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REVIEW

The historical ecology of the large mammal populations of Ngorongoro Crater, Tanzania, east Africa

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ABSTRACT

1. Ngorongoro Crater is an ecologically important protected area in Tanzania, east Africa. We review published and unpublished data on the crater's large mammal community from the first recorded visit by a European in 1892 to 2010.

2. Early estimates often exaggerated large herbivore numbers and regular scientific censuses have only been made since the 1960s. Since then, most large herbivore populations have declined, particularly wildebeest *Connochaetes taurinus*, which have been replaced by buffalo *Syncerus caffer* as the dominant herbivore in terms of biomass. The internationally important population of black rhinoceros *Diceros bicornis* has reduced from over 100 in the 1960s to around 30 in 2011. The lion *Panthera leo* population is genetically isolated, has declined since the 1960s and has consistently been held below carrying capacity.

3. Buffalo and warthogs *Phacochoerus aethiopicus* are relatively recent colonizers. Wild dogs *Lycaon pictus* were present in the 1960s but are probably now absent. Small numbers of elephants *Loxodonta africana* use the crater floor and cheetahs *Acinonyx jubatus* appear to be intermittent visitors.

4. Primary drivers of changes in herbivore populations are disease and vegetation change. Poaching has been implicated as the cause of decline in rhinoceros. Disease associated with anomalous weather conditions appears to be the main driver for population change in lions.

5. Recent scientific research on the large mammal community has largely been focused on lions and rhinoceros. The output of research on other species has not increased since the 1960s.

6. A wider dissemination of research on the crater's mammal populations would help to secure its status as an important site for conservation in the eyes of the wider scientific and conservation community.

Keywords: community ecology, ecosystem management, population dynamics, Serengeti, wildlife laws

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INTRODUCTION

Ngorongoro Crater is an internationally important wildlife site. It is part of a Biosphere Reserve (Anonymous 2010) and World Heritage Site (Anonymous 2011a). Despite its ecological importance, a comprehensive historical record of its large mammalian fauna does not exist.

Location and geomorphology

Ngorongoro Crater is a caldera (collapsed volcano) located in the East African Rift System in northern Tanzania (2°30′–3°30′ S, 34°50′–35°55′ E), adjacent to the Serengeti National Park (SNP) and within the administrative region of Arusha. It is situated within the Ngorongoro Conservation Area (NCA) which covers 8292km^2 and is divided geomorphologically into the crater highlands (including the crater itself), the Angata Salei Plains, the Gol Mountains, the Serengeti Plains and the Lake Eyasi Scarp (Homewood & Rodgers 1991). The crater (Fig. 1) is approximately 19km in diameter and contains a seasonal soda lake, Lake Magadi (Makat). The floor is 1800m above sea level, has an area of 250km^2 and is surrounded by an unbroken rim that ranges in height from 400 to 600m.

Climate and vegetation

The vegetation of the crater floor consists of semi-arid savanna containing grasses, notably *Chloris* spp., *Themeda* spp., *Cynodon* spp., *Digitaria* spp. and *Sporobolus* spp. (Herlocker & Dirschl 1972, Misana 1997), with scattered bushes and trees, the Lerai

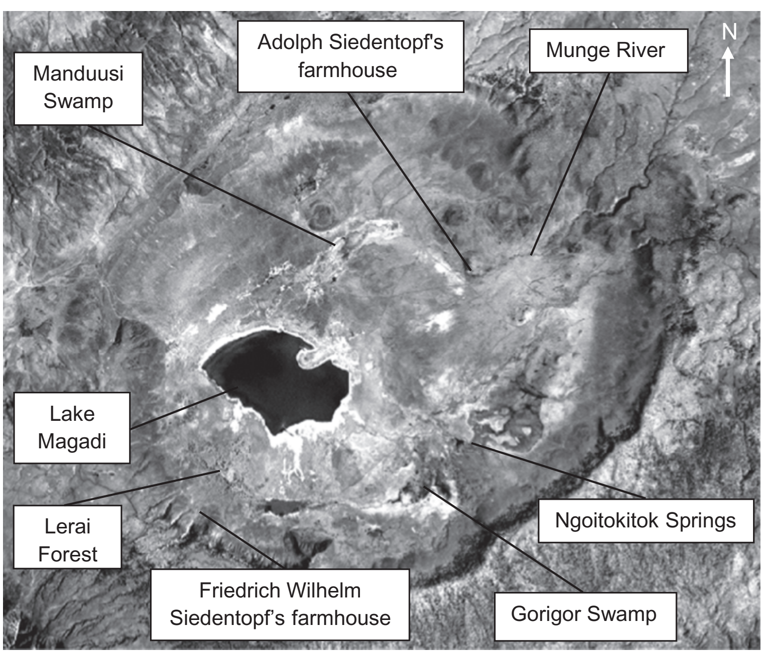

Fig. 1. Satellite image of Ngorongoro Crater, Tanzania, east Africa, showing the main features of the crater floor (source: USGS Earth Explorer). The crater, which is *c.* 19km in diameter, is in the East African Rift System in northern Tanzania (2°30′–3°30′ S, 34°50′–35°55′ E), adjacent to the Serengeti National Park and within the administrative region of Arusha, Tanzania.

and Ngoitokitok ground-water forests (comprised predominantly of the yellow-barked fever tree *Acacia xanthophloea*) and the Manduusi and Gorigor swamps.

The crater receives a short period of rains between November and December and a longer, heavier period between March and May. As the prevailing winds are from the east, the outer eastern slopes are considerably wetter (800–1200mm rain year^{-1}) than those in the west (400–600mm rain year^{-1}) and the crater floor (Estes et al. 2006). As a result, the eastern slopes are covered in dense forest, while the western slopes are mainly grassland interspersed with xerophytic species, dominated by *Euphorbia nyikae*, which give this ecotone its characteristic appearance.

Changes to legislation and land ownership

The first foreign visitor to the crater appears to have been the Austrian explorer Oscar Baumann in 1892 (Baumann 1894; translated in Organ & Fosbrooke 1963). The first Europeans to own land here were the German brothers Adolph and Friedrich Siedentopf, who entered the crater in 1899 and ranched cattle. They tried in vain to drive the large game herds from the crater (Grzimek & Grzimek 1960) and killed thousands of wildebeest *Connochaetes taurinus* in order to can their tongues (Herne 1999). The Siedentopfs left with the onset of the First World War and their land was subsequently bought by Sir Charles Ross, a big game hunter, who had first visited the crater in 1921 (Fosbrooke 1972).

In 1914, the German administration recognized the importance of the Northern Highland Forest Reserve as a water catchment area for the NCA and demarcated its boundaries (Homewood & Rodgers 1991). In 1921, the first Game Preservation Ordinance was passed which restricted hunting to permit holders throughout Tanzania (Anonymous 1957). In 1928, the crater became a 'Complete Reserve', in which hunting was prohibited on all land within the crater rim, except the former Siedentopf farms (Homewood & Rodgers 1991). However, Ross prohibited hunting on his land and as such was the first person to regard the crater as a sanctuary (Fosbrooke 1972). The National Park Ordinance of 1948 (implemented in 1951) created the SNP. However, this caused problems with the Masai and other tribes and an extended period of expert consultation culminated in the NCA Ordinance (1959) which separated the NCA from the SNP (Homewood & Rodgers 1991). The NCA was to be managed by the Ngorongoro Conservation Unit with consideration for both the wildlife and human inhabitants. The unit was disbanded in 1963 and Henry Fosbrooke was appointed as the NCA's first conservator. The NCA Authority (NCAA) was established by the Game Park Laws (miscellaneous amendments) Act, 1976 and owns the majority of NCA land, including the crater.

Early accounts and censuses of the large mammals of Ngorongoro Crater, and aim of this review

The first description of the crater was written in German by Baumann (Organ & Fosbrooke 1963) who visited in 1892, and the first English language account was by Barns (1921). Baumann referred to the presence of only four large mammal species: wildebeest, zebras *Equus burchellii*, hippopotamuses *Hippopotamus amphibius* and black rhinoceros *Diceros bicornis* (Organ & Fosbrooke 1963).

Historical accounts probably overestimated the number of animals living within the crater. In the early 1900s, FR Holmes (Holmes 1929) and Captain GHR Hurst (Fosbrooke 1972) estimated that the large mammal population numbered 100000 and 500000, respectively. Dr Hans Poeschel, who visited the Siedentopf brothers before the onset of the First World War, stated that, according to several experienced game hunters, the crater held over 20000 wildebeest (Grzimek & Grzimek 1960). In 1921, Major AR Dugmore estimated that there were over 75000 large mammals, while Barns suggested that wildebeest alone numbered 50000 (Fosbrooke 1972). Molloy and Harvey in 1959 estimated that the crater contained just 7800 wildebeest (Grzimek & Grzimek 1960). The first aerial census by Grzimek and Grzimek (1960) counted 8500 large mammals in 1958. A second aerial survey by Turner and Watson (1964) counted over 22000. Recent counts (1999–2005) show that the total number of wildebeest, buffalo *Syncerus caffer*, zebras, Grant's gazelles *Nanger granti* and Thomson's gazelles *Eudorcas thomsonii* alone fluctuates between 15000 and 28000 (Estes et al. 2006).

Early researchers debated whether migration occurred between the crater and the SNP (e.g. Grzimek & Grzimek 1960). Estes (1966) established that some wildebeest left the crater during the rains and it is now accepted that a number of species migrate out regularly (Estes & Small 1981). Several species found in the SNP are absent from the crater, including giraffes *Giraffa camelopardalis*, impalas *Aepyceros melampus*, topis *Damaliscus korrigum* and oribis *Ourebia ourebi* (Estes et al. 2006). Giraffes may be absent due to a lack of browse species (e.g. *Acacia tortilis*, *A. melifera* and *A. seyal*) and the open woodland preferred by impalas is absent (Fosbrooke 1972).

This paper is a review of published and unpublished data on the crater's large mammal community from the first recorded visit by a European in 1892 to 2010.

METHODS

A literature review was conducted which included peer-reviewed journal articles, books (notably Fosbrooke 1972), magazine articles (e.g. *National Geographic*) and grey literature (e.g. Proceedings of the Ngorongoro Black Rhino Workshop). Specialist collections were consulted including that of the Zoological Society of London, UK and the 'African Collection' at Edinburgh University, UK. Specialist data bases were also consulted (e.g. http://www.serengetidata.org). Census data were extracted from the annual reports of the NCAA (1964–90), obtained from the College of African Wildlife Management, Tanzania, and from peer-reviewed research papers (e.g. Estes et al. 2006). Additional records for 2003–06 were drawn from unpublished data (Rees et al. 2006).

The census methods used varied both within and between individual studies. For example Estes et al. (2006) concatenated estimates made using strip counts, aerial counts and total ground counts for five species, while Goddard (1966) made a total count using individual identification for rhinoceros. Estimates of the changes in the population size of any species which are derived from the concatenation of data from several sources are inevitably subject to errors. Where more than one record existed for a year from independent sources, an average was taken, except for rhinoceros, where studies using individual identification techniques were considered most reliable (Goddard 1967a).

RESULTS

Large mammal population trends

Changes in the large mammal community are presented in the form of the presence or absence of published records for 23 species (Table 1) – based on 62 sources

Table 1. Timeline of records in the literature for the presence of large mammal species (top: herbivores, bottom: carnivores) in Ngorongoro Crater

	1892	1921			1924	1954					1959	1960										1970										1980										1990										2000						2006
Wildebeest	•	•	•					•	•	•	•		•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•		•						•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Zebra	•	•							•	•				•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•		•						•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Grant's gazelle		•							•	•				•	•	•	•			•	•	•	•	•	•	•	•	•	•	•								•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Thomson's gazelle		•							•	•				•	•	•	•			•	•	•	•	•	•	•	•	•	•	•								•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Warthog																																•							•	•	•	•	•	•											•	•	•	•
Hippopotamus	•	•													•	•	•	•		•			•	•	•	•	•	•	•	•										•		•		•			•	•	•	•	•	•			•	•	•	•
Black rhinoceros	•	•							•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•				•	•	•	•	•	•	•	•		•			•	•	•	•		•	•	•	•
Hartebeest		•													•	•	•	•		•	•	•	•	•	•	•	•	•	•	•		•						•	•	•	•	•	•	•										•	•	•	•
Buffalo										•						•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•						•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Elephant									•	•						•	•	•		•	•	•	•	•	•	•	•	•	•	•						•	•			•	•	•		•									•		•	•	•	•
Eland									•	•					•	•	•	•		•	•	•	•	•	•	•	•	•	•	•		•						•	•	•	•	•	•	•										•	•	•	•
Waterbuck															•	•	•	•		•	•	•	•	•	•	•	•	•	•	•		•						•	•	•	•	•	•	•											•	•	•
Reedbuck		•																						•																																	
Oribi		•																																																							
Lion		•		•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•
Wild dog													•			•	•		•	•																																					
Golden jackal																	•																								•		•											•	•	•	
Black backed jackal																															•										•		•											•	•	•	
Hyena		•								•						•	•	•	•	•											•	•										•		•				•	•	•	•	•	•	•	•	•	•	•
Bat-eared fox																																																						•			•
Cheetah		•																																	•		•			•					•	•										•	•	•
Leopard																																																									•
Serval									•																				•	•	•	•	•																								

(Table 2) – and as graphs of population size for the five most common species and black rhinoceros (Fig. 2).

Herbivores

The wildebeest population increased between 1963 and 1974, from approximately 7500 to about 15000, and thereafter declined (Runyoro et al. 1995). Numbers declined by 58% between 1980 and 2005 from over 18000 to an average of 7522, with a temporary increase to a mean of 11441 between 1999 and 2002 (Estes et al. 2006).

The zebra population fluctuated between around 2500 and 6000 between 1963 and 1974 but subsequently declined by approximately 45% (from a mean of 4422 in 1972 to a mean of 2440 in 1998). The population then increased by about a thousand in 2002 and remained stable to 2005 (Estes et al. 2006).

Buffalo distribution in the crater has changed markedly since the late 1950s. The first buffalo to be recorded were observed by H Lamprey in 1958 (Rose 1975) who reported one herd of approximately 100 in the north of the crater. Prior to the 1960s, buffalo were rarely seen in the crater and inhabited the crater rim forests (Fosbrooke 1972). In 1968, Lamprey observed herds moving further into the open, and herd sizes increasing. There are published records of the presence of buffalo in almost every year since 1964, suggesting a continuous presence, and they were considered resident by the mid-1970s (Rose 1975). The first official count of buffalo in the crater was undertaken in 1964 by Turner and Watson (1964), who recorded 11 animals. Between 1964 and 1973, there was an exponential increase in buffalo numbers in the crater (Rose 1975). The population exceeded 1000 by 1973 and peaked at around 6500 in 1994 (Estes et al. 2006).

The Thomson's gazelle population increased between 1963 and 1974 (from approximately 1500 to 3900 animals; Runyoro et al. 1995) and subsequently decreased. Estes et al. (2006) estimated that it had decreased by two-thirds since 1978, from just over 3100 animals to an average of 1016 in 2005. From 1963 to 1974, the population of Grant's gazelles increased by 88% from 800 animals to around 1500. Subsequently, the population decreased to an average of 742 in 2005, a decline of 51% (Runyoro et al. 1995, Estes et al. 2006).

The crater black rhinoceros population was once one of the densest in Africa. Homewood and Rodgers (1991) described it as still the largest population in northern Tanzania, despite numbering approximately 11 individuals at the time of publication (Anonymous 1990). As black rhinoceros are currently listed as critically endangered on the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List (Anonymous 2011b) and in Appendix 1 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (Anonymous 2011c), the population in Ngorongoro Crater is biologically important for the species (Homewood & Rodgers 1991). As a result of this, conservation and research activities have led to many records of their presence in the crater. Rhinoceros numbers in the crater have decreased dramatically since the 1960s (Fig. 2f). They were once so abundant in the crater that 'they may well (have) be(en) classed as vermin' (Major Brown quoted in Barns 1921). Numbers decreased from approximately 110 animals in the mid-1960s to around 20 in the mid-1970s (Borner 1981). Goddard believed that the black rhinoceros in the crater form a sedentary, discreet population restricted to the crater and its walls (Goddard 1967b) and Moehlman et al. (1996) regarded the

Table 2. References used to compile Table 1

	Barns 1923	Holmes 1929	Hunter 1952	Pearsall 1957	Boyle 1958	Swynnerton 1958	Grzimek & Grzimek 1960	Organ & Fosbrooke 1963	Talbot & Talbot 1963	Grzimek 1964	Turner & Watson 1964	Walther 1965a, b	Estes 1966	Klingel & Klingel 1966	Estes 1967
Wildebeest	•	•		•	•	•	•	•	•		•		•		
Zebra	•						•	•			•				
Grant's gazelle	•				•		•					•			•
Thomson's gazelle	•				•		•					•			•
Warthog															
Hippopotamus	•							•			•				
Black rhinoceros	•						•	•			•			•	
Hartebeest	•										•				
Buffalo											•				
Elephant							•				•				
Eland					•		•				•				
Waterbuck											•				
Reedbuck	•														
Oribi	•														
Lion	•		•		•					•	•				
Wild dog															
Golden jackal															
Black backed jackal															
Hyena	•						•								
Bat-eared fox															
Cheetah	•														
Leopard															
Serval					•										

	Estes & Goddard 1967	Goddard 1967b	Fosbrooke 1972	Kruuk 1966, 1972	Schaller 1972	Estes 1976	Elliott & McTaggart-Cowan 1978	Tobias 1978	Estes & Estes 1979	Makacha et al. 1979	Borner 1981	Geertsema 1985	Anonymous 1989	Kiwia 1989a, b	Anonymous 1990
Wildebeest			•	•		•	•	•	•						
Zebra			•	•			•	•							
Grant's gazelle				•			•								
Thomson's gazelle				•			•								
Warthog															•
Hippopotamus															•
Black rhinoceros		•						•		•	•		•	•	•
Hartebeest				•			•								•
Buffalo				•											•
Elephant								•							•
Eland				•			•								•
Waterbuck				•			•								•
Reedbuck				•											
Oribi															
Lion			•	•	•		•								•
Wild dog	•		•		•										
Golden jackal				•											•
Black backed jackal												•			•
Hyena				•								•			•
Bat-eared fox															
Cheetah															
Leopard															
Serval												•			

	Averbeck et al. 1990	Brown et al. 1991	Packer et al. 1991b	Packer 1992	Brown et al. 1993	Anonymous 1993	Kabigumila 1993	Pusey & Packer 1994	Muller-Graf 1995	Heyworth 1995	Runyoro et al. 1995	Martin 1998	Selvaggio 1998	Packer et al. 1999	Gros 2000
Wildebeest											•				
Zebra											•				
Grant's gazelle											•				
Thomson's gazelle											•				
Warthog						•					•				
Hippopotamus						•					•				
Black rhinoceros						•				•	•				
Hartebeest						•					•				
Buffalo						•					•				
Elephant						•	•				•				
Eland						•					•				
Waterbuck						•					•				
Reedbuck															
Oribi															
Lion	•	•	•	•	•	•		•	•					•	
Wild dog						•									
Golden jackal						•									
Black backed jackal						•									
Hyena						•		•					•		
Bat-eared fox															
Cheetah	•											•			•
Leopard															
Serval															

	Mkenda & Butchart 2000	Maige 2001	Deocampo 2002	Honer et al. 2002	Ambrose 2003	Jourdain 2003	Kissui & Packer 2004	Cleaveland et al. 2005	Estes et al. 2006	Honer et al. 2006	Mills et al. 2006	Rees et al. 2006	Honer et al. 2007	Fyumagwa et al. 2008
Wildebeest									•			•		•
Zebra									•			•		•
Grant's gazelle									•			•		
Thomson's gazelle									•			•		
Warthog												•		
Hippopotamus			•									•		
Black rhinoceros	•	•			•						•	•		
Hartebeest												•		
Buffalo									•			•		•
Elephant						•						•		
Eland												•		
Waterbuck												•		
Reedbuck														
Oribi														
Lion							•	•				•		•
Wild dog														
Golden jackal												•		
Black backed jackal												•		
Hyena				•						•		•	•	
Bat-eared fox												•		
Cheetah												•		
Leopard												•		
Serval														

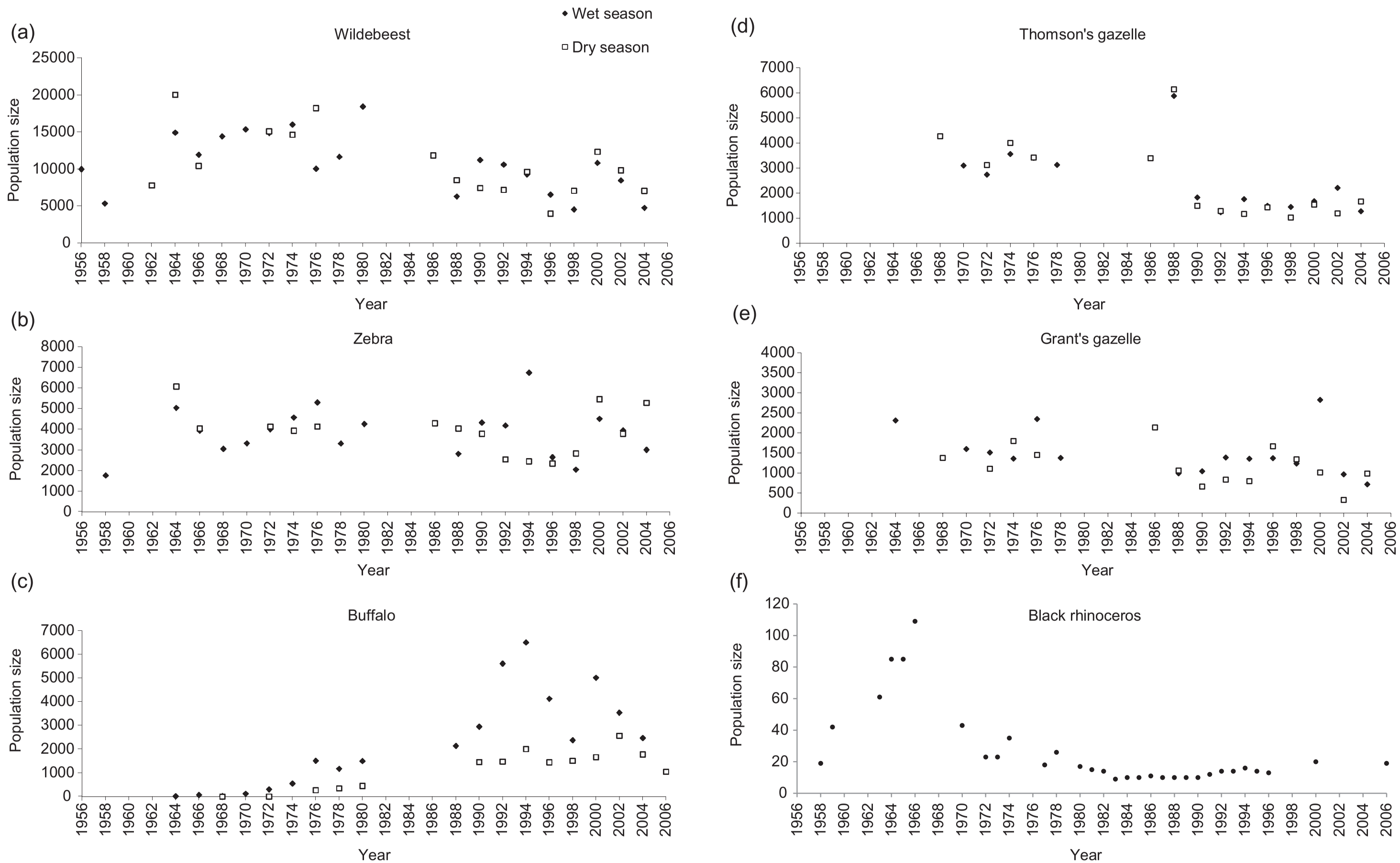

Fig. 2. Population trends of six large herbivore species [a – wildebeest *Connochaetes taurinus*, b – zebra *Equus burchellii*, c – buffalo *Syncerus caffer*, d – Thomson's gazelle *Eudorcas thomsonii*, e – Grant's gazelle *Nanger granti* (in wet and dry seasons) and f – black rhinoceros *Diceros bicornis* (annual counts)] in Ngorongoro Crater, Tanzania from 1956 to 2006, where data are available [based on data from Pearsall (1957), Grzimek & Grzimek (1960), Organ & Fosbrooke (1963), Talbot & Talbot (1963), Turner & Watson (1964), Goddard (1966, 1967a), Klingel & Klingel (1966), Anonymous (1980, 1989, 1990), Borner (1981), Estes & Small (1981), Kiwia (1989a), Homewood & Rodgers (1991), Runyoro et al. (1995), Moehlman et al. (1996), Estes et al. (2006) and Mills et al. (2006)].

population as an isolated relict. However, others have concluded that the population consisted of both resident and transient animals (Frame 1980, Kiwia 1989a). Klingel and Klingel (1966) believed that some rhinoceros moved out of the crater 'probably because of adverse conditions in the height of the dry season'. There are presently around 30 rhinoceros in the crater (P. Morkel, personal communication).

The first detailed studies of the rhinoceros population were conducted by Klingel and Klingel (1966) and Goddard (1966, 1967b, 1968). These researchers used an individual identification technique to establish the minimum number of rhinoceros which are utilizing an area (Goddard 1966). Goddard (1967b) found that 108 rhinoceros were using the crater floor and concluded that these animals were permanent residents, as none of the individuals was seen outside the crater walls. Recent researchers have predominantly used individual identification and ground counts. The Ngorongoro Ecological Monitoring Programme used a total ground count method in 1966 (Anonymous 1990), recording one more rhinoceros than Goddard. Runyoro et al. (1995) found that the rhinoceros population apparently fluctuated between zero and 52 prior to 1974 and declined significantly thereafter to an average of 13 in 1992. Kiwia (1989a) noted that, on some occasions, NCAA staff undertaking a total ground count recorded no rhinoceros while they were certainly present. The zero counts were undoubtedly the result of the use of a census method that, although it may have been suitable for other species, was not sensitive enough to detect rhinoceros occurring at relatively low density. Adult mortality between 1993 and 2003 was estimated to be 8%, while neonatal mortality was extremely high (between 25% and 45%; Mills et al. 2006).

Elephants *Loxodonta africana* have been recorded as present in publications since 1958. Individual bulls and small herds frequent the forests on the crater rim making it likely that the species has been continually present in the crater area for some considerable time. However, semi-annual counts conducted by the College of African Wildlife Management indicated that the elephant population reduced to zero in 1969 (quoted in Estes & Small 1981), and between 1963 and 1993 estimates of the elephant population fluctuated between zero and 87 (Runyoro et al. 1995). It has been suggested that only mature bulls (and rarely females) frequent the crater (Kabigumila 1988), however herds of up to a dozen elephants, including subadults, occur around the Lerai Forest and in the swamps, where they feed all year round (RD Estes, personal communication). As many as 56 bull elephants feed on the sedges and reeds of Manduusi and Gorigor swamps in all seasons without visibly diminishing their extent or productivity (Estes 2002).

There appear to have been no studies devoted solely to the hippopotamus population. Grzimek (1964) hypothesized that it may be a relict from thousands of years ago when hippopotamuses populated the entire area due to a wetter climate, since the crater is now isolated from other suitable hippopotamus habitat. Runyoro et al. (1995) found that the population increased by approximately 230% between 1964 and 1988 from 23 to 76 individuals, however this was based on only eight annual census results for the entire period. According to Estes (2002), hippopotamuses live in Gorigor Swamp but apparently not in Manduusi, which regularly dries up after the long rains. The total population is unknown because they are almost impossible to count in the tall dense *Cyperus immensus* and *Typhus laifolia* vegetation of Gorigor. Estes estimates the total population to be more than 200, including individuals that frequent the two hippopotamus pools and various springs, pans and 'puddles'.

During his study of spotted hyenas *Crocuta crocuta*, from 1965 to 1967, Kruuk included warthogs *Phacochoerus aethiopicus* in a list of animals absent from the crater (Kruuk 1972) and the species was still recorded as absent in 1978 (Martin 1998). Fosbrooke (1972) supports this conclusion by claiming that no warthogs were living in the crater, although he mentions this species being present in the past. Packer, writing in 1991, stated that warthogs had entered the crater in the previous 20 years (Packer et al. 1991b). Warthog numbers have been recorded in the crater since 1980 and the population apparently fluctuated between 35 and 336 between 1980 and 1992 (Runyoro et al. 1995). There is no apparent explanation for this relatively recent colonization.

The size of the common eland *Taurotragus oryx* population has apparently reduced from hundreds in the late 1960s to around 30 in 2005 (Moehlman et al. 1996, Estes et al. 2006). Runyoro et al. (1995) found that estimates fluctuated between 77 and 499 animals between 1963 and 1974, declining thereafter from an average of 268 in 1974 to around 18 in 1992. Captain GHR Hurst, a rancher who lived in the crater in the 1920s, stated that 'occasional eland' were present (Joelson 1928). In contrast, Hugo and Jane van Lawick-Goodall anticipated viewing 'huge herds of eland' within the crater before their arrival but did not record the actual number present (van Lawick-Goodall & van Lawick-Goodall 1970).

There are few data on reedbucks *Redunca redunca*. Elliott and McTaggart-Cowan (1978) reported that there were 'hundreds' in the crater but without supporting data (Runyoro et al. 1995). Runyoro et al. (1995) concluded that waterbuck *Kobus ellipsiprymnus* showed 'no change in mean population size' between 1963 and 1993, although estimates indicated fluctuations between 6 and 130.

Hartebeest *Alcelaphus buselaphus* have been included in the major censuses (Runyoro et al. 1995, Estes et al. 2006) but were not mentioned by any of the early explorers and hunters, except for in one record from 1921 (Barns 1923). Censuses suggest that the population increased between 1964 and 1974, from 20 to approximately 200, and then declined to an average of 157 in 1992 (Runyoro et al. 1995).

Oribis are only known from a single published record from 1921 (Barns 1921). Fosbrooke (1972) states that the Masai people remember a giraffe being resident in the crater but provided no date. No further records for giraffes in the crater have been located and several authors specifically note their absence (Fosbrooke 1972, Packer et al. 1991b, Estes et al. 2006).

Carnivores

Comprehensive accounts of the fluctuations in lion *Panthera leo* numbers between 1962 and 2002 are presented by Packer et al. (1991b) and Kissui and Packer (2004). The first published reference to lions is in 'The Highlands of the Great Craters, Tanganyika Territory' (Barns 1921), an account of a visit to the crater in 1921. Earlier records of lions may be absent due to the disturbance caused by the extensive hunting which took place in the crater prior to the First World War. The Siedentopf brothers hunted lions to such an extent that these animals would not approach human camps (Lithgow & van Lawick 2004), and Mrs Eva Wenkel, who lived with the Siedentopf brothers for a year, did not see any lions for the entire duration of her visit, although she did hear them at night (Grzimek & Grzimek 1960). When the Siedentopfs left, the lion population had a chance to recover. In the early 1920s, when the first game laws came into effect, lions were classed as vermin and could be shot by anyone (Fosbrooke 1972). Wright (1960) warned that overpopulation could become a problem after observing a single pride of 30 lions in the crater. Instead, the population began a gradual decline from which it has yet to recover fully (Kissui & Packer 2004).

A photographic identification and genetic study has established that the population is currently genetically isolated and that, in the past, immigration was rare (Packer et al. 1991b). Kissui and Packer (2004) identified four periods of decline. In 1962, the population declined from over 60 lions to just 15 individuals (Fosbrooke 1963). It subsequently recovered, reaching a peak of 124 in 1983, but then entered a gradual decline phase. Closely spaced die-offs in 1994, 1997 and 2001 have meant that the population has not had sufficient time to recover in between, resulting in fewer than 60 lions in the crater since 1994 (Kissui & Packer 2004).

Cheetahs *Acinonyx jubatus* have been described as being present intermittently in the crater (Homewood & Rodgers 1991) and it has been suggested that they were absent prior to *c.* 1988 (Martin 1998). However, Barns recorded their presence in 1921 (Barns 1921) and GHR Hurst described cheetahs as 'common' (Joelson 1928). Cheetahs were described by Laurenson (1991) as 'virtually absent', although they were recorded in 2004–06, and a ranger reported a cheetah being killed by a leopard *Panthera pardus* during a mammal census in 2006 (Rees et al. 2006). Too few records of leopards exist to draw any conclusions about their history in the crater. The first published record of servals *Leptailurus serval* appears to be from 1957 (Boyle 1958). A detailed study of serval behaviour was undertaken between 1977 and 1981 (Geertsema 1985), and the species was recorded by Rees et al. (2006).

Data on the spotted hyena population size are rare. Kruuk (1972) estimated the total at 430 individuals, including 385 adults. By 2000, the population had apparently declined to 139 (Estes et al. 2006).

Records for wild dogs *Lycaon pictus* are rare and they have been described as being present only intermittently (Homewood & Rodgers 1991). Fosbrooke (1972) describes the movements of wild dogs into and out of the crater between the years 1961 and 1966, and the species becoming completely absent in 1962–63. Estes and Goddard (1967) and Schaller (1972) also recorded that wild dogs were present in the 1960s. Packer et al. (1991b) state that they had been 'absent for nearly 20 years' and none was recorded by Rees et al. (2006) during censuses in 2003–06.

A small number of records exist for other canids. Golden jackals *Canis aureus* were first mentioned as present in 1965 by Kruuk (1972) and black-backed jackals *C. mesomelas* in 1979 (Geertsema 1985). Both canids were recorded by Rees et al. (2006) in 2003–05. Before 1994, the abundance of both species was similar, although *C. mesomelas* subsequently became dominant (Estes et al. 2006). Rees et al. (2006) recorded the bat-eared fox *Otocyon megalotis* in 2003 and 2006 but no other published records appear to exist.

Drivers of change in the crater

The most significant change in the dynamics of large herbivore populations in the crater has been the general decline in most grazing species since the 1970s, except for buffalo, which has replaced wildebeest as the dominant species in terms of biomass (Runyoro et al. 1995. Estes et al. 2006). There are several possible reasons for this and a number of drivers of other changes in the large mammal community (Fig. 3).

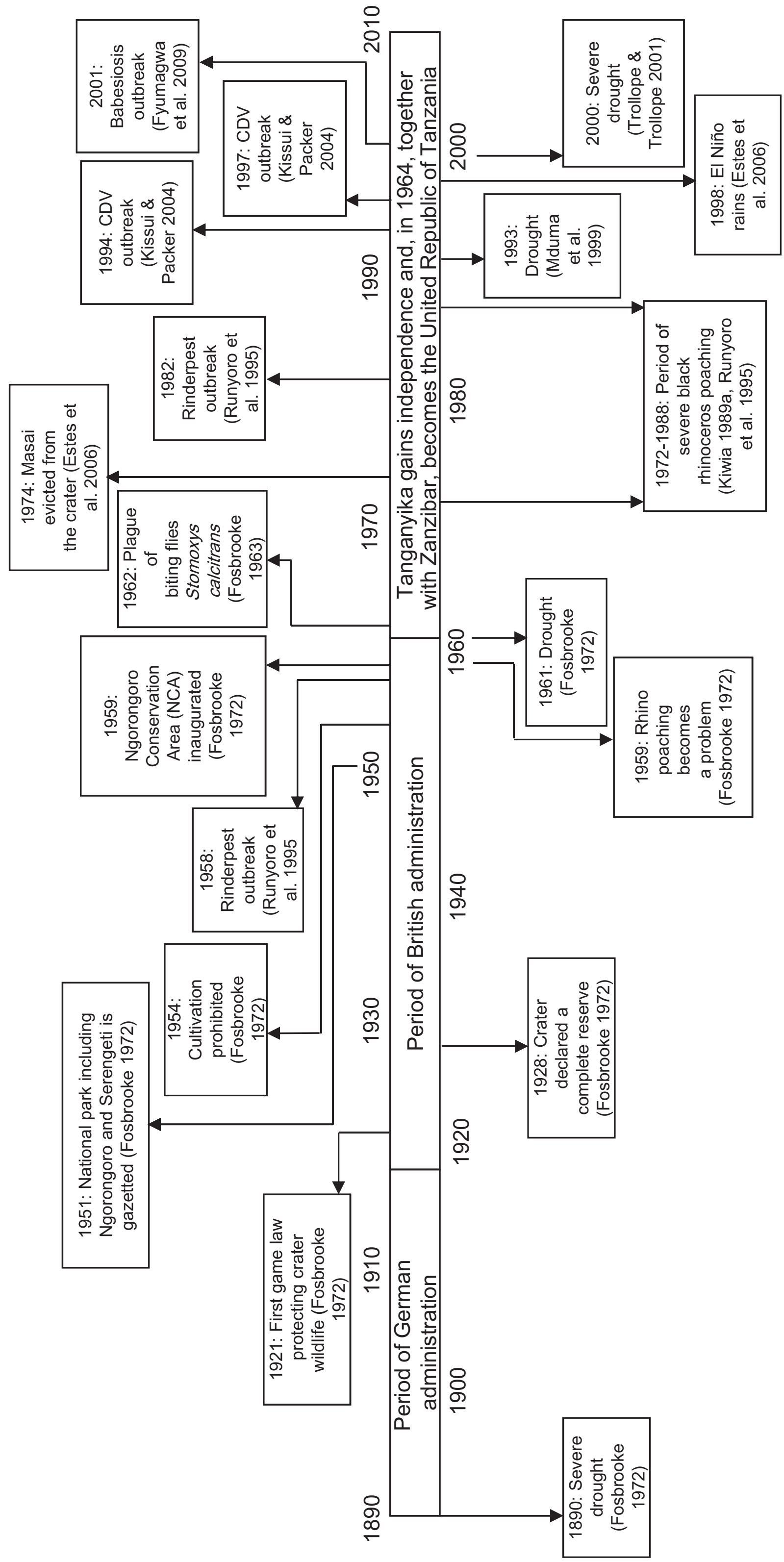

Fig. 3. Timeline of significant events that have affected the large mammals of Ngorongoro Crater. CDV, canine distemper virus.

Disease, climate and vegetation

Historically, wild herbivore numbers in Tanzania were regulated by rinderpest (an infectious viral disease of ungulates; Dobson 1995). Numbers of wildebeest and buffalo in the SNP increased rapidly during the 1960s and 1970s, while numbers of other grazers changed only slightly or not at all (Sinclair 1979). The increase coincided with the eradication of rinderpest in the wild ungulate populations in the early 1960s. Rinderpest had been suppressing wildebeest numbers in particular because of their high susceptibility (Sinclair 1979). Dobson (1995) believed that the disease may have affected the density of buffalo and wildebeest in the Ngorongoro area for most of the 1900s. There has been a significant increase in the number of buffalo in the crater since the eradication of rinderpest (Estes & Small 1981, Homewood & Rodgers 1991) and regression analysis suggested that wildebeest numbers increased by 38% between 1961 and 1973 (Runyoro et al. 1995). In 1958, a rinderpest outbreak caused declines in eland and buffalo populations (Dobson 1995).

Kissui and Packer (2004) concluded that disease, possibly exacerbated by an increased susceptibility due to inbreeding and an increasing human population, was the causative agent holding the lion population below carrying capacity. The 1962 decline was caused by a plague of biting flies *Stomoxys calcitrans* (Fosbrooke 1963) resulting from heavy rains (Kissui & Packer 2004). The bites weakened the lions, resulting in starvation. Some weakened individuals preyed on Masai livestock and were speared (Fosbrooke 1963). The 1994 decline coincided with an outbreak of canine distemper virus (CDV) in the Serengeti and was associated with a severe drought. Drought can bring more animals into contact at watering holes and at kills, while flood can improve conditions for the persistence of pathogens. The 1997 outbreak coincided with the El Niño rains but the exact cause of the decline is unknown (Kissui & Packer 2004). In 2001, a die-off in the lion population was attributed to a combination of CDV (Kissui & Packer 2004), the tick-borne protozoan disease babesiosis (Nijhof et al. 2003, Estes et al. 2006) and the weakening effects of a severe drought in 1999–2000 (Brett 2001, Mills et al. 2003, Kissui & Packer 2004). One thousand buffalo, 250 wildebeest, 100 zebras, 22 lions and five rhinoceros were recorded as having died (Brett 2001, Mills et al. 2003, 2006), with babesiosis confirmed in two of the dead rhinoceros (Nijhof et al. 2003, Fyumagwa et al. 2004). The loss of rhinoceros was regarded as serious enough to warrant the unprecedented action of treating the remaining population with the anti-protozoal drug Diminazine aceturate (Berenil Hoechst; Fyumagwa et al. 2004). The large mammals in the crater were observed to be carrying high tick and biting fly loads in 2001 (Fyumagwa et al. 2004). As buffalo numbered over 5000 individuals prior to the drought, it is possible that the species was at the upper limit of the carrying capacity of the crater and therefore more likely to succumb to the drought and associated disease (Estes et al. 2006). Additionally, an increase in human settlements in the area may have led to an increase in the number of domestic dogs (Kissui & Packer 2004), major carriers of CDV in Tanzania (Cleaveland et al. 2001).

Early explorers described luxuriant vegetation in the crater (e.g. Barns 1921). The removal of the Masai in 1974 may have been the cause of changes in the vegetation due to the associated removal of traditional grassland management, in which controlled burning and livestock grazing kept the grass sward short and palatable. Short grass suits small to medium grazers such as wildebeest (Demment & van Soest 1985) and browsers such as rhinoceros (Brett 2001, Mills et al. 2003, 2006). The grass sward subsequently became longer and less palatable, and therefore more suited to less selective feeders such as buffalo. Runyoro et al. (1995) found that buffalo and hartebeest numbers increased after the removal of the Masai, while wildebeest, zebras, Thomson's gazelles, Grant's gazelles, rhinoceros and elands declined. Both the presence of buffalo and the longer grass favour the growth and spread of disease-carrying ticks (Brett 2001, Mills et al. 2003). Fyumagwa et al. (2007) investigated the babesiosis outbreak and concluded that the eviction of the Masai, combined with the increased rainfall associated with the 1997–98 El Niño event, improved conditions for tick vectors. A decrease in the annual amount of rainfall from approximately 950mm in 1963 to 800mm in 2000 may have contributed to a reduction in available grazing and browsing for herbivores (Mills et al. 2003).

An increase in invasive weeds (e.g. *Gutenbergia cordifolia* and *Bidens shimperi*), possibly caused by the change in grassland management, may have reduced available food for many herbivore species (Henderson 2002, Trollope et al. 2002, Mills et al. 2003, Estes et al. 2006); this has been cited as a particular problem for rhinoceros (Brett 2001, Mills et al. 2003, 2006). Since the drought of 2000, efforts have been made to improve the grass sward for grazers and control invasive species by burning and mowing (Anonymous 2007). It is unclear whether these activities have been successful.

The Lerai Forest, previously an important calving refuge and home range for many rhinoceros (Goddard 1967b), has decreased in size and become fragmented (Fosbrooke 1972, Kabigumila 1993, Trollope et al. 2002) to such an extent that rhinoceros stopped using it (Mills et al. 2006). The lack of suitable calving areas is believed to have increased rhinoceros calf mortality (Mills et al. 2003). The forest's decline has been attributed to an increase in the salinity of the soil caused by the flooding of Lake Magadi (Fosbrooke 1972, Trollope et al. 2002, Mills 2006), a fungal infection in the trees and the action of elephants that remove tree bark (Trollope et al. 2002). Mills et al. (2003) recorded that forest regeneration towards the crater rim was occurring but was not producing suitable calving habitat.

Genetic constraints

Inbreeding depression may affect the crater's rhinoceros population (Moehlman et al. 1996, Mills et al. 2006) and Mills et al. (2006) reported that the dominant male had sired the majority (12 of 19 individuals) of the rhinoceros. However, neither Moehlman et al. (1996) nor Mills et al. (2006) found evidence of any deleterious effects resulting from inbreeding. Nevertheless, in order to address the possible future threat of inbreeding, five rhinoceros were moved from Addo Elephant National Park, South Africa to the crater in 1998. It is believed that these individuals were carrying babesiosis (Hilsberg et al. 2003, Mills et al. 2006). However, it is unclear whether two individuals that subsequently died of babesiosis during the drought of 2000 were residents as claimed by Fyumagwa et al. (2004) or translocated animals as claimed by Nijhof et al. (2003).

The Ngorongoro lions are an isolated population and the 1962 reduction in numbers, together with limited immigration of new individuals, resulted in a much reduced genetic diversity, confirmed by DNA analyses (O'Brien et al. 1987, Yuhki & O'Brien 1990, Packer et al. 1991b). Computer simulations have shown that the population may have passed through similar genetic bottlenecks prior to 1962. Inbreeding may increase the population's susceptibility to disease outbreaks (Packer et al.

1991b) and may reduce fertility through an increase in sperm and testicular abnormalities (Wildt et al. 1987, Munson et al. 1996). Strong coalitions of lions may have prevented immigration of other males and resulted in the genes of members of the coalitions being over-represented in the population (Packer et al. 1991a).

Poaching

Baumann described the shooting of five rhinoceros by his party and stated that 'several others' had also shot rhinoceros during their 5-day visit to the crater (Organ & Fosbrooke 1963). Several studies have suggested that poaching was the primary cause of recent rhinoceros decline in the crater (Moehlman et al. 1996, Mkenda & Butchart 2000, Mills et al. 2003, 2006). Poaching began in the late 1950s and 1960s when the Masai killed at least 19 rhinoceros in the period immediately after the inauguration of the NCA, probably in response to the severe drought (1959–60), which caused significant mortalities in Masai herds with a resultant increase in poaching to generate income (Fosbrooke 1972). The offer of a reward for information on poachers in 1961 reduced poaching dramatically (Grzimek 1964, Goddard 1967b, Fosbrooke 1972). However, poaching began again in the early 1970s (Makacha et al. 1979, Mills et al. 2006) and continued until the mid-1980s (Kiwia 1989a). Borner (1981) estimated that at least 25 rhinoceros were killed in the NCA by 'non-Masai' poachers for commercial gain. Between 1963 and 1965, 82% of crater rhinoceros were adults (total population = 61; Klingel & Klingel 1966) but this had declined to just 28% (total population = 27) by 1978 (Makacha et al. 1979). This may be evidence for heavy poaching, as commercial poachers select adult rhinoceros with large horns (Borner 1981). Increased ranger patrols in 1980 reduced poaching, however a subsequent deterioration in ranger activities allowed it to increase. The use of cash rewards for information leading to the conviction of poachers was re-established in the late 1980s and resulted in another decline in poaching (Homewood & Rodgers 1991). Runyoro et al. (1995) recorded that there had been no rhinoceros poached in the crater since 1988. However, in 1995, at least four were taken (Moehlman et al. 1996). This led to increased security and no further poaching was reported (Mills et al. 2006). Brett (2001) stated that poaching was still a problem for rhinoceros, but Mills et al. (2006) claimed that the population was the most secure in Tanzania.

Runyoro et al. (1995) concluded that poaching was not a significant threat to species other than rhinoceros, while Homewood and Rodgers (1991) believed that poaching and the poor relationship between the NCAA and the Masai threatened the future of the elephant population.

Interspecific and intraspecific interactions

Some carnivore species may be excluded from the crater due to the high density of hyenas and lions. The absence of wild dogs has previously been attributed to the high density of hyenas (Estes & Goddard 1967). Hyenas are known to steal kills from wild dogs and in certain circumstances this can be a considerable threat to packs (Fanshawe et al. 1991). Van Lawick-Goodall and van Lawick-Goodall (1970) suggested that cheetahs had been driven out of the crater by the high densities of hyenas and lions. The gradual decline in the lion population which occurred after 1983 has been attributed to a high rate of takeovers of prides by male coalitions, with an associated increase in infanticide (Packer et al. 1991b).

High losses of subadult lions have been attributed to density-dependent hostility from adults in their natal pride (Elliott & McTaggart-Cowan 1978). The recent decline in hyena numbers may be due to the decrease in available prey caused by the decline in many of the herbivore populations (Mills et al. 2003, Estes et al. 2006).

The rhinoceros population has not been able to sustain the recruitment rates observed during Goddard's study in the 1960s (Brett 2001), possibly due to their social interactions being governed by the density of the population (Moehlman et al. 1996). Low densities may allow for more persistent aggressive interactions between individual rhinoceros and therefore lead to increased immigration into the surrounding, less well-protected, habitat (Moehlman et al. 1996). Goddard hypothesized that being relatively sedentary may help small relict populations survive in protected areas which are bordered on all sides by human habitation. Predation has been identified as a potential limiting factor for rhinoceros and zebras. Rhinoceros numbers have failed to recover, partly due to high calf mortality (Mills et al. 2003). Frame and Goddard (1970) observed a hyena harassing a rhinoceros calf after hyenas had immobilized its mother. Goddard (1967b), van Lawick-Goodall and van Lawick-Goodall (1970) and Kruuk (1972) all witnessed predation attempts by lions and hyenas on rhinoceros calves. The degree of predation upon zebras reported by Elliott and McTaggart-Cowan (1978), who estimated that crater lions take 238 zebras per year, may be severe enough to affect zebra numbers seriously (Runyoro et al. 1995). Increased intensity of grazing by buffalo may reduce the availability of food for rhinoceros, and the latter may compete for browse with, and be disturbed by, elephants (Mills et al. 2003).

Human effects

Half a million tourists visited the NCA in 2007–08 (Debonnet & Wilson 2009). High numbers of tourist vehicles on the crater's road network have led to soil erosion and compaction, and illegal vehicle tracks have been created, affecting the quality of the habitat (Estes et al. 2006). In addition, the Masai are permitted to visit the crater floor with their cattle to use salt licks and water resources, increasing the local incidence of soil erosion (Anonymous 2007). The construction of roads in some parts of the crater has physically blocked water drainage onto meadows, reducing the amount of dry season grazing (Estes et al. 2006). A 2007 World Heritage Committee report on conservation issues in the crater acknowledged that measures had been taken to improve water drainage, recommended the use of a traffic management scheme for the crater and suggested that cattle access be limited or even denied (Anonymous 2007). Large mammal species can be disturbed by tourist vehicles. It has been demonstrated that tourist vehicles may cause a female rhinoceros to leave her calf and hinder her return, increasing the calf's risk of mortality (Mills et al. 2003). Adverse effects of tourist vehicles on the behaviour of some big cats have been reported from other parts of Africa (e.g. Hayward & Hayward 2009) and may occur in the crater.

The swamps that rhinoceros use for seasonal browsing have decreased in area, and this is regarded as a possible contributor to the rhinoceros population failing to recover from the decline in the 1970s (Mills et al. 2003). The changes in the swamps have been attributed to the diversion of water sources for the use of tourist lodges in the vicinity of the crater (Estes et al. 2006).

An exponential increase in the human population in the NCA from 1954 to 1994 (Kijazi et al. 1997) may have adversely affected wildlife corridors linking the crater mammal community with the wider area and, in the crater, may have been the cause of the decline in eland numbers and the low number of immigrant lions (Estes et al. 2006). The increase in buffalo numbers may have been the result of immigration from the surrounding forest in response to human encroachment and the implementation of crop protection measures in the early 1970s (Rose 1975, Runyoro et al. 1995).

Seasonal movements

Some wildebeest and zebras migrate out of the crater during the wet season to utilize grasslands in the highlands and the Olbalbal Depression, where they subsequently breed (Estes 1969, Estes & Small 1981, Runyoro et al. 1995). Some buffalo, elands, rhinoceros, waterbucks and elephants also leave during the dry season to search for better grazing areas (Rose 1975, Estes & Small 1981, Runyoro et al. 1995). While Estes et al. (2006) found a seasonal trend in Thomson's gazelle population estimates, they attributed these to anomalous results arising from different census techniques, as this gazelle is not thought to migrate out of the crater. Grant's gazelles have not been recorded migrating out of the crater, but migration is thought to occur, as large herds have been observed immediately outside the crater (Estes et al. 2006). Estes et al. (2006) proposed that many of the changes in the crater's herbivore populations may have been caused by natural population exchange with animals in the wider Serengeti ecosystem.

The relative popularity of large mammal species as subjects of research

Some species within the crater have been studied because the crater population itself has been of particular interest, e.g. lions (Gilbert et al. 1991, Munson et al. 2008), others because the crater has provided a discreet population for study, e.g. behavioural studies of servals (Geertsema 1985).

The number of research papers covering a single species published per year more than doubled, from seven in 1961–65 to 15 in 1991–95, with a drop to just one in 1971–75. It remained high thereafter but fell to eight in 2006–10 (Fig. 4). Almost all the increase since the early 1970s was due to the publication of work on rhinoceros and lions (Fig. 5). Lions account for 52% and rhinoceros 21% of all the papers published since 1961.

DISCUSSION

During the recorded history of the Ngorongoro Crater's large mammal community, several important changes have occurred. Early censuses show that in the 1960s, the dominant herbivore species were wildebeest and zebras, while lions and hyenas were the most abundant large predator species. Since then, the majority of the large herbivore populations have declined, and buffalo have replaced wildebeest as the dominant herbivore. Lions and hyenas, while remaining the dominant predators, declined over the same period. The decline of rhinoceros numbers from over 100 in the 1960s (Goddard 1967b) to around 30 in 2011 (P. Morkel, personal communication) is arguably the change of greatest conservation concern. In the last 50 years, the crater has been colonized by two large mammal species: the buffalo (*c.* 1960) and the warthog (*c.* 1980). While most

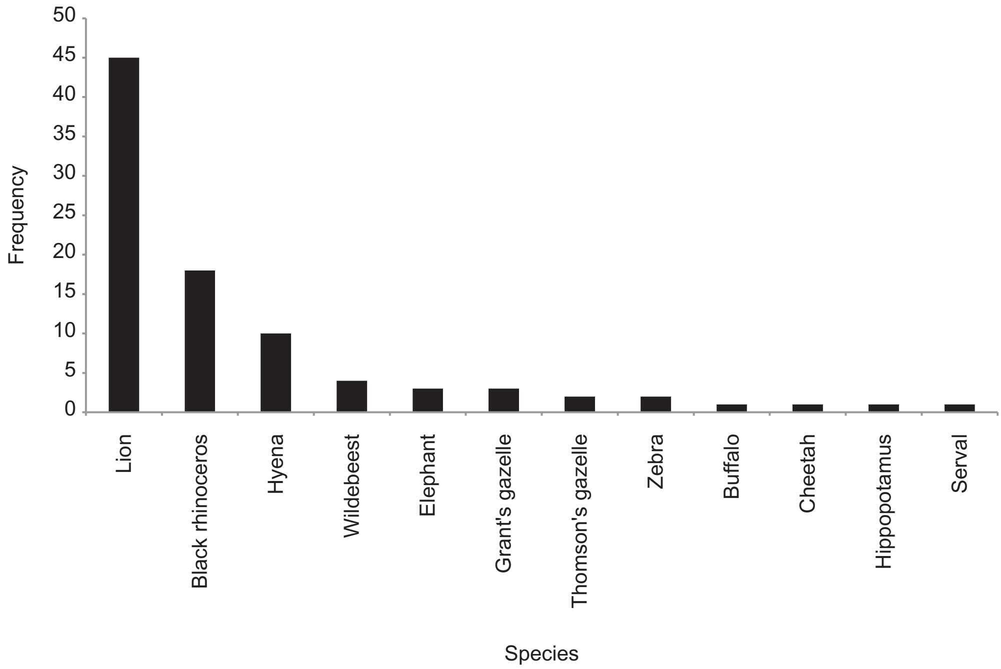

Fig. 4. The frequency with which the large mammal populations of Ngorongoro Crater have been the subject of research published in peer-reviewed journals ($n = 87$). Three papers each covering two species are included; all other papers cover a single species. Papers that report the results of general censuses are not included (e.g. Estes et al. 2006).

species are resident, cheetahs appear to be intermittent visitors to the crater floor, as were wild dogs in the past (Homewood & Rodgers 1991). In addition, there is some evidence that temporary absences of elephants from the crater floor may occur. It seems likely that the other species which currently inhabit the crater have been present throughout the period covered by this study, as any absence is likely to have been noted in major longitudinal and autecological studies (e.g. Runyoro et al. 1995, Estes et al. 2006).

Published records are extensive for some species but fragmentary for others. Baumann's (1894) description of the fauna of the crater was the result of a 5-day visit in 1892. Grzimek and Grzimek's 1958 census was a small part of a larger study of the Serengeti ecosystem. Turner and Watson's 1964 census was completed in 2 days (Grzimek & Grzimek 1960, Turner & Watson 1964) and marked the beginning of regular censuses by what became the NCAA. The absence of census data for 1980–85 may be attributed to the poor economic situation in Tanzania at this time (Meredith 2005); wildlife division wages were rarely paid, causing poor staff morale (Heyworth 1995).

The major influences upon the large herbivore populations appear to have been vegetation change (an increase in both moribund vegetation and invasive weed species) and disease. Poaching has particularly damaged the rhinoceros population, and disease has been identified as the primary reason for the lion population being consistently held below carrying capacity (Kissui & Packer 2004). Some of the apparent changes in numbers may be attributable to differences between census

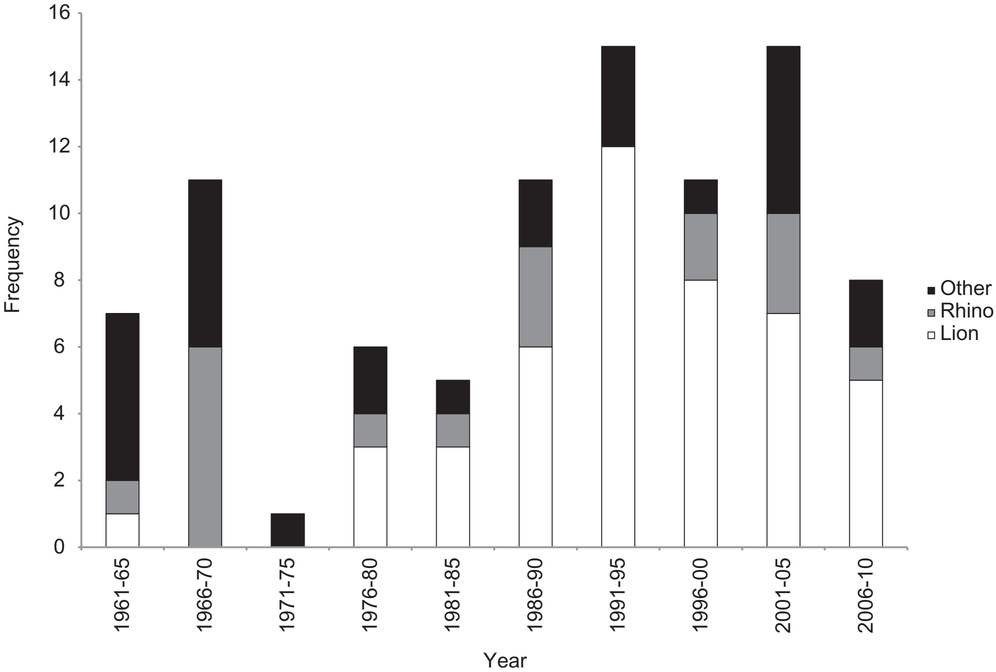

Fig. 5. The frequency of publication of peer-reviewed research papers on the large mammal species of Ngorongoro Crater between 1961 and 2010. Three papers each covering two species are included; all other papers cover a single species.

techniques and to differences in the accessibility of habitats (e.g. counts of reedbucks in forest and swamp may be low due to the dense habitat).

Although a considerable amount of information on the ecology of the crater undoubtedly exists in unpublished reports (e.g. Estes 2002, Henderson 2002, Mills 2003), very little of this finds its way into peer-reviewed journals. Consequently, this information is largely lost to the wider scientific community. There is no evidence of any significant increase in published research on mammals from the crater since the 1960s, with the exception of work on rhinoceros and lions. If the global importance of Ngorongoro Crater as a refuge for many of Africa's iconic species and the challenges it faces as a result of increased tourism, human encroachment, animal diseases and vegetation change are to be recognized, a wider dissemination of research on its ecology is essential.

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