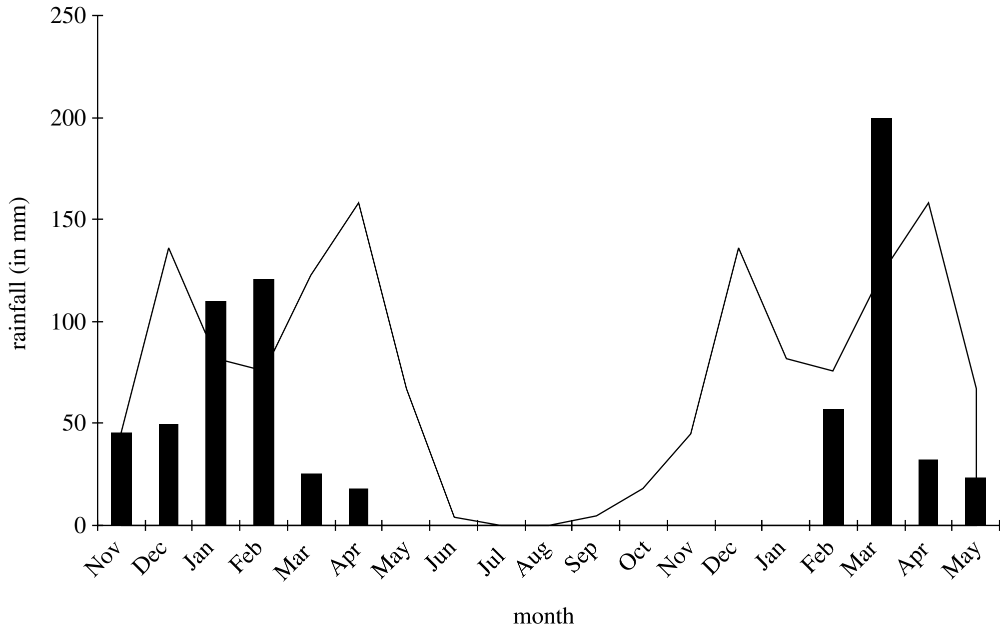

Figure 1. Monthly rainfall (in mm) in TNP. Black bars indicate monthly precipitations (in mm) from November 1992 to May 1994. For information on the usual rainfall pattern in the area, we have provided the average monthly precipitation from 1995 to 2004 (curve). Since the monthly precipitation from November 1992 to May 1994 covers a 19-month period, the average monthly precipitation from 1995 to 2004 has been duplicated when needed.

Table 1. Family group and clan affiliation, age of the matriarch in June 1993, number (no.) of calves per family group in June 1993, number (no.) of calves lost per family group during the drought (June 1993–February 1994) and percentage (%) of observation days (based on a 56 full-day monitoring) where the matriarch was seen in TNP for each of the 21 family groups considered. (Family group sizes include all adult females and all calves less than 8 years in age. For three family groups, not all family members were identified by June 1993: we have therefore provided in bracket the family size estimates for May 1994, when all members were identified.)

family group	clan	age matriarch 1993	no. calves per family June 1993	no. calves died	% days seen in the Park	no. adult females in June 1993	family size in June 1993
A	A	45	2	1	0	8	11
Cl	A	38	3	0	0	2 (6)	5 (11)
D	A	35	6	0	0	5	10
F	A	26	5	2	0	3	8
G	A	26	3	0	29	5	8
I	A	23	3	0	2	3	6
L	A	38	7	1	16	5	12
Na	A	26	3	0	0	1	4
Ol	A	26	2	0	2	1	3
Si	A	26	4	0	7	3 (6)	7 (11)
X	A	14	1	0	0	1	2
El	B	33	3	1	44	6	9
H	B	23	3	2	29	4	8
K	B	25	10	4	53	11	21
Ob	B	23	5	1	66	6	11
Ve	B	26	5	3	37	6	13
Y	B	20	1	0	16	2	3
Be	C	18	1	0	0	1	2
C	C	33	7	0	4	9	16
S	C	33	5	1	0	6	11
W	C	38	2	0	0	1 (4)	3 (9)

4. DISCUSSION

In the TNP elephant population, calf mortality during non-drought periods is generally extremely low, with an average annual mortality of 2 per cent over the last 12 years (C. Foley 2005, unpublished data). However, in 1993, 20 per cent of the monitored calves died within a 9-month period (table 1; appendix in the electronic supplementary material). The majority of calf deaths (at least 63%) occurred within the Park in the later stages of the drought.

As expected for a highly dimorphic ungulate species (Clutton-Brock *et al.* 1985), young males suffered most from the severe drought. In accordance with previous work on factors affecting early survival

Table 2. Parameter estimates from the generalized linear model considering survival of the calves (less than 8 years of age) as a function of the age of the mother, the family group migration pattern, the sex of the calf and the age of the calf (in years).

parameters	estimates	s.e.	*z*-value	*p*-value
intercept	−3.42	2.18	−1.57	0.12
age of the mother	0.22	0.10	2.23	0.03
migration	1.88	0.82	2.31	0.02
males	−2.22	1.16	−1.91	0.06
calf age	−0.30	0.28	−1.09	0.27
males × calf age	1.02	0.50	2.03	0.04

in mammals, calf mortality was moreover lower among experienced mothers than among younger mothers (Weladji *et al.* 2006). We also report high variability in the mortality patterns of calves among different family groups. Family groups that remained in the Park during the drought suffered heavy calf loss, compared with the family groups that left the Park. Mortality patterns during the drought and outside the drought are, however, different among families (appendix in the electronic supplementary material), suggesting that the families that did badly during the drought do not always have low calf survival.

During non-drought years, the whole ungulate migration pattern in TNP hinges on the availability of standing water in the main dispersal areas: if those are dry (i.e. during the dry season) then the elephants are found in the Park (TWCM 1998; Foley, C. A. H. 2002). During the 1993 drought, however, some families left the Park, and our results show that such a strategy was successful since those families experienced lower calf loss. This might suggest that family groups that left the Park were able to find sources of food and permanent water during their migration. This hypothesis is supported by the spatial distribution of permanent water points in the area and primary productivity estimates inside and outside the TNP (appendix in the electronic supplementary material). It is clear that the families that left were not migrating to their regular wet season dispersal area to the northeast of TNP during this time, as this area has no permanent water (Foley, L. S. 2002).

Food resource limitation leading to some families moving out of the Park is, however, not the only possible reason for the observed lower calf survival inside TNP. Lion predation on elephant calves during drought is known to increase (Loveridge *et al.* 2006): if predator density was higher in TNP than outside the Park, this difference might have contributed to generating the reported differences in calf mortality.

During the 1993 drought, family group migration was linked to clan affiliation: the majority of the family groups from the two clans (clans A and C; table 1) left the Park, while family groups from the third clan (clan B) remained in the northern area of the Park. The previous drought reaching the magnitude of the 1993 drought occurred in 1958–1961 (Foley, C. A. H. 2002). Few individuals experienced both the 1958–1961 and the 1993 droughts, since heavy poaching during the 1970s and 1980s led to the selective elimination of older, larger tusked individuals (Foley, C. A. H. 2002). Interestingly, clans A and C were the only clans with individuals aged 5 years or older during the first drought in 1958–1961. It might thus be possible that clan B remained within the Park during the 1993 drought because the sole surviving older female lacked knowledge of areas with forage and water outside the Park, while older matriarchs in the other clans were able to lead their groups, and probably other groups within the clan, to such refugia using their previous experience to guide them (Sukumar 1989). As previously stated, however, important differences occur between family groups and probably clans in terms of group sizes, proportion of animals of different age and sex classes and experience. Our results show that these differences are important in drought conditions, but we are unable to conclude which difference(s) led to higher calf survival in clans A and C.

Why did the family groups from clan B not follow those of other clans when they left the Park? The most likely reason is that, because clans separate during dry periods (Moss & Poole 1983), the probability of overlapping with family groups from other clans is reduced. Therefore, family groups belonging to clan B were probably unlikely to have been in the vicinity of other clans when the latter left TNP. This pattern of results might also be explained, if family groups from clan B were competitively excluded by members of clans A and C (Wittemyer *et al.* 2007). At the family group scale, we believe this hypothesis to be unlikely, since data from the area suggest that when resources are scarce dominant females will displace other individuals regardless of clan affiliation (Foley, C. A. H. 2002).

This study thus provides another example of how extreme climatic events such as droughts can strongly affect calf survival in elephant populations (Woolley *et al.* 2008). It also suggests that climatic change and extreme climatic events might act as a selection force on vertebrate populations, allowing only individuals with the appropriate behaviour and/or knowledge to survive.

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