Introduction: Burning for birds might seem absurd or even contradictory. How can the scorching heat of flames, which causes animals to flee and which burns and withers everything else within its reach, promote life? Fire events change resource availability, directly impact life cycles and modify vegetation structure. For a bird, this can mean a feast of insects flushed during a fire, a scorched nest in the grass, or a newly cleared habitat. Cumulative fire events can over the course of years influence the character and quality of habitats.

In this study we aimed to explore the short and long-term effects of fires on bird communities in the greater Serengeti savanna ecosystem in Tanzania. The study investigated the influence of recent fire history, (within one year), cumulative fire history (since 2000), and fire seasonality, on bird assemblages. We predicted that the occurrence of recent and cumulative fire history would influence bird communities, particularly through its impact on vegetation structure.

Understanding the impacts of fire on birds and on vegetation is critical to ensure appropriate management. Birds are highly influenced by vegetation complexity (MacArthur & MacArthur 1961). Fire, as a major determinant of vegetation structure is by extension a major indirect contributor to bird community composition, while also having direct impacts on life cycles.

In some ecosystems fire is indeed essential (Bond & Archibald 2004). Savannas, for example, are among the most fire dependent and geographically extensive of these fire driven systems. Their vast expanse through much of sub-Saharan Africa, South America, India and Australia can be attributed in large part to fire (Archibald 1995, Staver et al 2011). The savanna biome supports unique biodiversity in birdlife with important conservation implication for bird migrations, and endemic and range-restricted species.
Fires as ecological events occur within a historical pattern of fire attributes known as a ‘fire regime’. The nature of the regime determines the way in which fire influences the ecosystem. In particular, fire frequency, seasonality, intensity, and spatial scale all influence patterns of savanna vegetation structure (Smit et al 2010). The absence of fire, or simply the alteration of fire regimes can transform some ecosystems to alternate states (Bond et al 2005, Staver et al 2011) resulting in the loss of key habitats and the species they support.

This study was conducted in the complex ‘natural laboratory’ of the Serengeti ecosystem (Sinclair & Arcese 1995). A substantial proportion of the Serengeti is burned each year (see Appendix 1 Map 3) making fire an integral part of the system (Sinclair et al 2009). Fire in the Serengeti, is almost exclusively set by humans with no known incidence of lightning ignition (Sinclair & Arcese 1995).

The Serengeti is a designated large ‘Important Bird Area’, and an ‘Endemic Bird Area’ home to several avian endemics and range-restricted species (Baker & Baker 2001). These species of particular conservation interest include Grey-breasted Spurfowl (*Pternistis rufopictus*), Fischer's Lovebird (*Agapornis fischeri*), Usambiro Barbet (*Trachyphonus darnaudii usambiro*), Rufous-tailed Weaver (*Histurgops ruficauda*), Karamoja Apalis (*Apalis karamojae*), and Grey-crested Helmet-shrike (*Prionops poliolophus*). While there is new momentum with regard to fire decision-making, the focus remains on migrating herbivores and little attention has been given to addressing other conservation objectives.

Management decisions, though important, only play a one part in determining where and when fire events can happen. Bottom-up drivers, namely nutrient availability and rainfall influence how much fuel is available to burn and when it is dry enough to burn. Herbivores on the other hand compete with fire for consumable biomass (McNaughton 1985). The system is even more complex because of dynamic spatial and temporal patterns. Rainfall in the Serengeti is highly seasonal with dry periods between the short rains concentrated in November and December, and the long and heavier rains in March through May (Norton-Griffiths et al 1975). The mean annual rainfall is distributed across a broad rainfall gradient from ~150mm in the southeast to ~1400mm in the northwest (Norton-Griffiths et al 1975). The nutritional gradient broadly opposes the rainfall pattern with moist dystrophic conditions in the northwest and drier eutrophic conditions in the southeast (Holdo et al 2009).

Serengeti has impressively high populations of mega-herbivore grazers including around 1.3 million migrating wildebeest, 200,000 zebra, 440,000 Thomson gazelle, 70,000 buffalo, as well as eland, Grant’s gazelle, topi and others (Mduma et al 1999, Holdo et al 2007, Sinclair et al 2009). Browsers also play a significant role as top-down drivers with the most significant influence being exerted by the elephant population (Dublin et al 1990, Sinclair et al 2009). Rainfall, nutrients, and herbivory determine in large part the flammability and the available combustible fuel, and ultimately the effect of fire on the landscape.

**Aims & Hypotheses:** The aims of the project were to understand the impacts of different fire regimes on bird community composition across the Serengeti ecosystem. To investigate the relationship of fire and bird communities we tested whether:
1. Bird community composition was different in areas burned and in areas not burned within one calendar year;
2. Bird community composition changes in relation to the number of fire events since 2000. This was tested for three fire seasons: early (May-July), late (August-October) and short (February-April);
3. Abundance and diversity of birds was lower in areas that had a fire event in the last year, and if more fires impacted bird diversity and abundance.

We expected to find vegetation structure change in response to fire and a consequent response of birds to vegetation.

1. For recently burned areas we tested whether:
   a. Areas that were burnt in the last year would have low vegetation density, in the grassy understory;
   b. Bird community composition changes according to density of the understory.
2. For long-term effect of cumulative fire history over the course of 14 years we tested whether:
   a. More fires in general open up mid-upper level structure while few fires result in denser mid-upper level structure. We expected this effect to be strongest for late season fires that are hottest as opposed to cooler, patchier early season burns.
   b. Bird composition, density, and diversity change according to greater structural complexity in mid-upper level vegetation.

**Study area:** The study area included much of the greater Serengeti ecosystem in Tanzania (Appendix 1 Map 1), including a range of fire prone habitats, from dry eutrophic *Acacia*-*Commiphora* woodland and short grass plains in Makao Conservation Area, to the moist dystrophic *Terminalia*-*Combretum* woodlands and tall *Themida* grasslands in the Ikorongo and Grumeti Game Reserves. Fire is a major contributor to the ecology of this area with over 80% of the protected land area in the National Park and western protected areas experiencing a fire at least once since 2000.

**Fire data:** We obtained monthly 500-meter resolution MCD45A1 Burned Area satellite imaging for the complete times series (January 2000 – October 2013) from http://reverb.echo.nasa.gov, showing the spatial extent of the area affected by fire (Roy et al 2002, 2005, 2008). We mapped total number of fires, and number of fires in each fire season (Appendix 1 Map 2) Finally, we determined the number of seasons since the last fire occurrence (‘last burn’) to identify occurrence/non-occurrence of a fire event within one calendar year (Appendix 1 Map 3).

**Rainfall & Nitrogen data:** We extracted interpolated mean annual rainfall values from a map produced by Hopcraft et al (2012) using Serengeti Ecology Department monthly rainfall records (1960–2006). We extracted estimates of nitrogen for each sample site from a grass nitrogen map provided and described by Hopcraft et al (2012).
Sample selection: We used a suite of rapid sampling techniques to characterize bird communities and vegetation structure at 207 points from MODIS MCD45A1 product 500m burn pixels centroids using fire maps provided by Archibald et al (2010). We conducted the sampling during late September to early December 2013—at the end of the long dry season and beginning of the short rainy season (Appendix 1 Map 1).

Bird community sampling: We conducted standard 10-minute point counts (Bibby 2000) in the morning between 06:30 and 11:00 during peak bird activity for highest detection rates. During the 10-minute point counts, we recorded bird species, abundance count, and distance from observer for each visual or audible detection within distance bands of radius 0-10 m, 10-25 m, 25-50 m, 50-100 m, >100 m, and fly-overs.

Vegetation sampling: We conducted the Bitterlich variable-plot point sampling method (Cooper 1957) to provide a measure of tree density around each sample point. We used a wedge angle gauge: held at a fixed distance from the observers eye and rotated 360° around the sample point to obtain a count of trees and bushes whose trunk or stem diameter was visually wider than the wedge, which represents a fixed angle. Closer trees, and larger trees are counted proportionally more often. We then multiplied this count by a basal area factor according to the wedge size to give the total stand basal area (SBA) at breast height in m² per hectare at each sample point.

We measured horizontal visual obstruction caused by vegetation to characterize habitat structure using methods devised by MacArthur & MacArthur (1961), and modified from Ralph (1985), and Skowno & Bond (2003). We generated foliage profiles at each sample point using this simple method by estimating distance of horizontal visual obstruction at specific heights in a single direction. The distance we recorded at each height was an estimate of the distance at which an imagined 10x10cm board would be >50% visibly obscured by vegetation. The specific heights were 0.05, 0.25, 0.5, 1, 1.5, and 2 meters from the ground. We capped distances estimates at 250m. We took four foliage profiles in different directions systematically. Additionally, we also estimated maximal canopy height in each direction within 100m.

Finally we used a disc pasture meter (DPM) as a rapid method of measuring compressed grass height to give a proxy for the grass layer’s contribution to the vegetation structure (Bransby & Tainton 1977). We took ten DPM readings at 5-meter intervals in a random direction from the sample point, and focused analysis on the mean of these values. This provided a measure for a major component of the savanna habitat that is directly impacted by fire, herbivory, and abiotic conditions.

Data preparation: Using a distance sampling technique we converted raw bird abundances from point counts to density estimates for each species at each point. We calculated avian species total density, and Shannon diversity index (H) for each sample point. \[ H = - \sum p_i \log p_i \] where \( p_i \) is the proportional abundance for each species at a sample point (Shannon & Weaver 1949).
We summarized vegetation structure in two principal components using the package vegan (Oksanen et al 2013). This provided a single metric for each sample site foliage density at mid/upper level (53% of the variance), and a similar metric for low level vegetation (22% of the variance). We used these first two principle components as independent variables characterizing the two major vegetation structural components – lower grassy layer and mid-upper shrub/tree layer.

Analyzes: We divided analyses into two parts; the first relating to the composition, diversity, and abundance of birds as explained by fire, and the second concerning the indirect influence of fire on birds through its effect on habitat structure. To investigate the short-term and long-term impacts of fire on birds, we tested the direct ordination structuring effects and regression trends of recent fire occurrence and cumulative fires on bird community composition, diversity, and density. We expected fire to influence birds though its impact on habitat alteration, so we tested the structuring effects and regression trends of fire variables on vegetation structure. Finally we tested the effect of vegetation structure on bird communities. Each of these analyses involved incorporating the impacts of rainfall and nitrogen as underlying drivers.

Key Results: We recorded a total of 204 bird species excluding unidentified records at 207 sites with a mean of 18 species per site. Common species, contributing >1% to total density included 32 species.

Despite the high variation in bird community structure across sample sites, the occurrence of recent fire did explain a small but significant proportion of the variance in bird community composition. This effect was stronger if only common birds were included. Cumulative fire in each season also explained a small but significant proportion of the variance in bird community composition. This was also true for nitrogen & rainfall.

The specific effects of fire on bird diversity and density were often associated with an interaction with rainfall and nitrogen:

- Nitrogen had a weak negative effect on Shannon diversity when the last fire occurred recently, and a weak positive effect when the last fire occurrence was over one year ago.
- Cumulative short season burns was positively correlated to Shannon diversity especially in higher nitrogen areas. In contrast, cumulative burns in early and late fire season were not significantly associated with bird Shannon diversity. Rainfall was also negatively correlated with Shannon diversity.
- Cumulative short season burns was positively correlated to total bird density especially in lower rainfall areas. Cumulative late season fires showed a weak but significant negative correlation with bird density. Cumulative burns in the early fire season and recent fire occurrence were not significantly associated with bird density.
We expected to find vegetation structure change in response to fire and a consequent response of birds to vegetation. For recently burned areas we found that occurrence of recent fire explained a modest but significant portion of the variance in raw vegetation structure measures especially with nitrogen, and rainfall included in the ordination. However, variance in vegetation structure was not significantly explained by nitrogen or rainfall alone. Where fire had not occurred recently, nitrogen exhibited a weak effect of reducing grassy vegetation density.

Low-level understory vegetation structure parameters explained a small but significant percent of variance in bird community structure.

For long-term effect of cumulative fire history over the course of 14 years we found that:

- Raw vegetation structure measures were not significantly structured by cumulative fires in early, late, and short fire seasons collectively or individually.
- Cumulative burns in early, late and short fire season were not significantly associated with changes in low-level vegetation structure.
- The influence of fire on mid-upper level vegetation structure was generally weak. Cumulative short season burns was positively correlated with open, sparse mid-upper level vegetation in unburnt areas, but the effect was weaker in recently burned areas.
- Cumulative late season fires also exhibited a marginally significant positive correlation with open vegetation structure.
- Rainfall was negatively correlated with mid-upper level vegetation density.
- We did not find cumulative early season fires to be significantly associated with mid-upper level vegetation density.

Mid-upper level vegetation structure parameters explained a small but significant percent of variance in bird community structure.

**Discussion & Conclusions:** Despite a high degree of variation in bird communities and vegetation structure, our results suggested that fire regimes do indeed impact bird communities with important conservation implications. We detected the strongest changes in bird community structure, diversity, and density in response to the immediate impact of fire and post-fire regeneration processes, and weaker effects to cumulative fire history. Short fire season burning appears to have significant influence on birds and vegetation structure, and these preliminary findings warrant further investigation.
Our results suggest that both recent fire events and longer-term fire history are ecologically influential. Specifically, recent fire events were more important in influencing bird communities than cumulative fire history. Variation in bird community structure, diversity and density was correlated with the immediate impact of fire and post-fire regeneration processes. Cumulative fire history was also weakly correlated to bird community structure. The impact of fire on birds acts through alteration on habitat structure, to which birds respond. Given the post-fire changes in vegetation and bird community structure, we recommend against burning large expanses on a single day or even in a single season to allow some degree of continuity in the landscape. We also recommend that conservation managers think carefully about the expected habitat change in response to burning and the consequent changes in bird assemblages able to utilize the modified habitat. These decisions need to consider both short-term and to some extent long-term habitat impacts. Further research is required to elucidate the effects of herbivory and fire intensity on bird composition, and we advise focused research on species and functional groups of conservation interest.

Acknowledgements

I am deeply grateful to my supervisor Dr. Colin Beale for his dedicated support, from the initial invitation to work in Tanzania under the Serengeti Fire Project, through planning, fieldwork, data analyses, and writing. I could not have hoped for a more engaged and responsive supervisor. Likewise, I am sincerely thankful to my UCT supervisor Prof. William Bond for sharing his wealth of knowledge and ecological insight particularly in the initial planning and final writing stages.

Given the funding requirements for carrying out wildlife research in remote parts of the Serengeti ecosystem, I am profoundly grateful to my supervisors for support through their respective departments. I am also thankful to the African Bird Club through their Conservation Award program, to the Percy FitzPatrick Institute of African Ornithology, and the University of Cape Town – Travel Grant. This research would not have been possible with their support.

I express sincere gratitude for the competence and efficiency of Dassa Nkini at the Conservation Resource Center – Tanzania who facilitated all official processes necessary for conducting wildlife research in Tanzania. I am also thankful to Aurelia Mtui, Nelson Ole Kwai and Clarence Msafiri for their effort in this regard. I thank the Tanzania Wildlife Research Institute for granting me this opportunity to conduct research and for facilitating access to the study area.

I am grateful to the Brian Harris and Grant Burden through the Grumeti Fund, for enabling my stay in Grumeti and Ikorongo. I am equally appreciative for the support of Michel Allard, Julius Robinson, and Quinton Rochat through the Friedkin Conservation Fund and Tanzania Game Tracker Safaris for hosting me in Mwiba and Maswa. I am especially thankful to Mzee Nessa, my accompanying field assistant, throughout my fieldwork in Maswa.

For collaborative data sharing I owe my appreciation to Sally Archibald, who provided her Africa fire maps which I used in selecting sample sites, and to Grant Hopcraft for providing interpolated maps for estimates of rainfall and nitrogen, and for providing access to the Serengeti-Mara Database. I am also thankful to Howard Fredrick for his teaching assistance in using QGIS.

Finally, I am so grateful to my family, friends and classmates for their support. I am especially grateful to my father, Erwin Kinsey for use of his vehicle for research and for unwavering encouragement. Finally, I express heartfelt thankfulness to me wife, Jana Kinsey who selflessly encouraged me to pursue the masters program, and who remained a source of strength and dedicated encouragement throughout.
References:


Appendix 1 Map 1 Serengeti ecosystem protected areas in northern Tanzania and southern Kenya, including distribution of field sample points.
Appendix 1 Map 2. Cumulative fire occurrence between January 2000 - October 2013 summarized by fire season:
a. Early burn season in May-July (Julian days 121-212)
b. Late burn season in August-October (Julian days 213-304)
c. Short burn season in February-April (Julian days 32-120)
d. Cumulative burns across all fire seasons for the full time series.

Data from MCD45A1 Moderate Resolution Imaging Spectroradiometer (MODIS) Burned Area product at 500-meter resolution, obtained through the Land Processes Distributed Active Archive Center (LP-DAAC).
Appendix 1 Map 3 Recent fire occurrences over one calendar year (2013), showing burned areas in each fire season.