Dry Season Demography of African Elephants (*Loxodonta Africana)* in the Ngorongoro Crater, Tanzania

Jennifer Vickers, Drake University, jennofvenus@gmail.com

School for Field Studies, P.O. Box 304 Karatu, Tanzania, East Africa

ABSTRACT

The demography and distribution of the elephant population in the Ngorongoro Crater is poorly understood. To examine this issue, group size and type, sex and age of all individuals, habitat, cover type, and GPS coordinates were taken for all elephant groups observations were made from vehicles along roads in the Ngorongoro Crater during the dry season of 2016. In the Crater, significantly more adults were observed than sub-adults and young (Figure 2). Also, the population was composed of significantly more male elephants than females (Figure 3). The social structure of the population consisted of significantly more solitary males than bull groups, cow-calf groups, and mixed groups (Figure 5). A significant majority of elephants were seen on the floor of the Crater, and few were observed in the escarpment (Figure 6). On the Crater floor, elephants were only observed in swamp and acacia xanthophloea habitats. Overall, an average of 35 elephants were observed per day. This study is a baseline demography reference for management purposes and future studies of the elephant population in the Ngorongoro Crater.

Key words: elephant, demography, distribution, dry season, social structure, Ngorongoro Crater

INTRODUCTION

Elephants have broad home ranges that can include diverse ecosystems (Thomas et al. 2008). In addition, elephants are a transient species because their home ranges are driven by water and forage resources (Foley 2002). These home ranges are both inside and outside of protected areas (Chase et al. 2016), with protected areas playing a major role in elephant preservation (Hilborn et al. 2006). In Africa, only an estimated 16% of elephants occur outside of these protected areas (Chase et al. 2016), and this rate is continuously declining (Blanc et al. 2007). Because elephants tend to avoid areas of heavy human use (Barnes 1996), anthropogenic activities and land use changes are reducing elephant home ranges and confining elephants to protected areas (Newmark 2008).

Elephant societies are based on a fission-fusion pattern, where elephants come together into large groups in the wet season when resources are abundant and divide back into small family groups during dry seasons (Western & Lindsay 1984). Females remain with their natal herds comprised of closely related females and their calves throughout their lifetime, while males leave their natal herd between the ages of 12 and 20 when they reach puberty (Hollister-Smith et al. 2007). When males hit adulthood they live in loosely-associated groups with other males or remain solitary, and usually only interact with females around times of estrus (Poole 1994).

The population of elephants in the Ngorongoro Conservation Area (NCA) has been linked with populations in the adjacent Serengeti National Park (Mduma et al. 2014). Elephant counts of the meta- population in the southern part of the Serengeti- Mara ecosystem (including the Crater) have been estimated at 6,087 elephants (Mduma et al. 2014), and the population in this area is genetically diverse (Comstock et al. 2002). In the NCA, human land use for cattle grazing has restricted the elephant range to primarily the Crater (Homewood et al. 2009). In the Crater itself, several studies and speculations have varied greatly about the elephant population. Estes & Small (1981) states that the elephant population in the Crater was zero in 1969. Kambigumila (1993) claimed that “only mature males used the Crater” and that “females were rarely seen” but no demographic analysis was done. Sinclair & Arcese (1995) approximate that the population ranged between zero and 87 from 1963 to 1993. Most recently, Estes (2002) stated that up to 56 elephant males were observed in the Crater.

Sexual segregation is a frequent behavior of African elephants (Shannon et al. 2006 (1)). Three suggested explanations for this segregation are that it is due to forage selection, predation risk, and indirect competition (Shannon et al. 2006 (1)). Forage selection can play a role as larger bodied individuals can extract greater nutritional value from lower quality fibrous food (Stokke & du Toit 2000). This implies that adult bulls have the ability to settle for lower quality food. This increases the range of habitat that they are able to live in successfully, compared to cow-calf groups. For predation risk, there is data that shows that males are less susceptible to predation as compared to cow- calf groups (Bleich et al. 1997; Ruckstuhl & Neuhaus 2000; Corti & Shackleton 2002). Cow-calf groups prefer a habitat with more vegetation coverage than the bulls. Group sizes increase with more openness of vegetation, likely as a result of this same predation risk (Dublin 1996). In this area, the only predator is lions (Kingdon 1997). Finally, there is some indirect competition between bull and cow-calf groups. Clutton-Brock et al. (1987) showed that females will out-compete males when it comes to resource collection and force males into less ideal habitats. This implies that cow-calf groups are more likely to be found in areas of higher quality foraging.

The sex structure and size of elephant groups can also be variable (Selier 2007). The size of elephant groups is dependent on the seasons, with larger groups and family groups that include bulls usually forming during wet the seasons (Wittemyer 2001). Cow estrus coincides with the wet seasons which causes bulls to join the cow- calf groups to increase the likelihood of reproducing (Dublin 1983).

Another feature that influences sexual segregation is the differing male and female distribution patterns of elephants. Bulls tend to be more transient with larger, more evenly distributed home ranges (Wittemyer 2001). Cows are less transient because a higher quality of environment is needed for reproducing and supporting calves (Wittemyer 2001). Cow-calf groups settle in smaller, richer areas for longer lengths of time with a more patchy distribution. In addition to these factors, past and present human settlements also affect elephant distribution patterns (Barnes & Kapela 1991). All of this information culminates in the question; what is the structure of elephant populations in the Crater?

The objective of this study is to improve the understanding of the elephant population dynamics and distribution in the Ngorongoro Crater, Tanzania. The specific focus it to

understand the social structure, sex ratio and sexual segregation of this population. It is predicted that the population will be male dominated due to the higher incidence of male risk behavior and their tendency to have wider, more even distributions than family groups (Lee & Moss 1994; Hollister- Smith et al. 2007). Females with family groups are shown to prefer areas that are safer from predators with denser covering foliage (Corti & Shackleton 2002).

STUDY AREA

The Ngorongoro Crater, at a geographical position of 2°30′– 3°30′ S, 34°50′–35°55′ E, is located in the East African Great Rift Valley ecosystem in northern Tanzania (Oates & Rees 2012). The Crater is located in the NCA which is adjacent to the Serengeti National Park. The Crater itself is about 19 km in diameter and has a total area of 310 km^2 (Anderson & Herlocker 1973). In addition, there is an unbroken rim entirely surrounding the Crater floor. Inside the Crater is the seasonal alkaline Lake Magadi, which is also referred to as Lake Makat (Estes et al. 2005) (Figure 1).

A common human activity in the NCA is livestock herding (Homewood et al. 2009). The NCA is a unique location because it has a high concentration of wildlife that coexists with human communities (Akyoo & Nkwame n.d.). The value of the ecosystem in the Crater itself is immense due to its open habitat with high visibility making it a well-known and prestigious site for tourism (Akyoo & Nkwame n.d.). Furthermore, the NCA has been recognized as an essential location for black rhinoceros conservation and management, which also attracts tourism (Fyumagwa & Nyahongo 2010).

The vegetation in the Crater is semi-arid open savanna grassland with some trees and bushes with ground-water acacia xanthophloea forests and the evergreen swamps (Herlocker & Dirschl 1972; Anderson & Herlocker 1973) (Figure 1). This area has two wet seasons during the year and is dry the rest of the year. The short rains occur at the end of November through December and the long rains last from March to May (Oastes & Rees 2012). The Crater is hydrologically restricted so drainage is entirely internal. The perennial Oljoro Nyaki and Munge rivers, in addition to several springs and seasonal streams run into Lake Magadi (Anderson & Herlocker 1973).

Besides elephants, there are many other forms of wildlife in the Crater. This includes herbivore populations of wildebeest (*Connochaetes taurinus albojubatus*), zebra (*Equus burchelli*), buffalo (*Syncerus caffer*), Grant's gazelle (*Nanger granti*), Thomson's gazelle (*Eudorcas thomsonii*), hartebeest (*Alcelaphus buselaphus*), waterbuck (*Kobus ellipsiprymnus*), eland (*Taurotragus oryx*), warthogs (*Phacochoerus africanus*), bohor reedbuck (*Redunca redunca*), hippopotamus (Hippopotamus amphibius) and ostrich (*Struthio camelus*) (Sinclair & Arcese 1995).

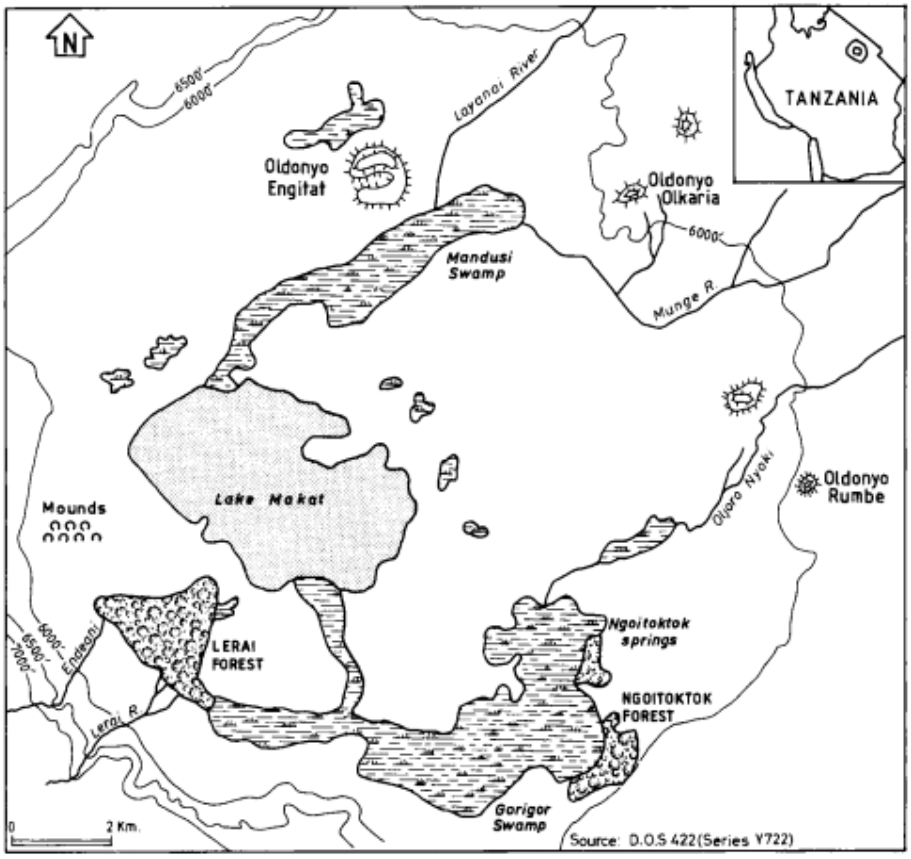

Figure 1. Map of Ngorongoro Crater and its location in Tanzania adapted from Kabigumila, 1988.

METHODS

Field Methods

Observations of elephants were made from vehicles. Total counts were taken of all individuals from all accessible areas to establish sufficient coverage in the Crater study area. Data was collected in the dry season on August 10th, October 24th, November 5th and November 16th, 2016. Each observation included group size and type, sex and age of all individuals, habitat, cover type, and GPS coordinates (Appendix I). Age and sex were determined based on physical attributes such as head shape, body shape and size, tusk size and features, and genitalia (Moss 1996). For group type, lone adult male bulls will be defined as "solitary males"; two or more adult male bulls will be defined as "bull groups"; adult females seen with sub-adults and young of both sexes will be defined as "cow/ calf groups" or "families"; and adults, sub-adults and young of both sexes will be considered "mixed groups" (Stokke and du Toit 2002). Group size will be the number of individuals in a given group. The location of elephant groups will be taken on a Garmin GPS unit.

Data Analysis

Sex and age ratios as well as comparisons of group types, social structure, and location were determined with the Chi-square goodness of fit test (Appendix II). Density was calculated by using the area and total counts of elephant individuals (Appendix III). Hurlbert's version of Levin's niche breadth test was used to determine habitat preference (Appendix IV). GPS points were plotted in ArcGIS to get the distribution (ESRI 2011).

RESULTS

Population Structure

Over the four days in the study area, 39 groups of elephant were observed consisting of 137 individuals. Of these, the age and sex were determined for 108 elephants. The daily number of elephants observed ranged between 16 and 51 individuals, with an average of 35 elephants observed per day. The density of elephants in the Crater was 1 elephant for every 9 kilometers.

Age Structure

Overall, there were significantly more adults than sub-adults and young elephants ($\chi^2 = 37.61$, $p < 0.05$, df = 2). The whole population consisted of 64% adult, 10% sub-adults and 26% young (Figure 2).

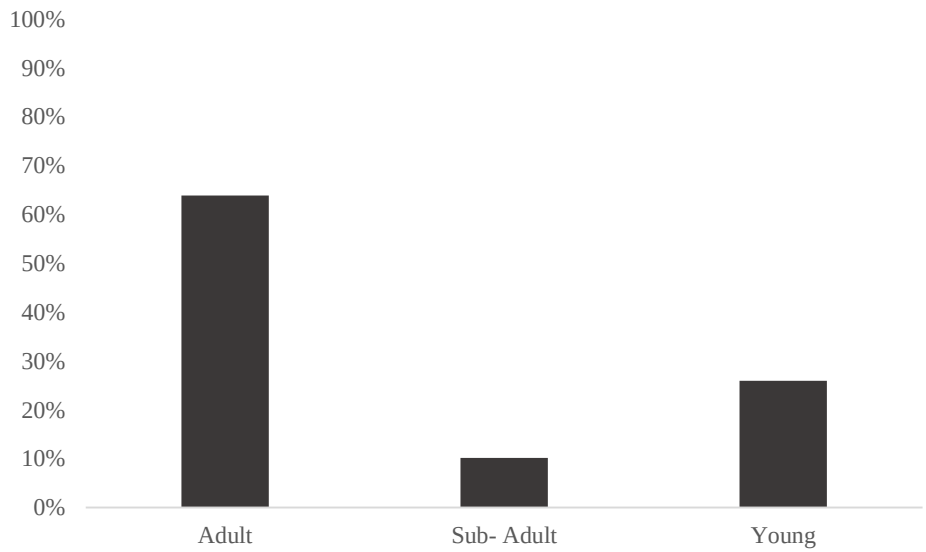

Figure 2. The proportion of adults, sub-adults and young in the Ngorongoro Crater elephant population (n = 108).

Sex Structure

The sex structure for the population was skewed towards males. In the entire population, the ratios of females to males differed significantly ($\chi^2 = 4.48$, $p < 0.05$, df = 1). The ratio of females to males was 1 female to 1.5 males (60% male). Among the adults, the proportion of males was even higher (68% males). In the sub-adult and young age classes, there were statistically equal proportions of males and females (Figure 3). The sex ratio in the cow/ calf groups was 73% female to 27% male (8 males) (Figure 4).

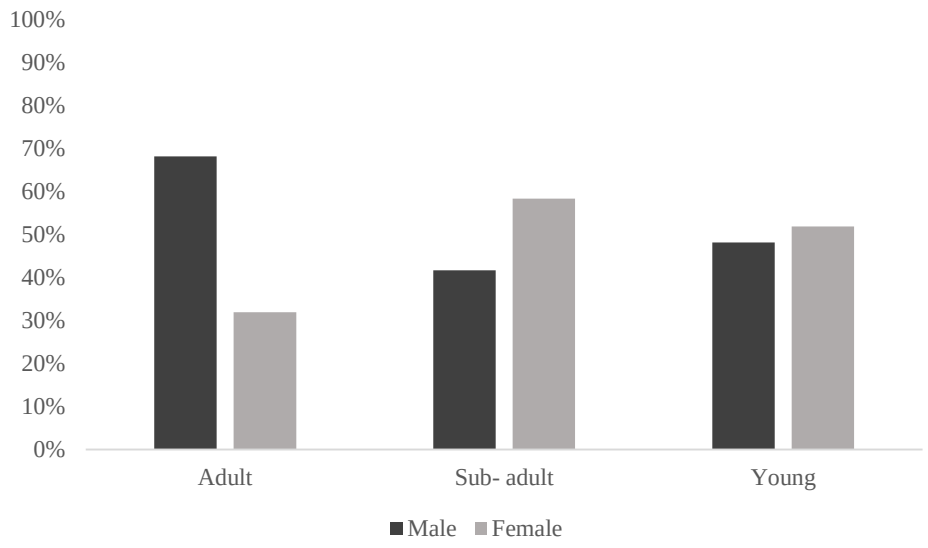

Figure 3. The proportions of the sexes for adults, sub-adults and young in the Ngorongoro Crater elephant population (n = 108).

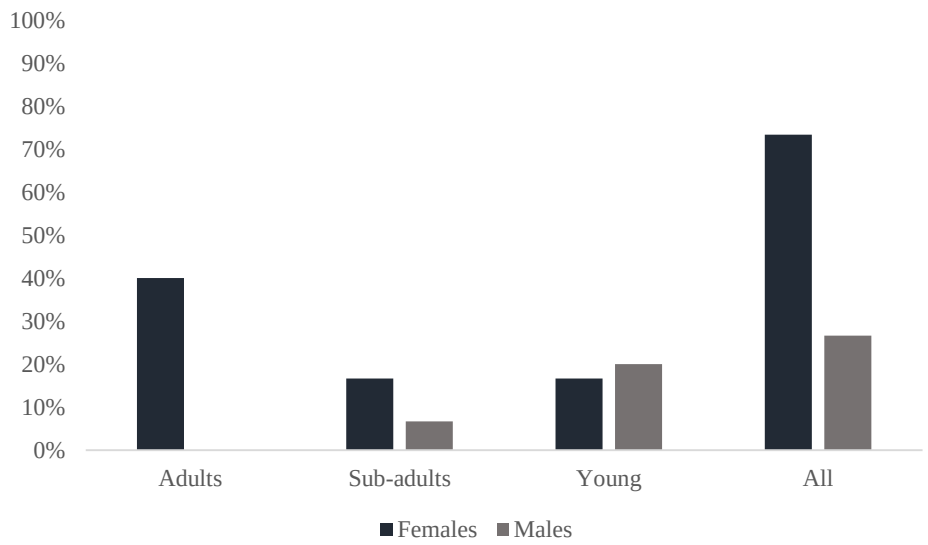

Figure 4. The proportions of the ages and sexes in the cow-calf groups in the Ngorongoro Crater elephant population (n = 30).

Social Structure

The 39 observed elephant groups included 24 solitary bulls, 9 bull groups, 5 cow-calf groups, and 1 mixed group with 62% of groups being solitary males. On average, 10 elephant groups were observed each day. Group sizes ranged between 1 and 25 elephants with an average group size of 4 individuals. There were significantly more solitary males groups encountered than bull, cow-calf or mixed groups ($\chi^2 = 31.05$, $p < 0.05$, df = 3) (Figure 5).

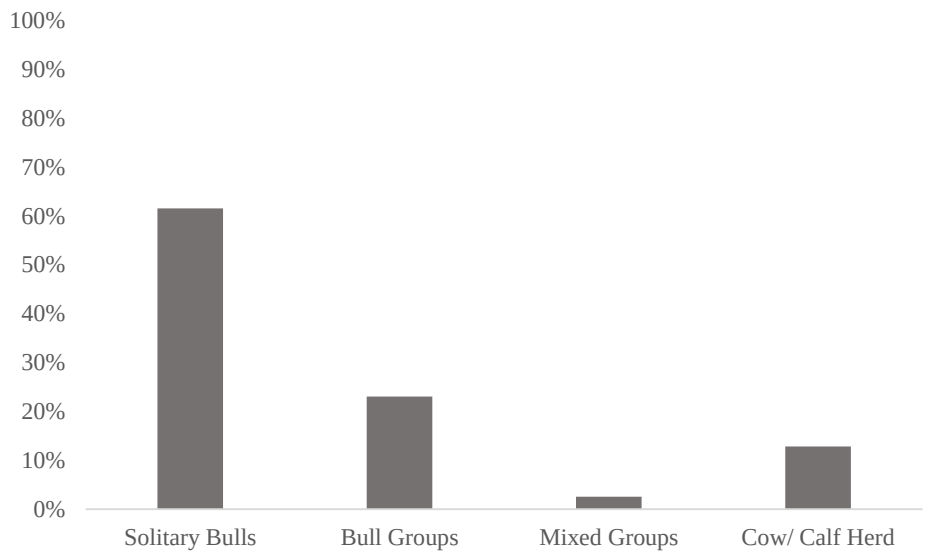

Figure 5. The proportions of the number of group types observed in the Ngorongoro Crater elephant population (n = 39).

Elephant Distribution

Out of the 39 groups, 17 were encountered in a swamp habitat, 11 were encountered in the bushland-shrubland habitat, and 11 were encountered in an acacia xanthophloea woodland habitat; however, their occurrence in these habitats did not statistically differ (Table 1; Figure 6). Significantly more elephant groups (29 or 74%) were found on the Crater floor compared to (10 or 26%) on the Crater escarpment ($\chi^2 = 7.41$, $p < 0.05$, df = 1) (Figure 7). When considering the availability of habitat, the elephant population showed preference for the wooded and swamp areas, and were not found in other habitats on the Crater floor.

Habitat	Solitary Males	Bull Groups	Mixed Groups	Cow-Calf Groups
Bushland- Shrubland	9	1	1	0
Swamp	11	6	0	0
Acacia xanthophloea forest	4	2	0	5
Grassland	0	0	0	0

Table 1. Numbers of each group type that were observed in each habitat.

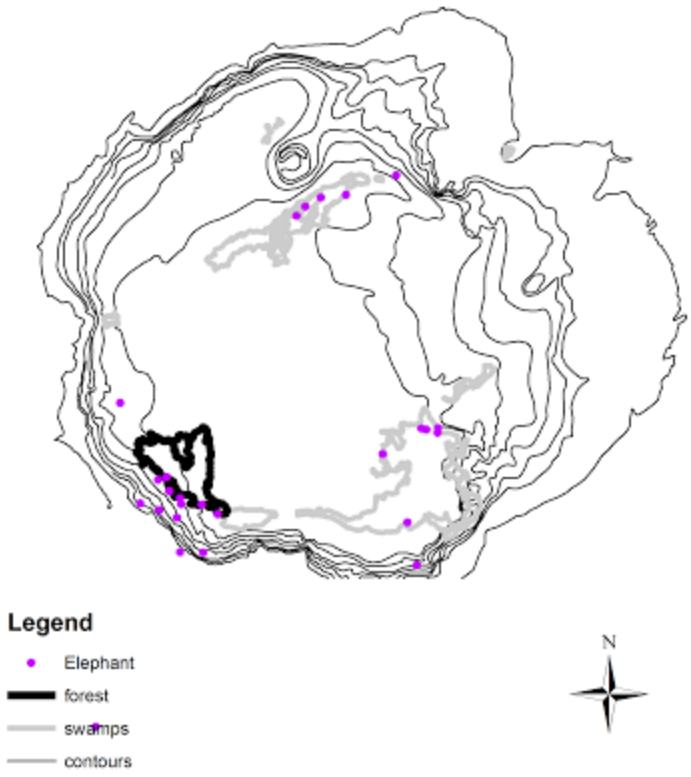

Figure 6. Distribution of elephant groups observed in the Ngorongoro Crater (n = 39).

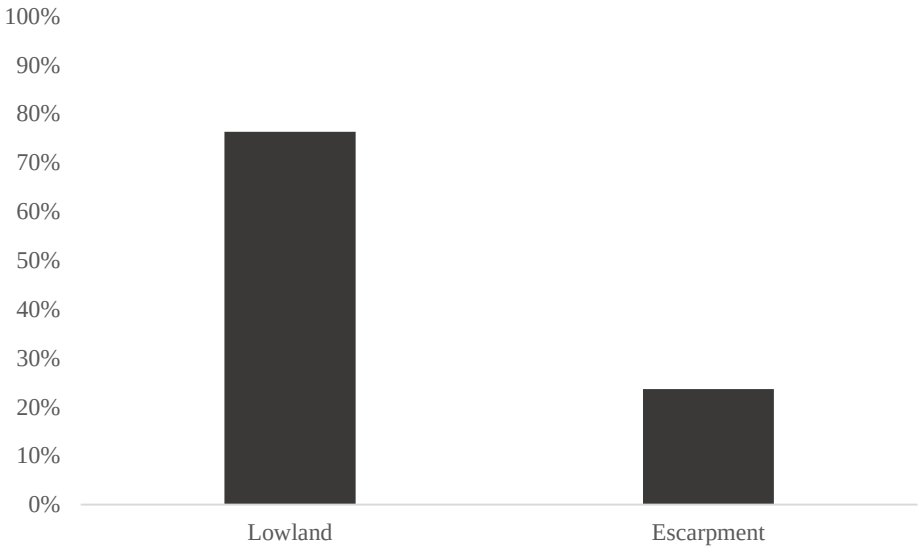

Figure 7. The proportions of where elephant groups were observed in different areas in the Ngorongoro Crater (n = 39).

DISCUSSION

The Ngorongoro Crater population was found to be male dominated. Recruitment in mammal populations is driven by birth rates and immigration (Dixon 2001). Lower numbers of females result in a low birth rate. This leads to a slow growth rate in a population. Male dominated sex ratios in elephant populations, such as that in the Crater, can suggest re-colonization (Ahlering et al. 2011). The total count numbers varied between days, so elephants are coming from outside the Crater. Immigration can increase recruitment (Dixon 2001).

Sex and age ratios of elephant populations greatly differ depending on habitat, forage and water availability, risk and other factors (Shannon et al. 2006 (2), Sitati et al. 2003, Shannon et al. 2009).While the Crater population differs greatly in population dynamics from other some elephants populations, it is not entirely unique. The Crater elephant population was found to be male dominated, as expected, and a great majority of the elephant groups observed were solitary bulls. Areas like the Crater, where there are increased risk factors such as a high density of lions and the presence of livestock grazing, tend to be male dominated (Kioko et al. 2013). The male dominated population also may be due to the transient tendencies of bulls as they have wider distributions that cover more ground (Wittemyer 2001; Hollister- Smith et al. 2007). Typical age structure in male dominated elephant societies tend to have a higher ratio of adults to young than female dominated societies (Kioko et al. 2013).

The Ngorongoro Crater elephant population is composed of mostly adults. The age structure is adult dominated because there are significantly more solitary males and bull groups. These types of groups are composed entirely of adults (Stokke & du Toit 2002). The sub-adult and young age classes are statistically equal in proportions because males remain with their natal groups and then disperse upon reaching a certain age (Hollister-Smith et al. 2007). Upon reaching maturity, bulls then disperse into areas with higher risk factors.

In the Crater, density was calculated to be 0.11 elephants per square kilometer. This is a relatively low density. Other studies conducted in Tanzania estimated density was between 0 and 1.2 elephants per square kilometer with a majority of the elephant range having more than 0.6 elephants per square kilometer (African Elephant Database 2013).

One habitat that was used by the elephants was the acacia xanthophloea forest. All of the cow- calf groups were observed in this forest (Table 1), so the habitat meets the needs of cow-calf groups. This forest has perennial water sources. This is important for elephants to wallow and drink. Acacia xanthophloea grow in areas high underground water table which keeps these trees green and full through the year (Orwa et al. 2006). This can provide a year round food source for elephants. It also gives shade and cover. Elephants, especially young, need to have access to shade throughout most of the day (Sukumar 1989; Daniel et al. 1995).

Another habitat where several groups were observed was the swamp. Solitary males and bull groups were found in this area more frequently than any other area (Table 1). The swamp has water source throughout the year and vegetation remains green because the water table comes above ground level (Banner & Mackenzie et al. 2000). There is year round forage and some cover in these areas. Family groups may not be found here because there is less shade because of the shorter vegetation.

Elephant of all ages and both sexes were observed using the bushland-shrubland on the escarpment of the Crater. This was surprising to see a mixed group that included young on the steep slopes of the escarpment. This is unexpected because some studies, such as Wall et al. (2006), have shown that elephants avoid steeper slopes and difficult terrain. This is not assumed to be the case for this population.

Cover is a major determinant of elephant distribution (Kalwij et al. 2010). Acacia xanthophloea, swamp and bushland-shrubland habitats areas all have more cover. The grasslands of the Crater are very open with high visibility and little shade. Elephants, especially young, need shade because it is hot and dry during the dry season.

The elephants were distributed mostly in the southern and eastern parts of the Crater (Figure 6). This is probably due to displacement by livestock grazing. Grazing occurs in the north-western parts of the Crater. The elephants were found in the acacia xanthophloea, swamp and bushland-shrubland habitats but none were observed in the grassland. This is likely because most lions can be seen on the grassland plains. This is important for cow-calf groups as their young are vulnerable to carnivore predation (Loveridge et al. 2006, Ruggiero 1991).

Implications and Recommendations

In summary, this study indicates that the Ngorongoro Crater elephant population is dominated by adult males, specifically by solitary bulls. In order to maintain an understanding of the Ngorongoro Crater elephant population, there should be annual censuses to monitor any fluctuations in the population's demography. It is also suggested that future studies investigate the demography of the elephant population during the wet season for a seasonal comparison. Further analyses of these elephants will indicate the influences of ecological factors on this elephant population and what drives the population's structure. Further studies on habitat type, forage quality, forage availability and biomass will deepen the understanding of habitat preference. Lion predation and anthropogenic activities may also pose a risk and pressure family groups to prefer certain habitats. In addition, observing the elephant population at night and looking for other elephant use signs such as dung, tracks and disrupted vegetation, may help to discover alternative habitat use. Finally, another studies may analyze the terrain and location of elephants in the escarpment as compared to the Crater floor.

ACKNOWLEDGEMENTS

I would like to thank John Kioko, PhD., Josen, and the management of the Ngorongoro Conservation Area, Tanzania. This study was conducted through the School for Field Studies-Karatu, Center for Wildlife Management Studies.

REFERENCES

AHLERING, M.A., MILLSPAUGH, J.J, WOODS, R.J. WESTERN, D. & EGGERT, L.S. (2011) Elevated levels of stress hormones in male crop-raiding elephants. *Animal Conservation*. **14**: 124–130.

AFRICAN ELEPHANT DATABASE (2013) African elephant range and population density. IUCN.

AKYOO, A., & NKWAME, M. (n.d.). Ngorongoro: A priceless asset (Tanzania, Ngorongoro Conservation Area Authority).

ANDERSON, G. D., & HERLOCKER, D. J. (1973) Soil factors affecting the distribution of the vegetation types and their utilization by wild animals in Ngorongoro Crater, Tanzania. *The Journal of Ecology*, **61**(3), 627.

BANNER, A., & MACKENZIE, W. (2000) The ecology of wetland ecosystems. Extension Note-British Columbia Ministry of Forests, 45.

BARNES, R. F. W. (1996) The conflict between humans and elephants in the central African forests. *Mammal Review*, **26**: 67–80.

BARNES, R. F., & KAPELA, E. B. (1991) Changes in the Ruaha elephant population caused by poaching. *African Journal of Ecology*, **29**(4), 289-294.

BLANC, J. J., BARNES, R. F., CRAIG, G., DUBLIN, H., THOULESS, C., DOUGLAS-HAMILTON, I., & HART, J. (2007) African elephant status report 2007: An update from the African elephant database. IUCN.

BLEICH, V., BOWYER, R. T., & WEHAUSEN, J. D. (1997) Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs*, **134**, 3-50.

CHASE, M. J., SCHLOSSBERG, S., GRIFFIN, C. R., BOUCHÉ, P. J., DJENE, S. W., ELKAN, P. W., . . . SUTCLIFFE, R. (2016) Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ*, **4**.

CLUTTON-BROCK, T. H., IASON, G. R., & GUINNESS, F. E. (1987) Sexual segregation and density-related changes in habitat use in male and female Red deer (*Cerrus elaphus*). *Journal of Zoology*, **211**(2), 275-289.

COMSTOCK K.E., GEORGIADIS N., PECON-SLATTERY J., ROCA A.L., OSTRANDER E.A., O'BRIEN S.J. & WASSER S.K. (2002) Patterns of molecular genetic variation among African elephant populations. *Molecular Ecology* **11**, 2489-2498.

CORTI, P., & SHACKLETON, D. M. (2002) Relationship between predation-risk factors and sexual segregation in Dall's sheep (*Ovis dalli dalli*). *Canadian Journal of Zoology*.

DANIEL, J.C., KRISHNAMURTHY, V., DESAI, A.A., SIVAGANESAN, N., DATYE, H.S., KUMAR, R., BASKARAN, N., BALASUBRAMANIAN, M. & SWAMINATHAN, S. (1995) Ecology of the Asian elephant. final report: 1987-1992. Bombay Natural History Society, Bombay.

DIXON, P. M. (2001) Population ecology. *Iowa State Statistics Preprints*. **80**(12), 2108-2117.

DUBLIN, H. T. (1983) Cooperation and reproductive competition among female African elephants. *Social Behavior of Female Vertebrates*, 291-313.

DUBLIN, H.T. (1996) Elephants of the Masai Mara, Kenya: seasonal habitat selection and group size patterns, *Pachyderm*, **22**, 25–35.

ESRI (2011) ArcGIS desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

ESTES R. D. (2002) Ngorongoro Crater ungulate study 1996–1999 final report. Unpublished.

ESTES, R., ATWOOD, J., & ESTES, A. (2006) Downward trends in Ngorongoro Crater ungulate populations 1986–2005: Conservation concerns and the need for ecological research. *Biological Conservation*, **131**(1), 106-120.

ESTES R. D., SMALL R. (1981) The large herbivore population of Ngorongoro Crater. Proceedings of the fourth annual African wildlife symposium. *African Journal of Ecology*, **19**, 175–185.

FOLEY, L. S. (2002) The influence of environmental factors and human activity on elephant distribution (Unpublished master's thesis). International Institute for Geo-Information Science and Earth Observation Enschede.

FYUMAGWA, R., & NYAHONGO, J. (2010) Black rhino conservation in Tanzania: Translocation efforts and further challenges. *Pachyderm*, **47**, 59-65.

HERLOCKER, D. J. & DIRSCHL, H. J. (1972) Vegetation of the Ngorongoro Conservation Area, Tanzania. *Canadian Wildlife Report Series*, **19**.

HILBORN, R., ACRESE, P., BORNER, M., HANDO, J., HOPCRAFT, G., LOIBOOKI, M., MDUMA, S., SINCLAIR, A. R. (2006) Effective enforcement in a conservation area. *Science Magazine*, **314**, 1266.

HOLLISTER-SMITH, J. A., POOLE, J. H., ARCHIE, E. A., VANCE, E. A., GEORGIADIS, N. J., MOSS, C. J., & ALBERTS, S. C. (2007) Age, musth and paternity success in wild male African elephants, *Loxodonta africana*. *Animal Behaviour*, **74**(2), 287-296.

HOMEWOOD, K., RODGERS, W. A., & ARHEM, K. (2009) Ecology of pastoralism in Ngorongoro Conservation Area, Tanzania. *The Journal of Agricultural Science*, **108**(1), 47-72.

KALWIJ, J. M., DE BOER, W. F., MUCINA, L., PRINS, H. H. T., SKARPE, C., & WINTERBACH, C. (2010) Tree cover and biomass increase in a southern African savanna despite growing elephant population. *Ecological Applications*, **20**(1), 222-233.

KAMBIGUMILA, J. (1993) Feeding habits of elephants in Ngorongoro Crater, Tanzania. *The African journal of ecology*. **31**(2), 156-164.

KINGDON, J. S. (1997) The Kingdon field guide to African mammals. Academic Press, London.

LEE, P. C., MOSS, C. J. (1994) Mammalian social learning: Comparative and ecological perspectives. Cambridge University Press, Cambridge.

LOVERIDGE, A. J., HUNT, J. E., MURINDAGOMO, F., & MACDONALD, D. W. (2006) Influence of drought on predation of elephant (Loxodonta africana) calves by lions (Panthera leo) in an African wooded savannah. *Journal of Zoology*, **270**(3), 523-530.

MDUMA, H., MUSYOKI, C., MALITI, K. D., NINDI, S., HAMZA, K., NDETEI, R, MACHOKE, M., KIMUTAI, D., MUTETI, D., MALOBA, M., BAKARI, S., AND KOHI, E. (2014) Aerial total count of elephants and buffaloes in the Serengeti-Mara ecosystem. Nairobi, Kenya: WWF-World Wide Fund for Nature.

NEWMARK, W. D. (2008) Isolation of African protected areas. *Frontiers in Ecology and the Environment*, **6**, 321-328.

OATES, L., & REES, P. A. (2012) The historical ecology of the large mammal populations of Ngorongoro Crater, Tanzania, east Africa. *Mammal Review*, **43**(2), 124-141.

ORWA, C., MUTUA, A., KINDT, R., JAMNADASS, R., & ANTHONY, S. (2009) Agroforestree Database: a tree reference and selection guide version 4.0. World Agroforestry Centre, Kenya. Acacia Xanthophloea, 1-5.

POOLE, J.H. (1994) Chapter 14. Sex differences in the behaviour of African elephants. — In: The difference between the sexes (Short, R.V. & Balaban, E., eds). Cambridge University Press, Cambridge, p. 331-346.

RUCKSTUHL, K., & NEUHAUS, P. (2000) Sexual segregation in ungulates: A new approach. *Behaviour*, **137**(3), 361-377.

RUGGIERO, R. G. (1991) Opportunistic predation on elephant calves. *African Journal of Ecology*, **29**(1), 86-89.

SELIER, S. J. (2007) The social structure, distribution and demographic status of the African elephant population in the Central Limpopo River Valley of Botswana, Zimbabwe and South Africa (Unpublished master's thesis). University of Pretoria.

SHANNON, G., DUFFY, K., PAGE, B., & SLOTOW, R. (2006) The consequences of body size dimorphism: Are African elephants sexually segregated at the habitat scale? *Behaviour*, **143**(9), 1145-1168.

SHANNON, G., PAGE, B., SLOTOW, R., & DUFFY, K. (2006) African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology*, **41**(1), 37-44.

SINCLAIR, A. R., & ARCESE, P. (1995) Serengeti II: Dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago. pp.148.

SITATI, N. W., WALPOLE, M. J., SMITH, R. J., & LEADER-WILLIAMS, N. (2003) Predicting spatial aspects of human–elephant conflict. *Journal of Applied Ecology*, **40**(4), 667-677.

STOKKE, S., & TOIT, J. T. (2000) Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography*, **23**(1), 70-80.

STOKKE, S., & TOIT, J. T. (2002) Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology*, **40**, 360-371.

SUKUMAR, R. (1989) The Asian elephant: ecology and management. Cambridge University Press.

THOMAS, B., HOLLAND, J. D., & MINOT, E. O. (2008) Elephant (Loxodonta africana) Home ranges in Sabi Sand Reserve and Kruger National Park: A five-year satellite tracking study. *PLoS ONE*, **3**(12).

WALL, J., DOUGLAS-HAMILTON, I., & VOLLRATH, F. (2006) Elephants avoid costly mountaineering. *Current Biology*, **16**(14), R527-R529.

WESTERN, D., & LINDSAY, W. K. (1984) Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology*, **22**(4), 229-244.

WITTEMYER, G. (2001) The elephant population of Samburu and Buffalo Springs National Reserves, Kenya. *African Journal of Ecology*, **39**(4), 357-365.