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**Author:** Huqa, Tuqa Jirmo  
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Synthesis, Conclusions, and Recommendations

6.1 Lion population response to environmental stochasticity and implications for conservation: A synthesis

The description and prediction of stochastic events and their impact on population dynamics in time and space is fundamental to ecology and conservation biology. Ecologists are increasingly aware of the importance of climatic variability in natural systems. Some authors have predicted that, with climate change, the frequency and severity of stochastic climate events will increase (Jededia et al., 2013). The dynamics of every population has both deterministic (predictable) and stochastic (unpredictable) components that operate simultaneously (MacArthur, 1972). Russell (1993) defined stochasticity as temporal fluctuations in terms of mortality and reproduction rate of all individuals in a population. A major challenge for ecologists is to predict the possible consequences of climate change in terms of an increase in stochastic events and based on this, to propose adaptation and mitigation measures (Wim et al., 2010). Climate change affects both the mean and the variability in climatic factors and the effect of changes in variability is poorly understood. Unpredictable catastrophes that suddenly reduce a population substantially, such as might occur in droughts, fire, floods, landslides, volcanic eruptions, or epidemics, are now classified as forms of stochasticity (Russell, 1993; Johst & Wissel, 1997).

Evolution is an expected response to environmental change, similarly, climate change and other environmental shifts are widely acknowledged to be important drivers of ecological change (Parmesan & Johe, 2003). Organisms are subject to selection imposed by the range of environmental variation experienced by their ancestors. Variability is a critical environmental factor and may therefore have consequences for vital population dynamics (Parmesan & Johe, 2006). Rainfall variability therefore is considered
important as it influences the dynamics of African ungulates, and change in rainfall variability equally affects carnivore abundance. Several studies have shown adverse impact of drought on predator biomass (Ottichilo et al., 2000; Georgiadis et al., 2007). Other factors regulating predator biomass are prey abundance, retaliatory killing and disease.

Fluctuations in population size often appear to be stochastic, or random in time as demonstrated by mortality, reproduction and dispersal (Parmesan, 2006). Stochastic environmental fluctuations can have important implications for the conservation of small single populations and for metapopulations.

Stochasticity also can interact with human exploitation of the environment or other factors such as disease and can cause the collapse of ecosystem, or it can cause deterministic extinction of a population harvested under a strategy, which deterministically would produce a sustained yield. The impact of environmental stochasticity may lead to extinction irrespective of the size of the population. Therefore, it constitutes an important risk for population decline, in all populations regardless of their abundance at a given location. Because organisms are subject to selection imposed by the range of environmental variations, therefore changes in the variability of a critical environmental factor may have consequences for survival rates and population dynamics.

Under stable climatic conditions, carnivore population dynamics depend more on prey – predator relationships and availability of prey and water than on climatic factors (Carbone & Gittleman, 2002). Consequently, one could assume that the diversity of carnivores would be less dependent on climatic-environmental conditions than that of herbivore abundance.

### 6.2 Lion population trends and response to environmental stochasticity

In my study in the Amboseli ecosystem, human-induced mortality and climatic variability had significant effects on lion pride organization and social structure. The drought affected the availability of prey, and as a result lion livestock predation increased, along with lion retaliatory killing. Loveridge et al. (2006) and Yamazaki (1996) found that social behaviour of prides was disrupted by the removal of pride males by sport hunters leaving gaps
within the territorial structure. In my study, the significant change in age structure after the drought year in 2009 was an indication of a growing lion population, with more juveniles than adults expected to fill this territorial vacuum. The changes in social structure I detected in my study, with a smaller group size after the drought and an increase in the Male: Female ratio, are an indication of a disturbed social structure. Previous studies have found that lion group size is correlated with prey size and prey availability and lion density is influenced by multiple factors, related positively to herbivore biomass, as well as annual, mean rainfall and with interactive effects between rainfall and soil nutrients (Schaller, 1972; Van Orsdol et al., 1985; Hanby et al., 1995, Ogutu et al., 2008).

In my study, the Vulnerability Index (VI) for lions as a function of Drought Severity Index (DSI) and Prey Availability Index (PAI) was highest in 2010, the year directly after the drought and showed a gradual increase during 2011 and 2012. My study also shows that the year directly after the drought (2010) was crucial for lion survival and determined the outcome in terms of mortality and lion population structure. My interpretation is that, although drought also affected livestock, people moved away with their livestock and returned after the rains, heightening predation and retaliatory killing. The drought Vulnerability Index can be used to plan mitigation measures and identify drought coping or adaptation mechanisms for lions in other areas.

6.3 Lion home range, movement patterns and connectivity provides opportunity for mitigation and adaptation

My study shows in many occasions, that both the collared male and female lions moved far from Amboseli NP into the surrounding communal group ranches. Furthermore, one of the males collared in this study spent a great amount of time in the neighbouring country of Tanzania, located south of the park. Evolutionary processes are not an alternative to range movement, but instead modulate the magnitude and dynamics of the range shift. My study indicated that the lion populations in Amboseli NP are not isolated, as wildlife corridors exist between the park and the group ranches and some of the lions even established new territories in Tanzania. This ability to disperse and survive in the surrounding landscapes and possibly connect with other lion populations serves an important function in the gene flow within the metapopulation. To restore the populations of prey species and thereby reduce the vulnerability of the lions in the face of climatic fluctuations,
there is need for concerted efforts to implement measures such as the establishment of community conservancies and corridors to other protected areas within the region.

This example shows how a complex interaction may occur in ecological responses to extreme climates and climate change. MacDonald (1983) suggested that resources and especially food dispersion are the main factors determining the home range size of large carnivores. During the wet season, when food is abundant due to the large herds of herbivores dispersing outside the park, the lions increased their home range. Due to the expansion and contraction of home ranges in response to prey availability, the total prey biomass within the home range may remain relatively constant. According to the finding of Bauer & de Jongh (2005), home range size is mainly determined by how food is distributed in space, while group size is determined by prey size and quality of food patches.

Ecologists have viewed species’ niches as static and range shifts over time as passive responses to major environmental changes (global climate shifts or geological changes in corridors and barriers) (Turner et al., 2005; McCarty, 2001). Patterns of change in the home range size (the size of the minimum area that can sustain the individual’s energetic requirements) over time can provide important insights into the ecological and evolutionary responses of mammalian communities to new environmental conditions (Van der Putten et al., 2010). Understanding the ability of species to shift their ranging pattern is of considerable importance, given current rapid climate change. Furthermore, a greater understanding of the spatial population dynamics underlying range shifting is required to complement the advances made in climate niche ecology. There is no doubt that climate plays a major role in limiting terrestrial species’ ranges (Turner et al., 2005; Wilson et al., 2005; Parmesan, 2006, Pearson & Dawson, 2003). There is a strong trade-off between climate tolerance and resource/habitat preferences on one hand and a relaxation of selection for climate tolerance (Turner et al., 2005; McCarty, 2001). Climate variability (change) can alter the setting of range limits, leading to range expansion or contraction (Owen-Smith & Ogutu, 2013, Ogutu & Owen-Smith, 2003). Many such range shifts have been reported over the past decades and this process is presumed to continue (Turner et al., 2005; Parmesan & Yohe, 2003; Easterling et al., 2000). Stochastic weather patterns can force wide-ranging species such as lions beyond current reserve boundaries, into areas where there will be greater conflicts with humans (Tuqa et al., 2014). Climate events affected the habitat quality, food
supply and access to resources (Wilson et al., 2005, Ogutu & Owen-Smith, 2003, Owen-Smitt & Ogutu, 2013), which in turn, as our results show, influenced the lions’ home-range and movement patterns.

The role of the Maasai community in conservancies such as Kitirua trust, Eselengei and Kitenden corridor are thereby crucial. An understanding of an animal’s ranging patterns provides an important insight on how it uses its resources. Under conditions of fragmented habitats, severe climate conditions such as severe drought can create new challenges for lion conservation due to effects on prey availability and subsequent influences on their ranging patterns.

**6.4 Lion prey availability and diet shift – a realized niche in constrained predator-prey relationships**

My research findings supports widely held perspectives that lions are opportunistic feeders, generally thought to prey on medium-to–large-sized ungulates. My study showed that lions are able to persist on a varied diet in a stochastic environment with extreme drought, by partially shifting or expanding their feeding niche and including smaller animals such as impala, warthog, or porcupine, and larger animals such as giraffe and buffalo as well as cattle. This partial shift and diversification of prey shows ecological resilience and the adaptability to a changing stochastic environment by lions. Much of ecology is built on the assumption that species differ in their niches and their responses to temporal fluctuations in the environment (Adler et al., 2006; Kneitel et al., 2004). Periodically, there are natural fluctuations in all seasonal parameters such as temperature, precipitation or the amount of vegetation cover (Wichmanna et al., 2005). We can assume that although the population dynamics of a species is well adapted to seasonal variations such as dry and wet, it might not be adapted to non-seasonal variation such as a stochastic drought phenomenon. Habitat use and prey selection by individual animals results from patterns ultimately driven by habitat-dependent fitness (Hirzel & Le Lay, 2008), that is, the fundamental niche is subjected to natural selection (Austin et al., 2013). For a niche to evolve, the new conditions must not lie too far outside the ancestral niche of any organism. In this case, natural selection tends to act upon principally as a conservative force (Holt & Gaines, 1992). In the case of gradually, directionally changing environmental conditions, a species is subjected either to track its environment across space or to go extinct (Lande & Shannon, 1996).
6.5 *Livestock predation trends, community knowledge and attitude*

My study results showed that prey abundance and seasonality in rainfall influences livestock predation rates. Further, my study also showed that most livestock predation attacks by large carnivores occurred during the wet season, with the exception of the drought year 2009. This applied to all livestock types: goats/sheep, cattle and donkeys, for which there were low predation rates in the years before and after the drought.

I found that, when herbivore numbers showed a significant decline during the drought year and during the years after the drought, carnivore livestock predation increased simultaneously. Wild herbivore decline was evident across the three categories; larger herbivores (buffalo, giraffe and eland) medium sized herbivores (wildebeest, zebra and waterbuck) smaller herbivores (Thomson’s gazelle, Grant’s gazelle, warthog and impala). Other studies, such as Patterson et al. (2004) and Woodroffe & Frank (2005) suggested that this trend may be ultimately driven by seasonal variation in the local availability of natural prey. Whether the wet or dry season causes increased depredation is then likely to be dictated by regional relationships between rainfall and natural prey. Various studies have demonstrated that livestock depredation is more common in areas with low prey abundance (Sillero-Zubiri & Laurenson, 2001; Polisana et al., 2003; Treves et al., 2003; Rabinowitz, 2005; Bagchi & Mishra, 2006; De Iongh & Bauer, 2008). Local environmental conditions such as rainfall (Patterson et al., 2004; Woodroffe & Frank, 2005), livestock husbandry practices (Madhusudan, 2003; Ogada et al., 2003; Polisara et al., 2003; Rabinowitz, 2005) and characteristics of attacked villages and livestock enclosures (Linell et al., 2001; Ogada et al., 2003) have been found to influence livestock depredation. Whereas the dry season in some regions is associated with increased natural prey and reduced livestock depredations, the inverse has been shown in areas where prey numbers peak in the wet season (Ikanda, 2005). In the northern region of Ethiopia, where the natural prey base were highly depleted spotted hyena depend entirely on anthropogenic food (Yirga et al., 2012; Kolowski & Holekamp, 2006).

Although multiple studies on Kenyan rangelands concluded that lions are the most serious livestock predator and that hyena predation is relatively infrequent (Frank, 2000; Ogada et al., 2003; Patterson et al., 2004), my study showed that lion predation rate were relatively low as compared to hyena.
To manage wildlife outside protected areas effectively, or even to secure protected areas themselves, the benefits of wildlife must outweigh the costs to neighbouring local communities. The compensation schemes introduced earlier have relatively positive impacts on community attitudes and have reduced lion killing in Amboseli. With the Kenya government policy change and introduction of wildlife compensation for life and property damage in 2014, we expect a significant positive impact on community tolerance for lions and all other carnivores.

Livestock continue to be a major source of livelihoods for the Maasai community around Amboseli NP. My result shows that a majority of the respondents depend on livestock. The major problems identified by all respondents was the problem of livestock predation by large carnivores. Hyena was identified to be the most problematic animal, followed by lion and cheetah in that order, while insignificant numbers perceived jackal to be a problem animal. Our result on predation trends show that jackal kills more livestock than lion in terms of numbers of young goats and sheep. Respondents recognized that there was a seasonal variation in livestock predation, indicating more predation during the wet season as opposed to dry season.

My results show that major community benefits of living next to Amboseli NP are the attraction of tourists, bursaries for schools children, and source of employment and “Social Projects” such as livestock/grazing and water provision. On the other hand respondents also reported problem animals, restricted movements, ranger arrest/harassment, loss of grazing land to be problems emanating from the park.

Management of the predation site (disposal of kills), a prompt response to community distress and predator kills are very important measures in resolving the conflict and reducing the frequency of predator attacks. Our results show that nearly all 94.6% respondents consume livestock meat killed by predators. This had significant impact on the immediate repeat attack of livestock, with varying time periods depending on whether the predator in question had fed on the kill or not.

The greatest impediment to pastoralism was identified as recurrent drought, predation of livestock diseases and diminishing pasture. The drought coping mechanisms identified were migration to other areas, sale of livestock
and diversification of livelihoods. The drought of 2009 was identified as worse in terms of livestock loss and poverty in the history.

I conclude that large carnivores create problems because of their feeding habits and wide-ranging requirements and the need for substantial prey populations, which inevitably brings them into conflict with people. Large protected areas or well-managed landscapes with corridors and conservation-friendly local communities can provide relatively long-term security for viable predator populations. To manage wildlife outside protected areas effectively, or even to secure protected areas themselves the benefits from wildlife must outweigh the costs to neighbouring local communities.

6.6 Conclusions

In my study, I discuss the response of lion populations to effects of climate variability (severe drought) and their strategy to persist and interact with people/livestock. I assessed several aspects of lion populations: lion population density and social structure, ranging patterns and movements, the diet and relationships with prey and livestock predation trends.

1 Severe drought had an effect on Amboseli lion social structure, with smaller group size and a decreased male to female sex ratio after the drought, a result of low food availability because of the drought. This increased the lion Vulnerability Index in 2010 as a result of increased human-induced mortality; furthermore, livestock predation by lions increased, as did retaliatory killing of lions.

2 Climate events such as drought affected the habitat quality, food supply and food access, which in turn influenced the lions’ home-range and movement patterns. Conditions of fragmented habitats can create new challenges for lion conservation due to effects on prey availability and subsequent influences on their ranging, far and wide beyond small protected area such as Amboseli. The long-term lion study through GPS/GSM collars has revealed useful information on corridors used by carnivores and herbivores within the Amboseli ecosystem and connectivity with other conservation areas.

3 My findings confirmed that lions are opportunistic feeders that are generally thought to prey on medium-to-large-sized ungulates, but are able to adapt to stochastic events such as drought. When preferred prey were not available, they partially shifted and fed more on smaller animals
such as impala, warthog, porcupine and expanded to larger prey such as giraffe in 2010 and 2011.

4 Prey abundance and seasonality in rainfall influenced livestock predation rates. The negative attitude of pastoralist community correlates with the intensity of livestock predation by large carnivores in Amboseli ecosystem. Annual herbivore numbers showed a significant decline during the drought year and during the years after the drought while livestock predation by carnivores increased.

5 Lion populations showed a high resilience in coping with drought stochasticity to survival by increased reproduction of cubs after the drought

6.7 Recommendations for conservation and management

The continued existence of large populations’ of lions and other large carnivore species in the Amboseli rangelands indicates the presence of a healthy and functional ecosystem. The majority of wildlife in this ecosystem lives outside the protected areas most of the year and is under intense pressure from human activities. These include the interaction with incompatible land use such as agriculture and high-density settlements. The increasing livestock numbers in the area forms another challenge, through competition for forage and water resources with wildlife especially during the dry season. Furthermore, poaching poses a threat to animals outside the boundaries of protected areas as they become easy targets. Wildlife species are generally adapted to their environments and slight changes in habitat or climate are often reflected in population changes.

- A climate-change strategy needs therefore to be developed: a science-based analysis of ecological factors that affect species’ adaptation and determines subsequent mitigation measures. The potential impacts of climate change in terms of stochastic events such as recurrent droughts should be assessed on a species by species basis for both carnivore and herbivore dynamics. This will enable the tracking of daily movements and seasonal migrations, and changes in vegetation conditions. Drought, being a driver of climate change, has the potential to alter migratory routes and timing, which may in turn lead to increased human-wildlife conflicts.

- Community participation in conservation and decision making is very important to ensure the survival of large carnivores and other wildlife within the group ranches. Trans-boundary ecosystems should be sup-
ported by the respective governments to establish buffer zones surrounding Amboseli NP and assuring connectivity to critical wildlife areas such as the Kitenden Corridor, linking Kilimanjaro national park with ANP. The Amboseli population may act as an important gene pool which might be prone to extinction, if passage through the corridor is blocked.

- Enforcement policies and legislation such as the Land use policy, the Draft land act, the Draft land registration bill, the Draft wildlife policy, the Wildlife conservation and management ACT 2013 are important. Other economic instruments, which ensure payment for ecosystem services, should be implemented as well, to secure the corridors and migratory routes of wildlife through easements, leases and direct purchases. The development of programmes that involve communities in wildlife conservation is an important tool for wildlife management.

- The promotion of community wildlife conservancies, game scouts, associations and other eco-tourism ventures will provide direct benefits. In order to meet both the conservation goals and livelihood needs of the communities, proliferation of awareness in conservation and public education is critical in promoting lion and other carnivore coexistence with people and to promote tolerance.

- Human-wildlife conflicts have increased in Amboseli NP as the park continues to be engulfed by unsustainable land use, including agriculture and infrastructure developments. During the dry periods, wildlife strives to survive in unfamiliar territories and becomes overwhelmed by intense competition for meager resources such as water, forage and space, and exposure to poaching and diseases. More research needs to be conducted in this field to find ways in which people can coexist with large carnivores.

- Further research is needed to confirm the low heterozygosity and genetic variability identified by Bertola (2015) of the Amboseli lion population. This management option requires extensive financial resources and expertise. For this to be feasible, the government should solicit financial support from international conservation donors.
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