Ecological assessment of a shifting conservation landscape in Kenya

Insights from a long-term assessment of mammalian community change in an African National Park

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Abstract

The Aberdare Conservation Area (ACA), located in the central Kenyan highlands, is one of Africa's flagship National Parks. The area harbors large amounts of African wildlife including several species of afromontane endemics that are of conservation concern. Since its inception, the ACA has experienced explosive human population growth at its margins, with associated domestication of the surrounding landscapes. Both processes have led to a *de facto* isolation of the ACA from other natural areas. Even before the establishment of the national park, local authorities started collecting systematic wildlife records. These nightly surveys, conducted by trained professionals using standardized protocols over a period of approx. 50 years, provide a unique opportunity to evaluate the effects of various conservation measures including the construction of a perimeter fence.

Here I analyze two exceptionally long-term nightly datasets on the diverse mammal community (46 spp.) collected in two different locations, one close to the edge of the protected area (Treetops Lodge) and one closer to the core of the park (The Ark Lodge). I found not only clear difference in the two species communities, but also differentiation in the temporal changes of wildlife populations between the two sites. Five taxa (bushy-tailed mongoose, coypu, reedbuck, impala, and eland) appeared in the resident mammal community during this study, while eight species (aardvark, bushpig, bongo, civet, Harvey's duiker, jackal, lion, and zorilla) disappeared. The species that have disappeared from the ACA are either intrinsically rare taxa or savanna species that have had a marginal existence within the limits of the ACA. I find strong evidence for edge effects with the site closest to the border of the ACA (Treetops); this site registered the strongest losses in total wildlife population numbers, aggregate wildlife biomass, species richness, and compound indices of species diversity. Establishment of a fence around the area starting in 1989 led to temporary increases in wildlife populations near the park margins, but in the last 10 years these gains have been reversed and wildlife populations have continued to decline near the edge of the park. In contrast, wildlife populations near the core areas (The Ark) appear to have remained relatively stable over the years.

Keywords: Aberdare National Park, biodiversity, generalized additive models, species richness, species abundance, community turnover, edge effects

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Introduction

The Aberdare mountain range is one of Africa's flagship conservation areas; its natural value lies in its plentiful water resources, abundant forests, and endemic biodiversity. Aberdare National Park is world renowned for its high concentration of megafauna, which in turn has made it a prime target for conservation and ecotourism activities. These conservation efforts, culminating most recently in the fencing of the perimeter of the Aberdare mountain range, have had important implications for the management of the protected area. Many have hailed these changes as a win-win for the wildlife inside the protected area and the human communities that have become established at the margins of the ecosystem. Although the value of Aberdare bioregion has been recognized, surprisingly little has been done in quantifying the biodiversity of the protected area. In particular, little work has been done to document long-term changes in wildlife populations or investigate the general effects of conservation management on the biodiversity of the region.

Here I analyze two previously unpublished long-term datasets that document wildlife populations in this biodiversity hotspot. The purpose of this study is to explore spatial and temporal patterns in the mammalian communities at two study sites located within Aberdare National Park (Figure 1) across the duration of the datasets. The wildlife observation records from Treetops and The Ark lodges within Aberdare National Park provide 80 cumulative years of sighting data (data records span from 1963-2011 and include 48 years of data from Treetops and 32 years of data from The Ark). I explored the time series data using population and diversity measures to identify long-term trends in the resident mammal communities. In addition the analysis provides the rare chance to evaluate the effectiveness of an electric fence that was built around the perimeter of the ACA on wildlife using long-term historical data. Given the increased use of such fences around protected areas, this study can provide important before and after data that can inform further conservation planning.

Population monitoring across a mammalian community

Standardized long-term survey data are used regularly to monitor changes in species populations, especially for taxa of conservation interest (Fedy & Aldridge, 2011; Rendon, Green, Aguilera, & Almaraz, 2007). However, such data have been used less often to investigate population dynamics across multiple taxa, let alone entire species communities[1] (for exceptions see Waite et al., 2007 and Kirkland, 1990 (a metanalysis)). This dearth of long-term whole-community datasets is understandable given the immense methodological, logistical and fiscal challenges that such investigations pose. The wildlife surveys of Treetops and The Ark, obtained on a daily basis, provide an unusual opportunity to delve into questions concerning the stability and changes in a mammalian community over a long-term time period. I employed methods similar to previous studies that utilized long-term population data in order to provide a historical timeline of species abundance and diversity in this system.

Diversity: a measure of an ecosystem

Growing concerns over the state of ecosystems have rekindled interest in integrative measures of biological diversity that can be used to evaluate potential disturbances and change on these systems (Mugarran & Henderson, 2010). Measures of biodiversity have been used to evaluate such factors as ecosystem productivity and stability (Tilman, 1996; McNaughton, 1977), as well as overall ecosystem health (defined here as the actual state of an ecosystem

[1] This statement is based upon a literature review that included a key word search (mammal community data conservation) and an extensive reference search of key articles.

relative to the state desired by management). Here I use indicators of diversity to investigate the following general questions:

(1) Do diversity measures of the mammalian communities vary spatially?

(2) Do diversity measures of the mammalian communities vary temporally?

(3) Relatedly, do changes in diversity correspond to the construction of the electric fence that encloses the Aberdare ecosystem?

The wildlife datasets allow us to calculate such diversity values across the two study sites as well as across the timeline of observations. I accomplish this investigation of diversity change by utilizing measures of species richness and species abundance. Species richness and abundance (or evenness) are two broad measures that have traditionally been used to assess the biodiversity of an ecosystem. There are also a variety of indices used to measure species diversity which are useful when one wants to describe both the evenness and richness of a species community with one value (Magurran, 2004). I employed the Shannon-Wiener diversity index, defined as *H'*, to compare diversity between the two study habitats across the time series data.

Brief overview of Aberdare National Park

Aberdare National Park is a 776 km² protected area located within the larger Aberdare Conservation Area (ACA; 2185 km²). Even before its establishment as a national park in 1970, the Aberdare range was recognized as a priority region critical for the protection of forest, wildlife (particularly charismatic megafauna) and water resources. Recent estimates suggest that the Aberdare range harbors 50+ mammal species, 270 species of birds, and over 770 species of vascular plants (Butynski, 1999). Aside its global importance as a cradle of biodiversity (the Aberdare Range belongs to the 'Eastern Arc and Coastal Forests of Tanzania and Kenya' biodiversity hotspot (Myers et al., 2000)), the Aberdares mountain range provides valuable ecosystem services to local communities through its provisioning of an abundant and stable water supply. The Aberdare mountain range is considered one of the five major water towers of Kenya with five of country's seven major rivers originating in this range. The area serves as a catchment for the Sasumua and Ndakaini dams and provides most of the water and energy resources for Kenya's capital, Nairobi (Lambrechts, Woodley, Church, & Gachanja, 2003).

The lush tropical forests and abundance of wildlife make the Aberdare Range and the Mt. Kenya region a popular tourism destination in Kenya. Tourism is traditionally ranked as the second most important industry (behind agriculture) with 1 million tourists in 2010 and foreign exchange revenue of over 800 million U.S. dollars (Ministry of Tourism, Nairobi, Kenya). While much of the tourism and its associated benefits are based on intact natural ecosystems and wildlife viewing, intense agriculture and high population density in areas adjacent to the ACA, as well as illegal exploitation of forests and wildlife inside the conservation area, threaten the protection of these resources (Rhino Ark, 2011; Lambrechts, Woodley, Church, & Gachanja, 2003).

The management in the Aberdare Conservation Area

The vulnerability of the Aberdares landscape coupled with the high value of its natural resources have resulted in a complex history of wildlife and habitat management. Like many Eastern African landscapes, the Aberdares has faced many threats that have impacted its wildlife. This includes heavy poaching of rhinos for their horns causing a population crash in the 1970's (Western, 1982; Walpole, Morgan-Davies, Milledge, Bett, & Leader-Williams, 2001). In addition, there has been illegal exploitation of the forests inside the protected area including such activities as logging, livestock grazing, marijuana cultivation, and charcoal kilns (Rhino Ark, 2011), and increased agricultural intensity and urbanization in areas adjacent to the Aberdares. These events have triggered aggressive single-species management initiatives, as well as a major fencing initiative (discussed in detail in the next section).

Much of past conservation management has focused on two rare and charismatic taxa: the mountain bongo (*Tragelaphus euryceros*) and the black rhino (*Diceros bicornis*). The mountain (or eastern) bongo, endemic to the Aberdare and Mt. Kenya mountain ranges, is considered the Aberdares “flagship” species. It’s estimated that globally less than 100 individuals remain in the wild due to poaching and human encroachment (Estes, Okin, Mwangi, Shugart, 2008). Lion control efforts were used in the 1990s to reduce predation on the bongo population (Charles Mathenge, pers. comm.). Other efforts include the translocation of a number of individuals from Florida zoos to revitalize wild populations and the monitoring of collared individuals for ecological studies (i.e. Estes, Okin, Mwangi, & Shugart, 2008; Faria, et al., 2011).

Other conservation efforts have also targeted the black rhino populations in the Aberdare range. These efforts have primarily been led by the Rhino Ark, a NGO established in 1988. Both in the ACA specifically, as well as in Kenya in general, black and white rhino populations have experienced a dramatic decline (Western, 1982). As a result, a rhino fence was commissioned by Rhino Ark to help protect black rhinos in the Aberdares. The original proposal would have isolated black rhinos inside the ACA but would have allowed for movement of other wildlife species across the ACA boundaries (Rhino Ark, 2011). However, the scope of the fence project was soon expanded to an electric fence with the increasing concern about conflict among farmers and wildlife, as well as the increasing exploitation of the protected forests (Lambrechts, Woodley, Church, & Gachanja, 2003).

The Aberdare fence

In a report chronicling the destruction of the Aberdare range, Dr. Newton Kulundu for Kenya's Ministry of Environment, Natural Resources, and Wildlife describes the Aberdares as an invaluable ecosystem facing a range of threats: increasing agricultural intensification at the edges of the protected area, increasing urbanization of the neighboring city of Nyeri, and illegal exploitation of wildlife and forests inside the protected area (Lambrechts, Woodley, Church, & Gachanja, 2003). In an effort to protect the Aberdare ecosystem, a non-governmental organization called Rhino Ark was established in 1988 to oversee and coordinate wildlife conservation efforts. These included plans to stop illegal exploitation of wildlife inside the park (in particular the poaching of black rhino) as well as reduce human-wildlife conflicts at the edges of the protected area. Reports (Butynski, 1999; FAO, 1998) have concluded that the best way to reduce these conflicts would be to physically separate wildlife from the agricultural and urban areas that surround the Aberdare range. In the 1970's, a game ditch (Prickett, 1974) had been used to discourage wildlife from leaving the park in the direction of the surrounding agricultural fields and the nearby town of Nyeri (see reference Figure 1). However, these ditches proved ineffective: elephants destroyed the walls of the moats and most other animals could jump across the ditch (Thouless & Sakwa, 1995). The need for a more effective and manageable solution, particularly near the two wildlife lodges where megafauna populations were most heavily concentrated, gave justification for the construction of an electric fence.

This major conservation initiative was carried out by the Rhino Ark and other partners, including the Kenya Wildlife Service, from 1989-2009 and helped to establish the Aberdares as a successful conservation example in Eastern Africa. The fence was completed in eight phases, and at 400 km it functionally isolates the ACA from the surrounding landscape. The first phase of the Aberdare fence was built around the perimeter of The Salient, a 70 km^2 area where our two study sites are located (Figure 1). This area was an obvious choice for the first portion of the fence; it has the highest concentration of megafauna in the Aberdare ecosystem, lies in the immediate vicinity of Nyeri, and is the focus of most of the tourist activities in the area.

Physically separating protected areas from the surrounding environment is not a novel approach and fencing has been shown to be one of the most effective short-term solutions for reducing human-wildlife conflict (Parker et al., 2013, Thouless & Sakwa, 1995; Kenya Wildlife Service, 1990; Taylor and Martin, 1987; O'Connell-Rodwell, Rodwell, Rice & Hart, 2000). However, largely due to lack of data, there has been little opportunity to investigate in a quantitatively rigorous manner the effects of fence establishment on the numbers and composition of the local wildlife populations. Given the high costs of fencing, there is usually little money remaining to evaluate the effects of the fence and instead management plans are often carried out on a trial-and-error basis (Thouless & Sakwa, 1995). The wildlife datasets available at Treetops and The Ark provide us with this rare opportunity to investigate the potential long-term effects of an electric fence. Because the portion of fence around our study region was completed in 1991, a sufficiently long period of time has elapsed to evaluate the potential long-term effects of the fence on the local wildlife populations.

Methods

1. Study Area

Aberdare National Park (ANP; 776 km²) is located in the Aberdare mountain range in the Central Province of Kenya. The Aberdare range lies southwest of Mt. Kenya and runs roughly in a north to south direction, thus forming the eastern rim of the Great Rift Valley. Together with the Aberdare Forest Reserves (1411 km²), ANP comprises the larger protected area known as the

Aberdare Conservation Area (ACA) (2,185 km²). The Aberdare ecoregion has two rainy seasons; the long rains occur during April-June, whereas the short rains occur during the November-December season. Annual precipitation totals average 956 mm (SE= 80.9; n= 12) near The Ark wildlife lodge (The Ark Lodge, *unpubl. data*). Mean daytime temperatures range from 16°C (July) to 21.8°C (February) (The Ark Lodge, *unpubl. data*).

Ten distinct vegetation zones exist along the elevation gradient of the Aberdare Range (1,850-4,000 m); they can be grouped into three broader categories (Rhino Ark, 2011). The montane forests occur at the lowest elevations (1,900-2,400 m) and include the highest diversity of flora and fauna in the Aberdare Range. This is followed by the bamboo zone (2,400-3,000 m), and then the high elevation moorlands (dominated by *Hagenia*, *Hypericum*, and various ericaceous species) at the highest reaches of the range.

This study focuses on a section of the Aberdare NP known as the Salient. The Salient is a 70 km² spur of the mountain range that extends towards the east (Figure 1). The area is dominated by montane forest at higher elevations and transitions into one of the few savanna areas of the region towards the far eastern edge of the NP (Sillero-Zubiri & Gottelli, 1991). The Salient is known for its exceptionally high concentration of megafauna and has been the focus of most tourism and conservation activities in the area. Two wildlife lodges, The Ark and Treetops, are located in this area and they are the two sites where standardized records of wildlife sightings have been collected on a daily basis since the mid-1960s.

Treetops

Treetops lodge sits at the edge of The Salient and Aberdare National Park and is located less than 1 km from the edge of the park (Figure 1). Treetops lodge has a history that begins well before the establishment of Aberdares national park in 1949 (Pullan, 1988). It began as a simple tree stand in 1932 and expanded to its current 50 room capacity in the 1950's. The lodge's viewing decks provide a 360° view of the surrounding environment and the watering hole that lies adjacent to the lodge. Treetops lodge lies along a now defunct wildlife migratory route connecting the Aberdares with Mt. Kenya (Prickett, 1974).

Located at a relatively low elevation (1,996 m asl) Treetops lies below the zone of montane forest. Consequently, and also because of a history of deforestation, the lodge is surrounded by one of the few areas of grassland in the ACA (Prickett, 1974) which in turn attracts a number of savanna species otherwise rare in the area. On the other hand, the proximity to the park edge and the lack of montane forest habitat discourage the presence of some of the park's more elusive, high elevation species such as the mountain bongo (*Tragelaphus eurycerus isaaci*). Being located so close to the boundary of the ACA also means that the site is fully exposed to possible edge effects.

The Ark

The Ark lodge, opened in 1970, overlooks a salt lick and a watering hole deep in the Aberdare forests. Located 7.25 km from the entrance of the park, the site was chosen because of its seclusion from human activities. At 2,316 m above sea level, the lodge lies within the montane forest zone and is visited by a variety of high elevation forest taxa such as the mountain bongo (*Tragelaphus eurycerus isaaci*) and the giant forest hog (gfh) (*Hylochoerus meinertzhageni*).

2. *Data collection*

Nightly observation data have been collected by trained employees termed 'hunters' for all wildlife visiting the watering holes and salt licks at each site. Aside from an approx. 10-year gap in the Ark data (1985-1996) and a few other small gaps in the records (see Fig. 3) the data records have been continuously collected since 1963 at Treetops and 1970 at The Ark. Despite the exceptional length of the data series, a full analysis of these records has never been undertaken. Aside from Sillero-Zubiri and Gottelli's extensive work on the population trends and behavior of black rhinos (*Diceros bicornis*) and spotted hyenas (*Crocuta crocuta*) (Sillero-Zubiri & Gottelli, 1991; Sillero-Zubiri & D., 1992; Sillero-Zubiri & Gottelli, 1987; Sillero-Zubiri & Gottelli, 1992), there has been little published on the long-term changes in the whole species community documented at the two lodges.

The wildlife sightings are tallied everyday into the official log book at each lodge. The 'hunter' on duty records animals frequenting the watering hole from approximately 3pm-8am everyday (to coincide with the arrival, overnight stay, and departure of tourists). All visible animals that approach the waterhole and saltlick are counted. At night, visibility is restricted by the limit of the floodlights that are turned on after darkness falls, and during the day by the line of trees that delimit the edge of the clearings where the two lodges are situated. Special effort is being made to avoid double counting of animals; this is achieved by using sex, group size and morphology to identify recurrent groups and individuals. Because of the excellent visibility and the close range of observation, it is generally easy to unambiguously assign species identity. The one exception is marsh mongoose (*Atilax paludinosus*) that can be confused with melanistic individuals of the white-tailed mongoose (*Ichneumia albicauda*); in this case, species identity was determined by the time of day an individual was observed (white-tailed mongoose tend to be nocturnal) and by its behavior (marsh mongoose tend to feed in the water). Also, I combined all three resident hare species (*Lepus capensis, L. microtis* and *L. saxatilis*) into one general *Lepus* spp. category because it was not clear that observers were always able to distinguish these taxa in the field.

The methodologies for recording and organizing the wildlife sightings are nearly identical between the two lodges. Richard Prickett, a famed hunter and naturalist, was first an employee of Treetops and then joined The Ark when it opened in 1970, thus ensuring that comparable methods were used (see Figure 1 of the Appendix). I took digital photographs of each page of the logbooks (26,116 images in total) during the duration of the month of July 2011. These files were stored in external hard-discs and transported to the University of Michigan, where over 250,000 data points were gradually entered into spreadsheet format by me and five undergraduate students. To ensure that data were transferred correctly, every data enterer checked the entered species counts against the species counts shown in the original photographs for each daily entry. Additional random checks were performed both by double checking entered data and by visual inspecting long series of all data entered for spurious values.

As with most long-term datasets, there were missing data points. The most significant gap is from 1985-1996 at The Ark. Lodge managers theorized that the books were lost or thrown away due to water damage (Philip Nyagah, manager at The Ark, pers. comm.). There are further small gaps in the dataset (partial years) most likely due to lodge closures for renovations and/or repairs.

Since 1999, The Ark management has also been recording daily weather information at the lodge. AM temperature, PM temperature, and cumulative rainfall data have been recorded on a consistent basis. I collated these data to explore local patterns in climate seasonality (see Table 1 in Appendix for monthly temperature and rainfall averages).

3. Data analyses

Generalize Additive Models

In order to plot population and diversity trends in a usable way, I utilized Generalized Additive Models (GAMs) to smooth the daily time series data. GAMs are defined as flexible extensions of generalized linear models (GLMs); the linear predictor of GLMs is replaced by an additive predictor thus allowing for a more flexible trend since the change in mean abundance is not constricted to a linear curve (Fewster, Buckland, Siriwardena, Baillie, & Wilson, 2000).

Because of this flexibility, a GAM is considered a better representative of underlying data when compared with classical Gaussian distributions (Guisan, Edwards, & Hastie, 2002) and it is accepted as a method for detecting abundance change for data characterized as long-term and nonlinear (Fewster, Buckland, Siriwardena, Baillie, & Wilson, 2000). It allows the analyst to choose the level of smoothing and thus display trends that show either greater linearity or more fine fluctuations of the data. More recent literature has also shown that GAMs can effectively describe trends with up 50% of the data missing (Atkinson et al., 2006) making it an especially effective analytic method for observer-based survey data.

For these reasons, GAMs have become a widely used method in analyses of long-term population trends (Wood, 2006). Examples of GAMs used for the analysis of long-term survey data include the Breeding Bird Survey (Fewster, Buckland, Siriwardena, Baillie, & Wilson, 2000), long-term greater sage-grouse data in Wyoming (Fedy & Aldridge, 2011), and the British Butterfly Monitoring Scheme in the United Kingdom (Rothery & Roy, 2001). Using analyses similar to these studies of long-term trends in wildlife populations, I applied a GAM to smooth the raw daily observation data and diversity data. R statistical software (v. 2.15.2) was used to configure the GAMs.

Summary measures of the mammalian community

Beyond the population trends of individual species, I tried to obtain an overall understanding of changes in wildlife populations at each site as a whole by employing a variety of summary metrics: total population size, heat maps, rank-abundance graphs, species richness, species diversity and aggregate biomass.

Total population size. First, I calculated a summary population metric of all species by tallying the total of the number of individuals seen at each site on a given day. A GAM smoothed the aggregated raw data, thus allowing a better visual representation of the total wildlife population trends at both sites.

Heat maps. To further visualize species presence and abundance in a summary way, I constructed heat maps of the two mammalian communities ordered by species commonness. These heat maps display the log(Abundance) (i.e. log(1+smoothed counts)) of all mammalian species across time at each site, ranked from the globally most common (at the bottom of the graph) to the least common (at the top).

Species richness. The total number of species seen was calculated on a daily basis for each site. These raw data were smoothed using a GAM which I then used to determine any significant temporal changes at each site.

Rank-Abundance Curves. I used measures of species abundance to compare the evenness (or equitability)(E) of each species community. One of the simplest ways to compare the evenness of communities is to construct rank-abundance curves (Heip, Herman, & Soetaert, 1998), which ranks species based on their abundance relative to all the other species in the community. Rank abundance curves can be used to compare species communities spatially or temporally. To compare communities across time, I constructed "snapshot" abundance curves based on annual species data for a periodic time intervals across our study period.

Shannon-Wiener Diversity Index (SWDI) (H'). To quantify the level of diversity in this mammal community, I calculated Shannon-Wiener Diversity Index (for a more complete discussion on methodologies for evaluating diversity, see Magurran, 2004 or Kindt & Coe, 2005). The Shannon index accounts for both species richness and evenness and measures the likelihood that a randomly sampled individual belongs to a given species within a set community. The Shannon index (H') is calculated by the equation:

$$H' = - \sum p_{i\,*} \ln p_i \qquad \text{Eqn. 1}$$

where *i* is the proportion of individuals in the *i*th species (Magurran, 2004). As evident by Eqn. 1, if there is only one species in a given community, then H=0. A nonzero value indicates that the community consists of more than one species because the probability that an individual animal belongs to a certain species is less than 1. For biological communities, the diversity index often varies between 1.5-3.5 (Margalef, 1972); values further from zero indicate a more diverse community. H-values were calculated daily based both on the daily species richness and on the total daily sighting counts for each species.

Biomass. Lastly, I evaluated the performance of the whole community by calculating aggregate biomass for all species take together. Total biomass of the community at a given time was calculated my summing the products of population size and average body mass for each species.

Changes in a mammalian community

To obtain a comprehensive view of the patterns of change in the overall mammal species in the greater Salient region (and possibly the whole ACA) I also analyzed species presence/absence in the combined Ark and Treetops datasets. Over the period of the study, 40 species were recorded at Treetops and 40 species at the Ark for a grand total of 46 mammal taxa for the whole ACA.

A species was considered to be extant in the ACA on a given year if it was seen at least once in one of the two lodges in that year. Some taxa, however, were so rare, or present only in particular habitats, that they were not recorded every year despite their continuous presence. Such species were still recorded as present in the ACA in years they were not seen, as long as they were recorded at least once in a subsequent year. While it is conceivable that 'filling in' such gaps may have erroneously mask repeated extinction-colonization cycles as continued existence, this is unlikely. Because of the isolated nature of the ACA (even before the establishment of the fence, the surrounding landscape was used intensely for agriculture and urban settlements making it inhospitable for wild animals) it highly improbable that there has been recent natural colonization by wildlife originating from external populations. However, 8 species (African golden cat, bat-eared-fox, blue duiker, cheetah, gray duiker, honey badger, wild dog, and zebra mouse) were observed so rarely (less than 6 times over the 48 years of the study) that they were excluded as it was deemed that there were not enough data to justify further analyses.

I classified a taxon as having gone extinct if the species was missing from recent records for at least a period longer than any previous absence (i.e. gap in the record) and it was no longer seen in the record up to the last day of available records. For example, if species A was absent for the last 8 years it was recorded as having gone extinct if the previous absence was less than 8 years long. I classified a colonization event when a species that was absent from earlier records began being observed consistently at least one of the two lodges. Finally, core species are defined as species regularly seen throughout the period of study.

Results

1. *Changes in total wildlife population sizes*

My analysis reveals clear fluctuations, both across space and time, in the aggregate resident mammalian populations. Despite their relatively short distance between the two lodges (approx. 6km), there are striking differences between them, both in individual species populations and in the aggregate population sizes.

Overall population numbers have been relatively stable at the Ark over the study period while they have fluctuated strongly at Treetops. Until the mid-1970s, there was a rapid increase in wildlife populations at Treetops (as well as to a lesser extent at the Ark) most likely following the eradication of rinderpest in the area (Figure 3). During the first 40 years of the study, but especially early on, Treetops harbored much larger wildlife populations than The Ark. Using the sum of the raw individual species population data to compare the two sites at specific time points, I found that the average annual population at Treetops ($\bar{x}$ = 126,592.5) is significantly greater than the average annual population at The Ark ($\bar{x}$ = 39,780.8) for the baseline years of 1970-1975 (two-sampled t-test, $t=10.03$, $df=10$, $p<0.001$). Comparatively, looking at the most recent five-year span (2006-2011), I find that there is no significant difference (two-sample t-test, $t=1.59$, $df=10$, $p>0.05$) between the average annual population at Treetops ($\bar{x}$ = 34,096.5) and the average annual population of The Ark ($\bar{x}$ = 46,046.5). The total wildlife population at Treetops has decreased dramatically (by approx. 73% from the highest count in 1973) and it has now fallen below the mean population size at The Ark, which has remained relatively steady over the years. Nevertheless, comparisons of total wildlife population sizes between the two sites at a given moment in time should be interpreted with caution since the geography of each site (Treetops is more open) results in different detectability of species at each site.

Heat maps (Figure 4) provide a more detailed account of the individual time series data and give a clearer picture of how the makeup of the two communities has fluctuated across time, including the appearance or disappearance of species in each community. This species turnover is especially evident in the second half of the Treetops dataset, where there is evidence of a drastic population decline. From 1991-2011, there are seven species that show significant decreases in abundance (giant forest hog, hyena, black rhino, genet, Sykes monkey, bushbaby and colobus monkey) while during the same time period there are six species that have significant but ultimately only transient increases in abundance (baboons, eland, impala reedbuck, slender mongoose).

2. Patterns in biodiversity

Biodiversity

Species richness varied greatly between the two sites, as well as over the time period investigated. In general, the spatiotemporal patterns in species richness mirror closely the patterns observed in aggregate wildlife population numbers, with species richness at The Ark being much more stable over time relative to Treetops. The number of species seen on a given day range from $S = 3$ to $S = 16$ at The Ark and $S = 1$ to $S = 17$ at Treetops with $\bar{x} = 10.31$ at The Ark and $\bar{x} = 10.28$ at Treetops. A GAM (Figure 5) showcases the trends of daily species richness at Treetops and The Ark. For Treetops, following an initial rise through the mid-1970s, most likely caused by the eradication of the rinderpest from the region, species richness starts a long decline which appears to have accelerated in the last 10 years. Overall, species richness appears to have been much more stable at the Ark relative to Treetops.

To understand dynamics within the community, I also used rank-abundance measures. A rank-abundance curve can provide information regarding the evenness of each community as shown by Figures 6 and 7. Treetops and The Ark each have 40 species across their respective datasets. Across the first 20 ranked species, Treetops has a slightly more even species community (indicated by the more horizontal curve). The set of species ranked 20-40 (thus the rarer species) show less differentiation between the two sites, and there is more similar evenness across the communities. I also prepared annual “snapshots” of rank-abundance to investigate change in the evenness of species across our timeline (Figure 7). These curves show relatively consistent evenness in the species communities at both study sites across time with the most significant species loss occurring at The Ark after 1970.

The results of our Shannon-Wiener diversity analysis show evidence of a loss of diversity at Treetops occurring in the second half of the dataset. Using the raw data to calculate annual Shannon-Wiener diversity indices (SWDI), I find that the largest difference in diversity values between the two sites occur in back-to-back years: 2010 ($H'_{\text{Ark}} = 2.85$ and $H'_{\text{Tree}} = 2.35$) and 2011 ($H'_{\text{Ark}} = 3.00$ and $H'_{\text{Tree}} = 2.44$). Figure 8 shows the smoothed SWDI trends for each site; for the period 2001-2011, there is evidence of decreasing diversity at Treetops while diversity is increasing at The Ark. It is also important to note that the diversity index values at Treetops are considered biologically low. Most biological datasets show diversity values that range between 1.5-3.5 (Magurran, 2004) and values and the smoothed data shows diversity values at Treetops hovering around 1.5 with values dipping below 1.5 in the last five years of the dataset.

Biomass graphs (Figure 9), which display changes of aggregate biomass in each community, also reveal interesting patterns of change particularly at Treetops. Across the timeline at Treetops, there is a steady decrease in total biomass and a near disappearance of the biomass of most species excluding elephants and buffaloes. At the same time there is an increase in the proportional biomass of elephants. The Ark also shows an increase in the proportional biomass of elephants, although there is less of an overall loss in the biomass of other species.

Community Changes

As shown by Figure 10 and the accompanying Table 1, the mammalian community of the Salient region (and potentially the whole of the ACA) experienced significant shifts in its composition over the duration of this study. With the exception of 8 taxa (see Methods) that were observed so rarely (defined as seen <6 times across both lodges across the 80 cumulative years of data) that they could not considered to have a stable presence in the region, there was a regularly recorded community of 46 species. Of these species, 33 constituted the core group of species (seen consistently across the entire study period). Additionally, over the course of the study 5 species were added to the community while 8 species went extinct.

Discussion

The objective of this study was to investigate potential community-level changes in population and diversity as a way of providing ecological guidance regarding past and upcoming wildlife management. Previous research utilizing long-term datasets has been primarily focused on single species analysis. Given the breadth of the Aberdare datasets, I was able to expand on methodologies commonly seen in long-term data analysis to investigate broader patterns of biodiversity change. Measures of diversity are gaining importance as tools for assessing the status and productivity of ecosystems (Cardinale, B., Srivastava, D., Duffy, J., Wright, J., Downing, A., Sankaran, M., & Jouseau, C., 2006; Loreau, 2010), especially in habitats facing rapid environmental change. The Aberdare datasets provide a rare opportunity to investigate long-term population and diversity change in a protected area with a complex history of resource extraction and conservation.

The composition of the mammalian community in the ACA changed due to the appearance and the disappearance of several species. Of the 5 species joining the community, one, the coypu (*Myocaster coypus*), is considered an invasive species that likely became established by itself in the Aberdares early on. The coypu was introduced to Kenya (the species is native to South America) as part of the fur trade in the 1950s. Feral populations were soon established and the Kenya government unsuccessfully attempted to eradicate the species (Venter, 2011). The species is known for converting vegetated wetlands into open water by destroying aquatic plants and thus degrading freshwater habitats for native species (Venter, 2011). Three other species that appeared in the Aberdares community are large-bodied antelopes: eland (*Taurotragus oryx*), impala (*Aepyceros melampus*), and reedbuck (*Redunca fulvorufula*). They were likely intentionally introduced given that at the time of their appearance, the fence was already in place, precluding a natural colonization event. These charismatic species have historically been an important part of Kenya's tourism industry, as they are popular both for wildlife viewing as well as for hunting (Steinhart, 1989).

Of the species that went extinct, most were probably rare and or had otherwise small populations, and therefore a tenuous existence within the protected area. For example, both aardvark (*Orycteropus afer*) and jackal (*Canis adustus*), even though not intrinsically rare, occur mostly in grassland areas, which are found only marginally within the limits of the ACA. Other species are either meso- (zorilla, jackal, civet) or apex predators (lion) and thus by virtue of their trophic position particularly susceptible to extirpation. Interspecific interactions coupled with anthropogenic changes were most likely responsible for additional extinctions: the disappearance of two other taxa, the bushpig (*Potamochoerus larvatus*) and the bongo (*Tragelaphus eurycerus isaaci*), coincided with increases in the resident lion population, as well as habitat destruction and increases in human activity at the margins of the protected area (Lambrechts, Woodley, Church, & Gachanja, 2003). When considering extinctions and colonizations together, it is clear that while there have been some additions of new species, there have been more extinctions. In addition, while additions of new species have been tapering off due to the isolation from the fence, extinctions have continued. This follows a typical pattern of community relaxation following habitat isolation as has been observed in other systems (Foufopoulos, Kilpatrick, & Ives 2011; Newmark 1987; Brashares & Sam, 2005; Brashares et al., 2004).

Our results also show evidence of spatial and temporal change in the two mammalian communities in the Salient region. Across the timeline, there are parallel decreases in the total population and diversity of the mammalian community at Treetops with the most significant declines occurring in the second half of the dataset (after the mid-1990s). Interestingly, I did not observe similar decreases at The Ark in the second half of the dataset and in many cases I observed there increasing trends in population and diversity. These conflicting trends were observed across the board in measures of total population, species richness, and species abundance (as shown by the results of the SWDI analysis). The results from our heatmaps and biomass graphs provide further evidence of the diverging results between the two study sites for the second half of the dataset timeline. Additionally, I recorded an overall decrease in biomass at Treetops, with a near disappearance of biomass representing all other species besides elephants and buffaloes resulting in a moderate increase in the proportional biomass of elephants.

What is the reason for these broad decreases, evident in several types of metrics at Treetops over the last twenty years? One possible explanation is the close proximity (<1km) of the lodge to the edge of the ACA. Considering that Treetops has been subject to more disturbances, it is likely that these changes are due to local habitat experiencing more edge effects. A recent aerial report by Lambrechts, Woodley, Church, & Gachanja details the causes and extent of anthropogenic destruction mostly at the edges of the ACA. At the time of the report**,** habitat destruction due to illegal activities, particularly charcoal production and illegal logging, was continuing unabated. With increasing human population and intensifying land use at the edges of the park, there is more incentive to exploit the relatively untouched forests and vegetation inside the park (Lambrechts, Woodley, Church, & Gachanja, 2003). Additionally, poaching, particularly for rhino horns, remains a constant threat. Consequently, we might be seeing the increases in population and diversity at The Ark because it is acting as a "biodiversity beneficiary" as individuals move away from the edge (Treetops).

Beyond vegetation destruction due to human activities, there is some evidence to suggest that changes in elephant populations may play a role in transforming the vegetation in environments similar to the ACA. Large herbivores such as the elephant have the potential to transform the vegetation of an ecosystem and the Aberdare forests are a prime example of a high density population of elephants that have transformed much of the climax forests into secondary forests (Laws, 1970) (see Figure 11). Laws's seminal paper on elephant behavior in increasingly human-mediated environments showed the potential destruction resulting from elephant feeding behavior as shrinking habitat space results in increased mean group size**.** The unspecialized nature of the bush elephant can have devastating effects on the habitat for specialized species; as there are less ideal habitats to support such large mammals as the elephant, the largely forested habitats can become transformed and thus have ripple effects on other forest-dependent taxa (Laws, 1970).

Many of the changes evident in the data series are the result of individual species management plans. Some of these efforts have been concentrated on the protection of the critically endangered mountain bongo, the flagship species of the Aberdare range and a bioindicator of healthy mountain forests (Mwangi, 2010). The Rare Species Conservatory Foundation introduced 18 mountain bongos from captive facilities in the U.S. to the Mt. Kenya forest ranges as a way to revitalize the critically endangered wild populations (Rare Species Conservatory Foundation, 2002). In addition, lions were eradicated from the Aberdares in the late 1990's and early 2000's in an effort to protect bongos from predation, as bongo populations plunged when lion populations increased earlier (Charles Mathenge, pers. comm.). This course of action was not publicized but was common knowledge among managers and hunters at the two wildlife lodges and is reflected in the sighting datasets (see Appendix). Even with these measures, bongos have not reappeared in our sighting datasets since the mid 1980s and it is not clear whether the species still exists as a viable population in the ACA.

Aside from the struggle to revitalize and protect future bongo populations, the actions taken to reduce predation on these valuable species may have unforeseen effects on the species communities. Along with hyenas, lions were considered a primary predator of the Aberdare range (Sillero-Zubiri & Gottelli, 1987) and the loss of a keystone predator can have ripple effects across an entire ecosystem. It can cause trophic cascades and result in surges in the populations of grazing species which in turn can alter the vegetative landscape, as shown by the classic wolf-elk-aspen studies in Yellowstone National Park (see Fortin, D., Beyer, H., Boyce, M., Smith, D., Duchesne, T., & Mao, J, 2005 or Ripple, Larsen, Renkin, & Smith, 2001). The loss of lions from the Aberdare range coupled with the isolation of wildlife due to the fence may have drastic effects on the populations and behavior of other species in the short- and long-term, particularly with concerns related to the density of grazing and browsing species that already make up the highest proportion of the mammalian biomass in this ecosystem (Figure 9).

While further investigations are clearly needed, our results implicate the existence of edge effects in the differences between Treetops and The Ark across the study period. There is evidence of population decline and community turnover, particularly at the edges of the protected area (Treetops) as well as evidence of extinction and colonization events. Continued wildlife monitoring and population analyses can aid in providing evidence and justification for ongoing management. And as previously stated, the fence has major, positive implications for more than just wildlife.

Conservation Implications

Fencing: a solution for wildlife conservation?

There is broad consensus that the remaining forested areas of the Eastern Arc and Coastal Forests of Tanzania and Kenya, including the Aberdare Range ecosystem, are critically endangered and constitute a global conservation priority (Myers, Mittermeier, Fonseca, & Kent, 2000). Most of these areas are now protected, and while this protection is a great achievement for conservation, it is unclear how to best manage these ecosystems for long-term habitat and wildlife conservation. In particular, fencing protected lands is becoming one of the most popular methods for long-term management of human-wildlife conflict and habitat protection especially in Africa. In a meta-analysis looking at the fate of lion populations in fenced and unfenced lands, authors concluded that fencing was critical to help conserve lion populations and that half the lion populations in unfenced lands face extinction in the next 20-40 years (Parker et al., 2013). Similarly, experts concluded the most effective way to protect the Aberdare ecosystem and its wildlife was a physical barrier isolating the wildlife and forests from the dangers of the surrounding habitat matrix (Butynski, 1999; FAO, 1998).

Perhaps the simplest way to evaluate the role of the Aberdare fence in protecting wildlife is to briefly discuss the case of the black rhino. Protecting black rhinos and rebuilding their population in the Aberdares was arguably the most important mission of the fence. Rhinos have long been the focus of conservation efforts to protect wildlife from poaching. Their well-documented population crash in the 1970's (visible in the black rhino population graph in the Appendix) is largely attributed to poaching and there is now a concern that the remaining populations are not genetically viable (Sillero-Zubiri & Gottelli, 1991). In the twenty years since the first phase of the fence was completed around the Salient, the black rhino population has not rebounded but has remained low and stable with animals in the single digits recorded at both sites (see Appendix for the black rhino population graph). While the lack of population increases for black rhinos seems dispiriting, it points to the importance of continued conservation efforts beyond the construction of the fence. The fence is a major step in protecting wildlife and reducing human-wildlife conflict, but the complex constellation of issues surrounding the conservation of this ecosystem is not solved by the construction of a fence alone.

Considering issues such as poaching and illegal forest exploitation that have consistently plagued this environment (see Figure 2), there is clear that there is a need for better enforcement and management beyond the fence. It is clear from our results that the establishment of the fence in the early 1990s halted the previous declines in wildlife numbers and even led to a temporary increase in wildlife populations. However starting in the late 1990s, wildlife declines have resumed and wildlife population numbers, species richness, and other metrics of diversity at Treetops (but not at The Ark) are at their lowest value since measurements started. These data suggest that wildlife poaching and/or vegetation degradation continue along the edge of the

Salient. Unless these issues are managed, wildlife numbers at Treetops will continue to decline to the point where the lodge will lose its attractiveness to tourists and its ability to generate revenue.

While the fence has been critical in protecting wildlife populations along the edge, by itself it is currently an insufficient conservation tool and stricter management is needed to prevent further declines. Such management needs include not only stricter enforcement but also more outreach and education for communities living outside the ACA. In addition, by providing shared revenue of tourism dollars to the communities residing at the margins of the ACA, it could be possible create financial incentives to protect the habitats at the edges of the protected area.

While many of the habitat management initiatives have been molded around goals to protect rare and valued wildlife, this ecosystem provides vital ecosystems services that benefit from ambitious habitat protection. The scope of this paper made it inappropriate to give a detailed discussion of the value of the forest and water resources of the Aberdare mountain range, however, given our conclusions about the potential impacts of the electric fence, it is important to reiterate that the value of the fence extends beyond just wildlife conservation. In line with its objectives, the fence has helped protect indigenous vegetation through reduced forest exploitation (including logging, charcoal kilns, livestock grazing, etc.) (Lambrechts, Woodley, Church, & Gachanja, 2003), as well as vegetation recovery at the edges of the protected area, as shown by secondary vegetation growth at Treetops (Rhino Ark, 2011).

The Aberdares has a history of aggressive wildlife conservation and protection efforts and the fence is perhaps the greatest example of these efforts. Combined with further scientific assessment and continued wildlife management, the analyses carried out on the Aberdares datasets can be used as a model for other protected areas. It is also an example of the importance of taking a broad approach to managing a conservation area. The fence, while immensely important for the protection of the area, is not sufficient to protect the ACA. It should not be considered the final solution but rather part of a broader approach that needs to include increased enforcement, expanded community outreach, and continued monitoring.

Figures

Figure 1: Map of the greater Aberdare Conservation Area (ACA) and the surrounding fence. Each phase of fence construction is indicated with a different color and the year of completion. The area designated as Aberdare National Park is outlined in light purple. The first phase of the fence enclosed the Salient region, where Treetops and The Ark are located. The stippled line between Phase 3 and Phase 8 denotes a line of cliffs where no fence was built.

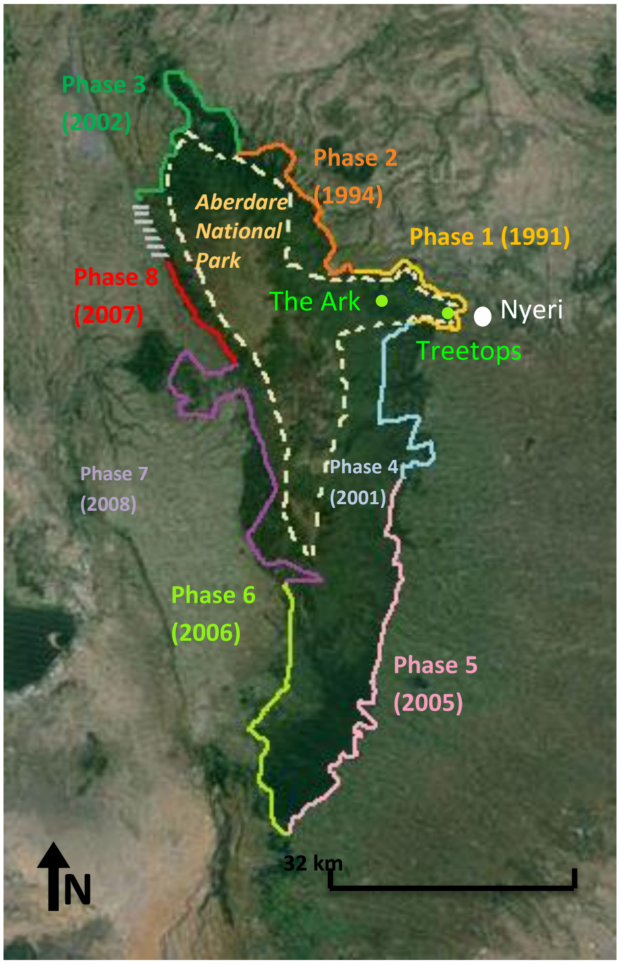


Figure 2: Aerial image of the edge of the ACA (here the far east end of the Salient). The electric fence in the middle separates the protected area (L) from the agricultural matrix (R). Note the absence of mature trees within the protected area caused by illegal logging near the border of the ACA. Treetops lodge is located at a comparable distance from the edge of the park less than 3km to the North of this image (Left).

Figure 3: Change in total animal populations across time. The number of individuals was totaled daily for each site after which a GAM was used to smooth the raw data. The trends are bounded by 95% confidence limits (estimated by +/- 2SE confidence intervals) shown by the shaded regions surrounding the trendline.

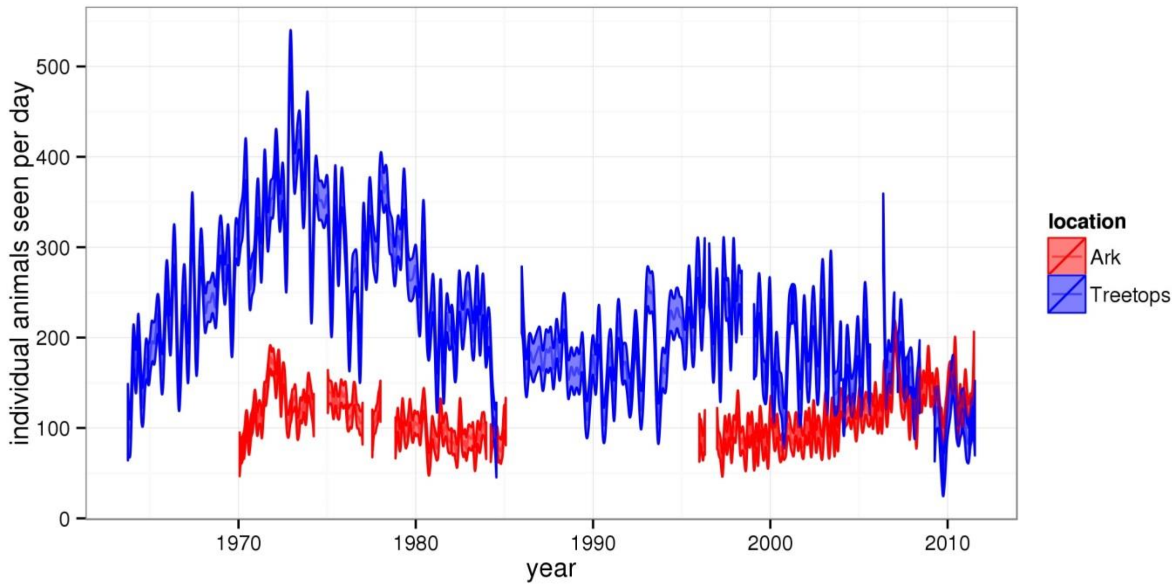


Figure 4: Heat maps of species abundances at The Ark (top panel) and Treetops (bottom panel). Species are organized by global abundance with the most abundant species at the bottom of each panel and the least abundant species at the top of each panel. The log(1+smoothed count) was used to quantify the abundance of each species and assign color. Bright red coloration indicates high abundance; lesser abundance is indicated by cooler (blue) colors. Gaps in the datasets are shown by the gray bars, with the width of the bars corresponding to the duration of the data gaps.

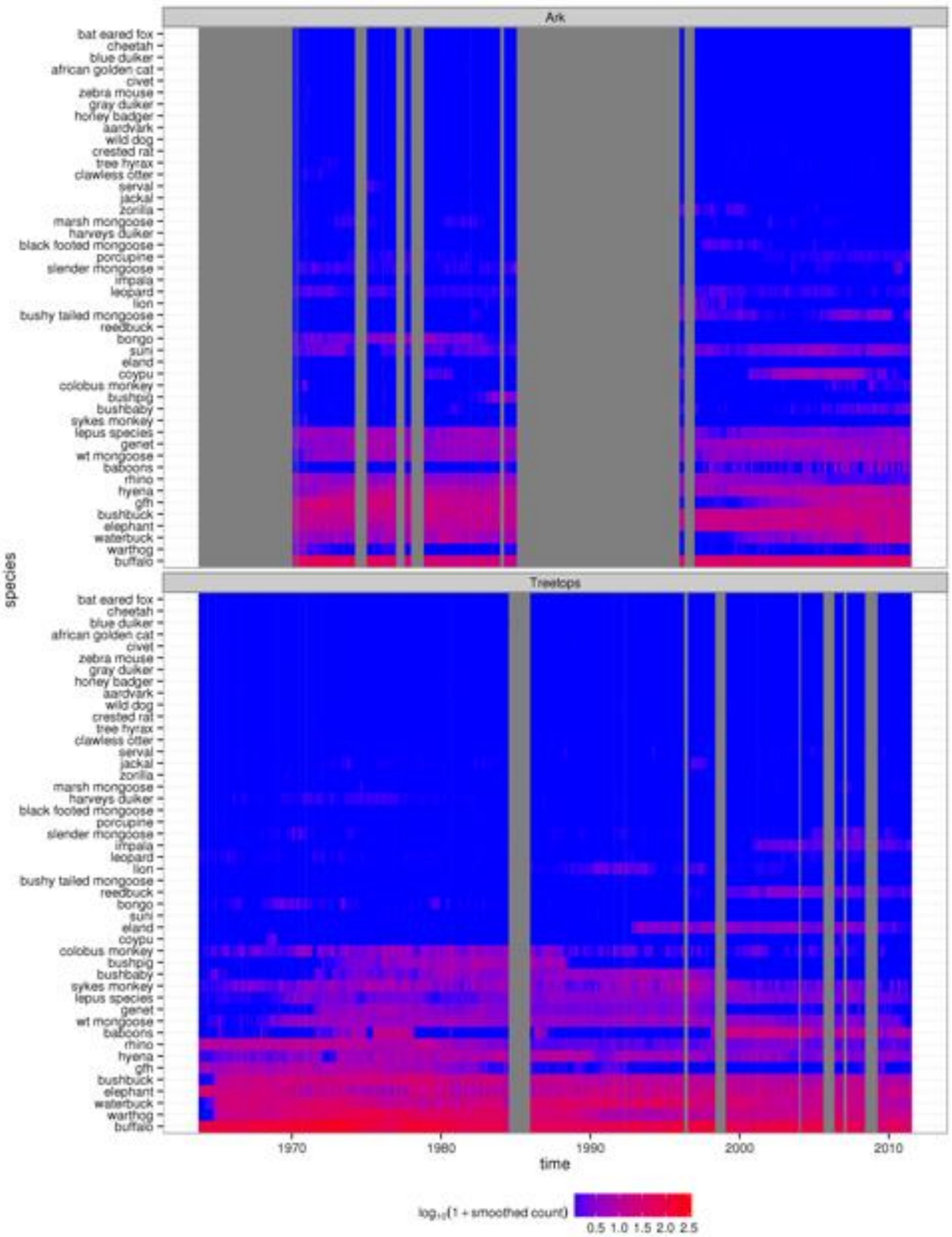


Figure 5: Change in species richness values across time. The number of species was totaled daily, after which a GAM was used to smooth the data and produce mean species richness numbers. The trends are bounded by 95% confidence limits (estimated by +/- 2SE confidence intervals) shown by the shaded regions surrounding the trendline.

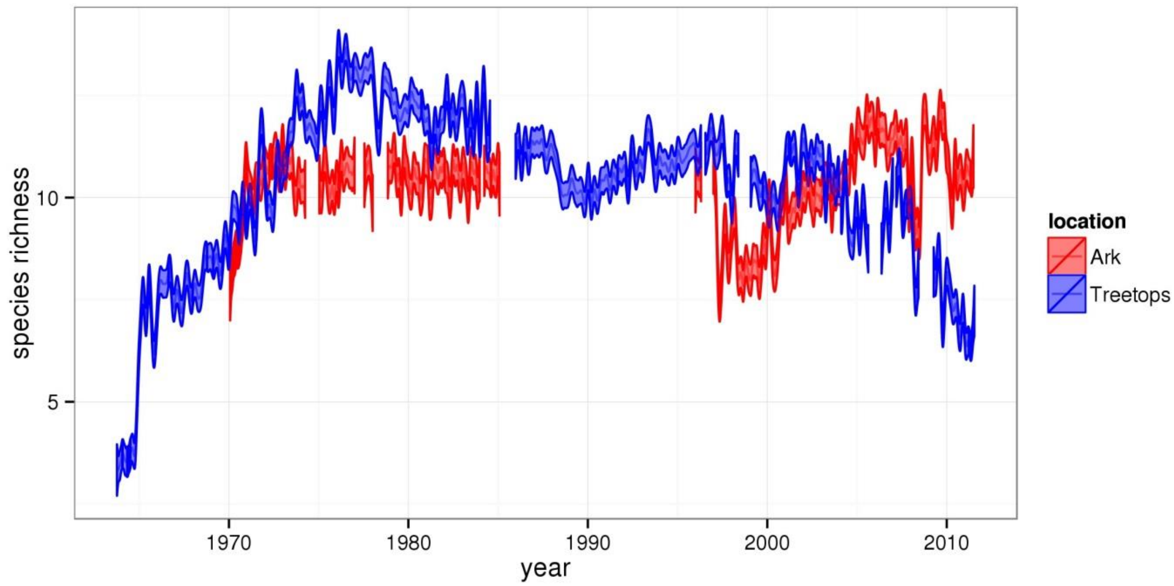


Figure 6: Species abundance curves for the mammalian communities at The Ark (red line) and Treetops (blue line) for the total individuals seen across the entire study period. Each point (indicated by circles for The Ark and triangles for Treetops) represents a species. Species richness is the same for both sites (S = 40). Both curves show similar steepness suggesting that the two sites have similar equitability of individuals among species.

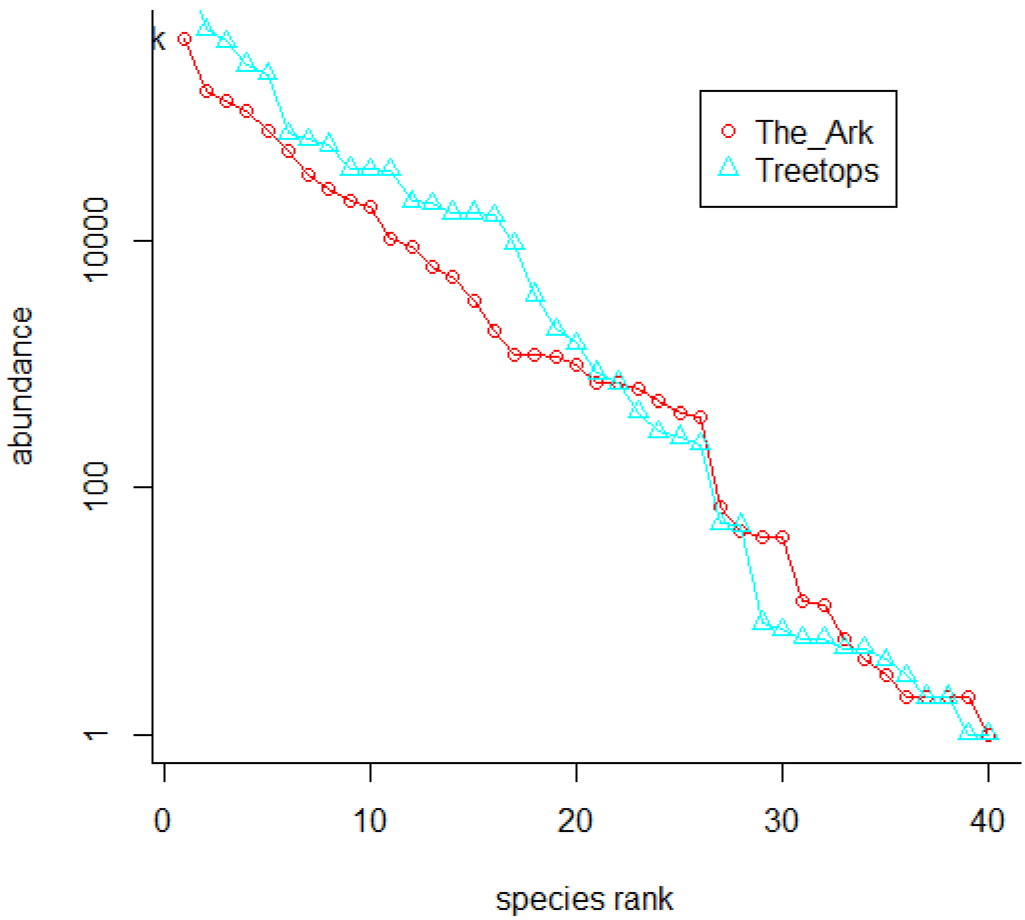


Figure 7: Species abundance rank curves calculated at intermittend intervals to obtain periodic "snapshots" of community evenness across the timeline of the study. The rank abundance curves for The Ark are shown on the left while the rank abundance curves for Treetops are shown in the right panel.

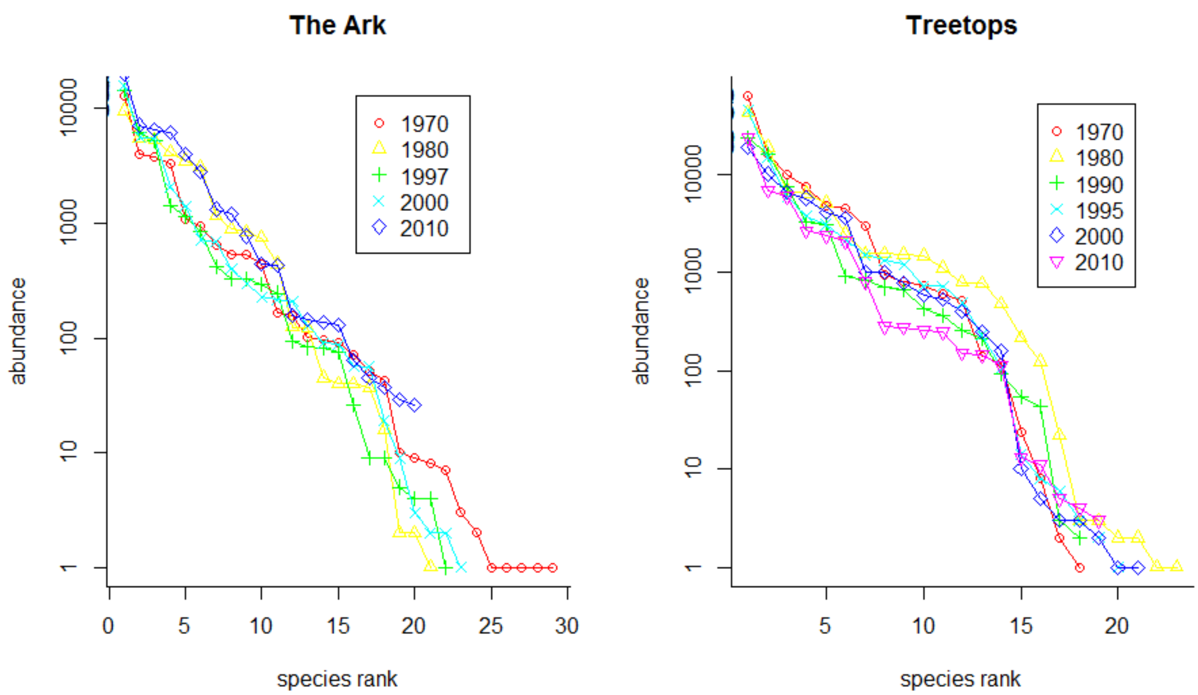


Figure 8: Change in Shannon-Wiener diversity indices (SWDI) across time. SWDI were calculated on a daily basis; after that a GAM was used to smooth these index values and produce the trends shown above. The trends are bounded by 95% confidence limits (estimated by +/- 2SE confidence intervals) shown by the shaded regions surrounding the trendline. A value of zero indicates no entropy across a community (thus a community comprising of one species). As values move further away from zero, the probability that an individual is from any one species decreases and the community is considered more diverse.

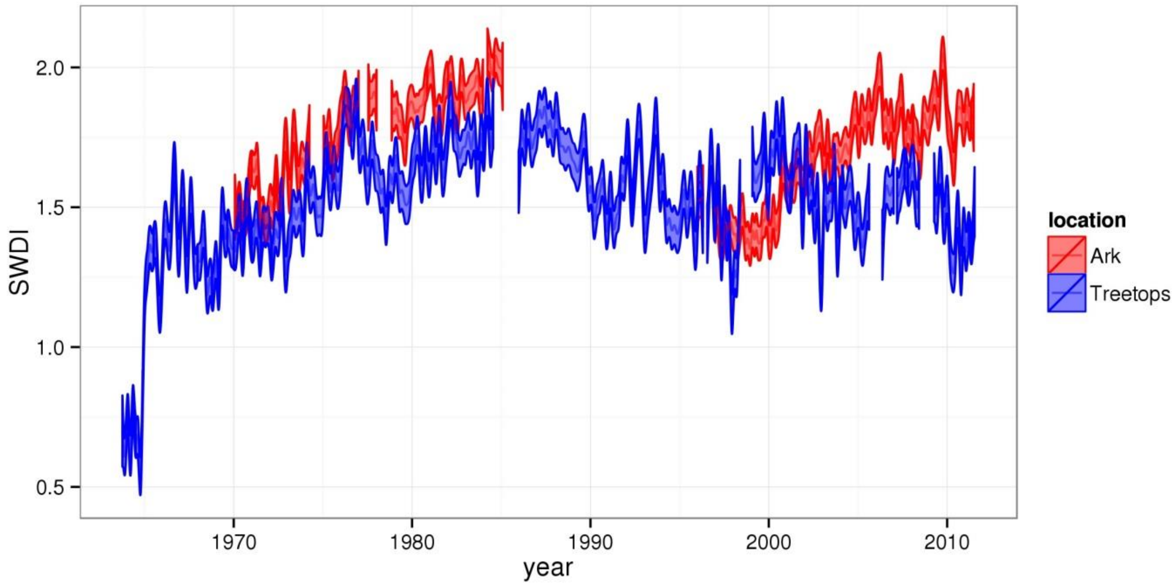


Figure 9: Change in biomass of the two species communities across time. Total biomass is proportionally dominated by elephants at The Ark and buffalo at Treetops.

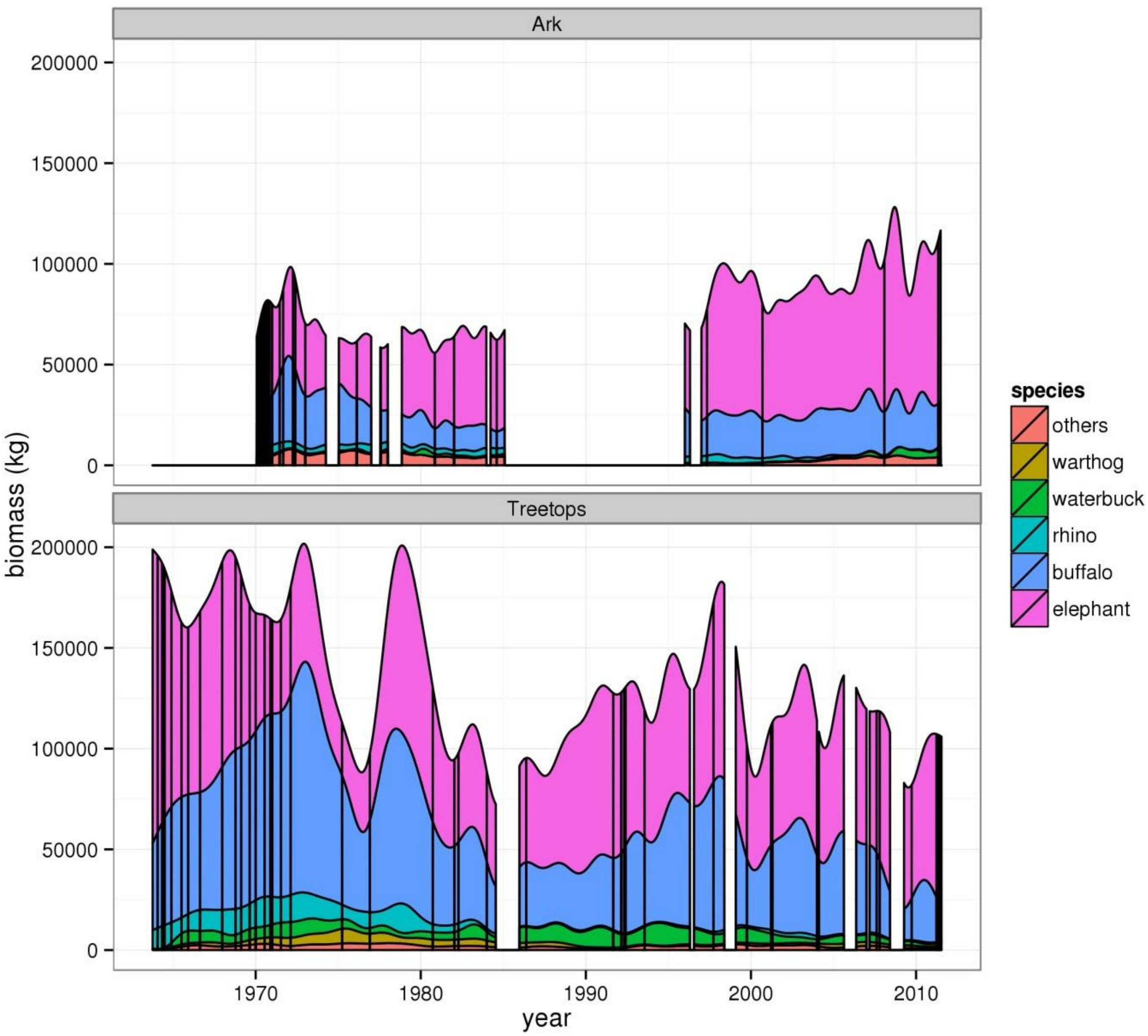


Figure 10: Summary of changes in community composition at the ACA across the study period. Core species are defined as a taxa whose presence is based upon reliable data and which have been recorded consistently over the duration of this study. Species have been classified as extinct if they were once consistently recorded and are now no longer observed in the data record. The timing of the extinction event is set arbitrarily as one year after last definitive record of a species. A colonization is defined as a species that started being recorded at some point after the beginning of this study. Excluded from this graph are 8 transient species that do not have a permanent presence in this ecosystem. See also Table 1 in the Appendix for the complete species list.

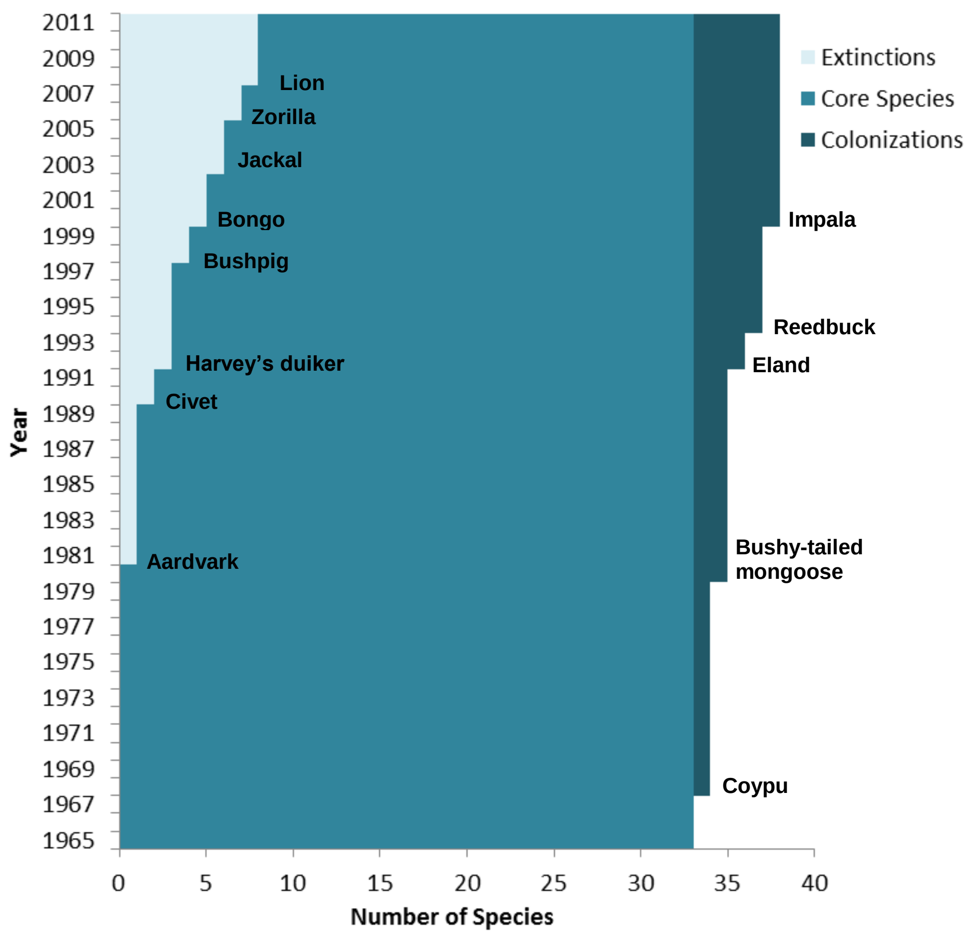
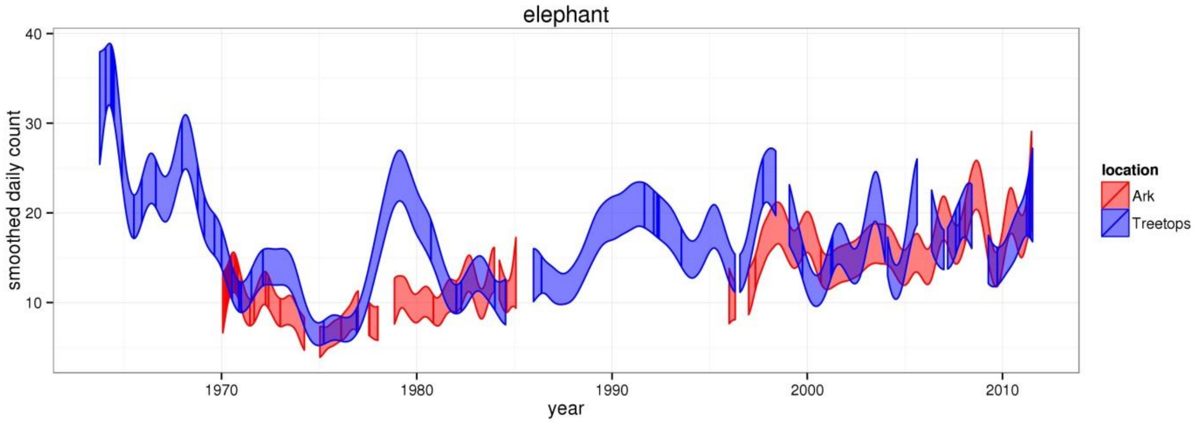


Table 1: Regular species that are seen consistently throughout the data records. Eight species extinctions have occurred in the ACA, in addition to five colonization events.

Core Species	Extinctions	Colonizations	Mass (kg)	Seen at The Ark?	Seen at Treetops?
Baboons (*Papio anibus*)			25	X	X
Black-footed Mongoose (*Bdeogale nigripes*)			2	X	
Buffalo (*Syncerus caffer*)			500	X	X
Bushbaby (*Galago senegalensis*)			0.5	X	X
Bushbuck (*Tragelaphus scriptus*)			50	X	X
Clawless Otter (*Aonyx capensis*)			19	X	X
Colobus Monkey (*Colobus angolensis*)			18	X	X
Crested Rat (*Lophiomys imhausi*)			1	X	X
Elephant (*Loxodonta africana*)			4000	X	X
Genet (*Genetta genetta*)			2	X	X
Giant Forest Hog [gfh] (*Hylochoerus meinertzhageni*)			200	X	X
Hyena (*Crocuta crocuta*)			63	X	X
Leopard (*Panthera pardus*)			55	X	X
Lepus spp.			2.5	X	X
Marsh Mongoose (*Atilax paludinosus*)			3.2	X	X
Porcupine (*Hystrix africaeaustralis*)			24	X	X
Black Rhino (*Diceros bicornis*)			1180	X	X
Serval (*Leptailurus serval*)			12	X	X
Slender Mongoose (*Herpestes sanguineus*)			1	X	X
Suni (*Nesotragus moschatus*)			7	X	X
Sykes Monkey (*Cercopithecus mitis*)			5	X	X
Tree Hyrax (*Dendrohyrax arboreus*)			2.5	X	
Warthog (*Phacochoerus africanus*)			70	X	X
Waterbuck (*Kobus ellipsiprymnus*)			210	X	X
White-tailed Mongoose (*Ichneumia albicauda*)			3.5	X	X
Aardvark (*Orycteropus afer*)	X		61	X	X
Bushpig (*Potamochoerus larvatus*)	X		70	X	X
Bongo (*Tragelaphus eurycerus*)	X		270	X	X
Civet (*Civettictis civetta*)	X		12	X	X
Harvey's Duiker (*Cephalophus*	X		14.5	X	X

harveyi)					
Jackal (*Canus adustus*)	X		11		X
Lion (*Panthera leo*)	X		160	X	X
Zorilla (*Ictonyx striatus*)	X		0.5	X	X
Bushy-tailed Mongoose (*Bdeogale crassicauda*)		X	1.5	X	
Coypu (*Myocastor coypus*)		X	7.5	X	X
Eland (*Tragelaphus oryx*)		X	570		X
Impala (*Aepyceros melampus*)		X	54		X
Reedbuck (*Redunca fulvorufula*)		X	30		X

Figure 11: Generalized additive model of total number of elephants seen daily across time. GAMs were configured based on data organized by 52 knots (approx. a knot for every year of data) across the time range of the datasets. The trends are bounded by 95% confidence limits (estimated by +/- 2SE confidence intervals) shown by the shaded regions surrounding the trendline.



APPENDIX

Figures

Figure 1: Example of a typical daily entry of wildlife sightings at Treetops (L.) and The Ark (R.) wildlife lodges. Each set of logbooks is organized in the same fashion: a species name is listed in the left most column followed by counts that are totaled at the end of the night in the right most column. Each daily entry is signed by the hunter on duty.

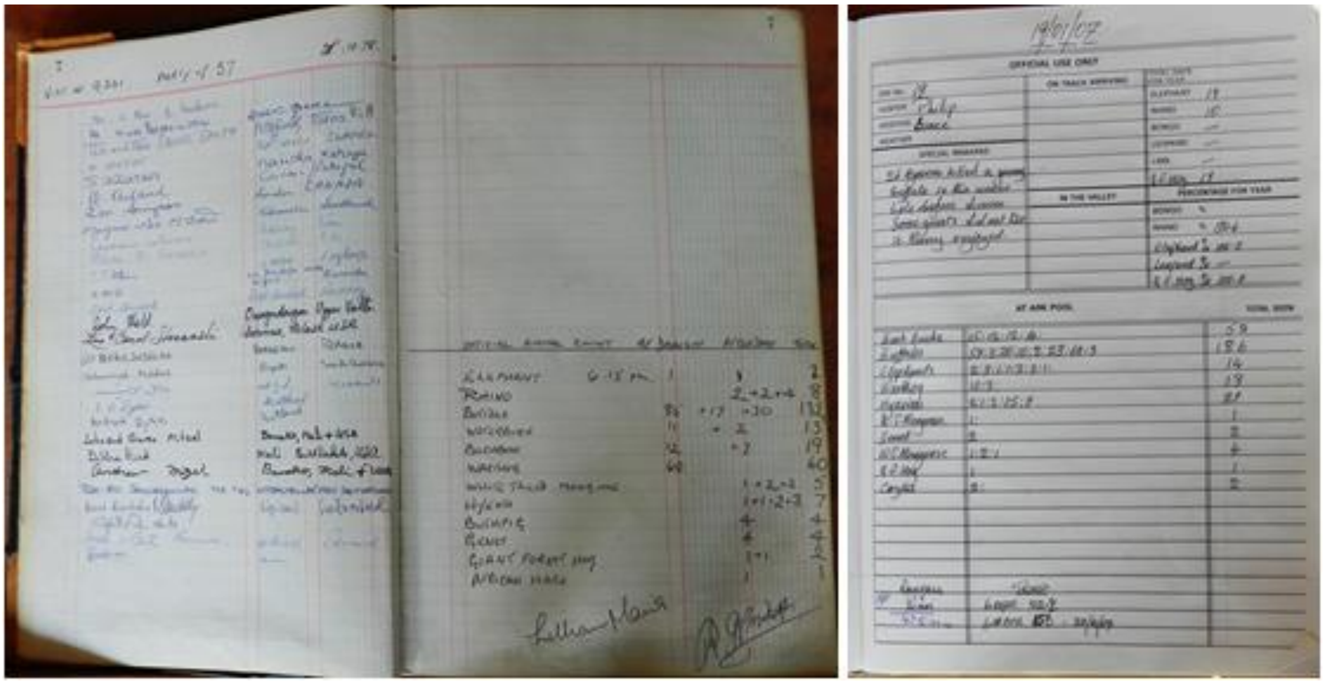


Table 1: Climate data (1999-2011) for The Ark study site. Monthly averages are shown for precipitation, AM temperature, and PM temperature. (Continued)

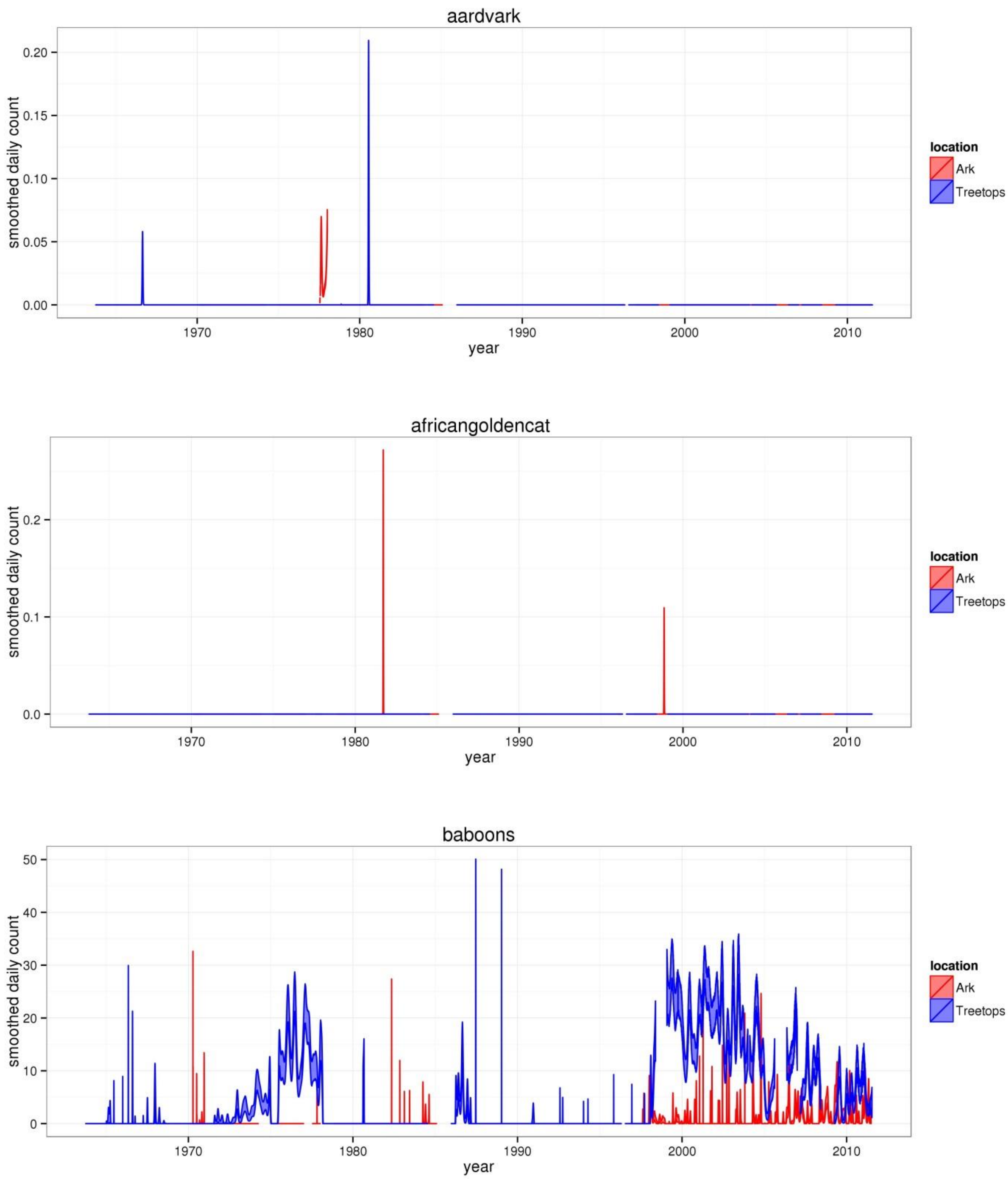
Year	Month	Average monthly precipitation (mm)	Average monthly AM temperature (°C)	Average monthly PM temperature (°C)
1999	January	50.6		
	February	18.2		
	March	79.9		
	April	50.2		
	May	78.7		
	June	8.0		
	July	18.6		
	August	56.5		
	September	48.5		
	October	22.9		
	November	84.4	13.857	17.714
	December	24.7	13.571	18.42857143
2000	January	5.2	13.500	21.000
	February	50.3		
	March	143.1	14.500	22.667
	April	78.0	15.000	21.500
	May	56.0	14.231	20.615
	June	13.6	13.556	20.111
	July	9.6	13.280	20.120
	August	26.1	13.032	19.194
	September	8.5	11.931	18.931
	October	44.4	11.000	19.567
	November	89.0	14.536	19.862
	December	99.4	14.517	20.355
2001	January	102.2	13.935	20.387
	February	47.4	13.643	21.964
	March	44.5	14.172	20.548
	April	193.6	14.107	18.933
	May	26.2	12.967	18.233
	June	15.2	11.300	16.900
	July	42.6	11.581	15.258
	August	19.7	12.161	16.323
	September	37.3	14.167	18.733
	October	44.2	14.310	19.300
	November	136.6	14.964	17.733
	December	120.2	17.724	20.516

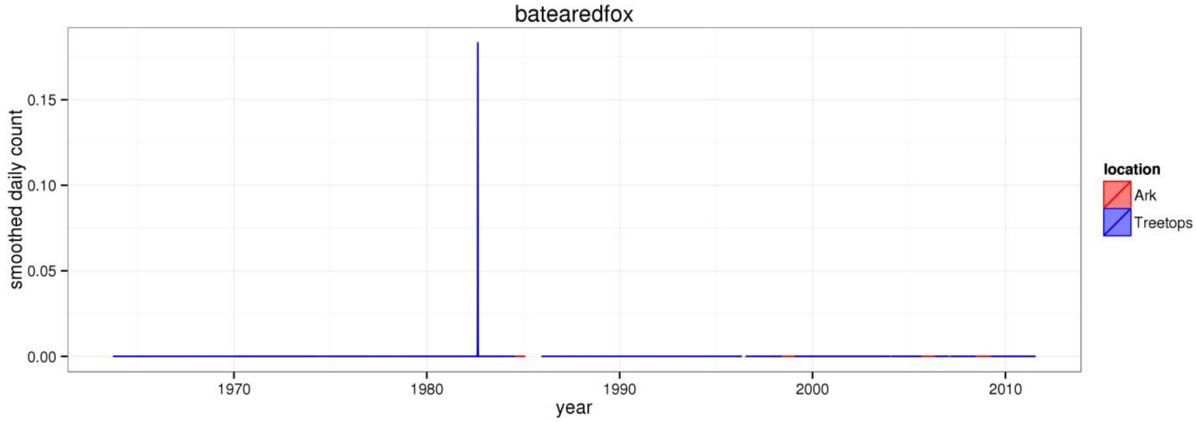
2002	January	42.6	17.767	21.516
	February	24.5	17.963	22.607
	March	79.5	17.806	21.226
	April	191.3	16.067	19.367
	May	75.1	14.586	18.167
	June	27.1	12.448	16.567
	July	25.4	12.276	16.200
	August	11.6	11.367	14.677
	September	38.5	13.071	17.633
	October	79.5	14.345	18.516
	November	205.3	16.067	18.933
	December	156.1	17.774	20.451
2003	January	43.8	21.548	21.968
	February	22.7	18.185	23.571
	March	84.4	16.968	22.258
	April	175.2	16.000	20.000
	May	171.7	14.903	18.258
	June	14.2	13.167	16.633
	July	7.1	11.967	15.613
	August	90.1	12.484	14.871
	September	10.6	12.929	17.300
	October	174.5	14.250	18.323
	November	105.8	14.367	18.467
	December	27.9	14.645	19.839
2004	January	43.5	15.613	20.194
	February	56.9	16.481	20.241
	March	52.5	15.267	20.613
	April	248.8	15.000	18.700
	May	54.4	14.700	18.645
	June	8.0	12.033	16.067
	July	55.7	10.964	16.226
	August	23.4	11.871	15.419
	September	44.0	13.621	18.867
	October	54.1	14.310	17.567
	November	171.5	13.276	18.000
	December	134.4	15.065	19.774
2005	January	19.7	15.600	20.742
	February	48.1	16.074	21.857
	March	111.4	16.533	21.065
	April	94.0	15.321	19.667
	May	202.8	14.767	18.130
	June	19.7	13.607	16.167
	July	59.8	11.800	14.323

	August	29.5	12.516	15.129
	September	58.8	12.138	15.767
	October	44.7	12.846	17.871
	November	111.5	13.483	18.300
	December	4.2	14.774	19.871
2006	January	49.2	14.600	20.290
	February	29.2	15.577	21.464
	March	137.9	15.935	20.387
	April	220.8	15.167	18.900
	May	114.8	14.950	17.839
	June	34.7	13.000	17.172
	July	70.5	10.419	14.258
	August	46.9	11.548	15.452
	September	54.6	12.667	16.893
	October	105.3	13.828	18.071
	November	488.5	14.828	18.069
	December	225.1	14.733	19.484
2007	January	75.2	15.387	20.655
	February	98.2	16.143	20.852
	March	43.4	15.679	20.462
	April	117.1	15.379	18.950
	May	130.7	14.000	17.452
	June	45.2	12.571	16.267
	July	81.9	11.733	14.821
	August	77.5	12.516	14.500
	September	74.9	12.310	17.500
	October	99.1	13.871	18.645
	November	200.7	14.483	20.059
	December	33.6	15.233	20.448
2008	January	52.8	14.367	20.520
	February	54.3	15.034	20.345
	March	126.6	15.129	20.000
	April	109.2	14.185	19.433
	May	97.1	13.452	18.871
	June	11.9	12.000	15.769
	July	59.8	10.905	14.053
	August	29.9	11.419	15.774
	September	61.4	13.448	19.267
	October	127.8	14.065	18.581
	November	148.2	14.600	19.767
	December	38.1	15.333	21.200
2009	January	107.3	15.097	21.355
	February	54.6	15.107	21.643

	March	41.0	15.500	21.806
	April	42.8	15.133	20.433
	May	78.7	14.931	19.742
	June	22.4	13.310	18.655
	July	14.3	11.226	17.129
	August	13.5	11.667	16.387
	September	16.9	13.333	18.933
	October	208.9	13.933	18.065
	November	114.3	14.667	19.667
	December	144.2	15.677	19.452
2010	January	86.0	15.290	20.968
	February	160.6	16.250	21.429
	March	193.4	15.645	20.355
	April	199.0	15.233	19.633
	May	240.9	14.548	18.742
	June	34.7	13.897	16.333
	July	42.2	11.935	14.774
	August	50.8	11.806	15.000
	September	53.1	12.867	17.267
	October	135.6	14.613	18.742
	November	191.6	14.733	18.267
	December	24.6	14.871	19.733
2011	January	45.9	15.125	20.875
	February	41.7	15.148	21.893
	March	106.5	15.742	21.258
	April	58.4	15.467	20.000
	May	112.6	14.367	17.800
	June	74.4	13.750	17.857

Figure 2: Abundance of mammal species across time based on daily observation data at each lodge. GAMs were used to smooth the data and were configured based on data organized by 307 knots (approx. a knot for every month of data) across the period of the datasets. The trends are bounded by 95% confidence limits (estimated by +/- 2SE confidence intervals) shown by the shaded regions. Data for all three hare species are aggregated under Lepus spp. Giant forest hog abbreviated as gfh. (Continued)

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location
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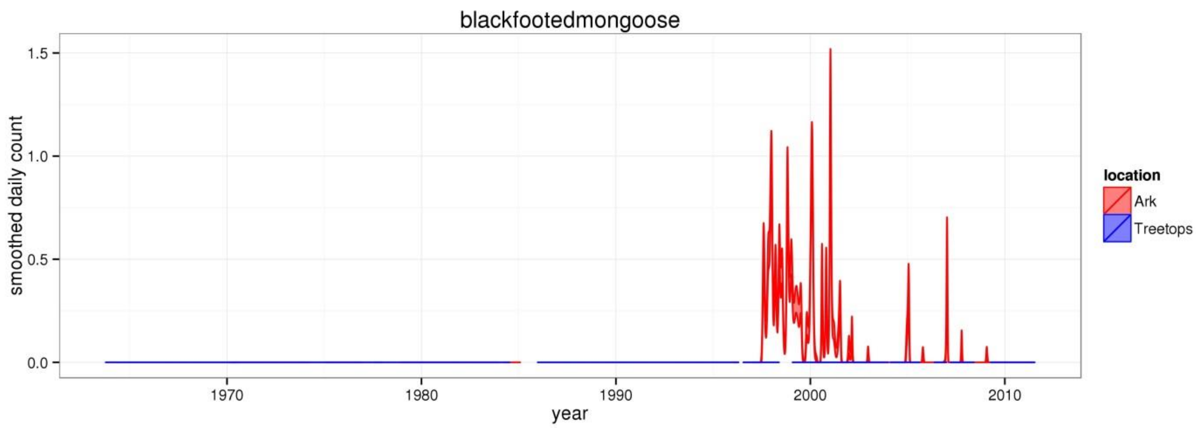
Treetops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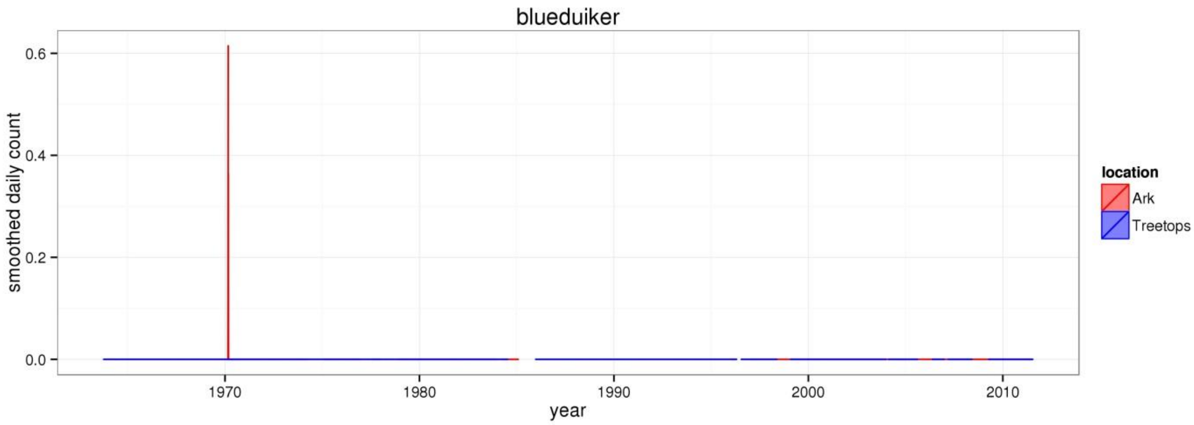
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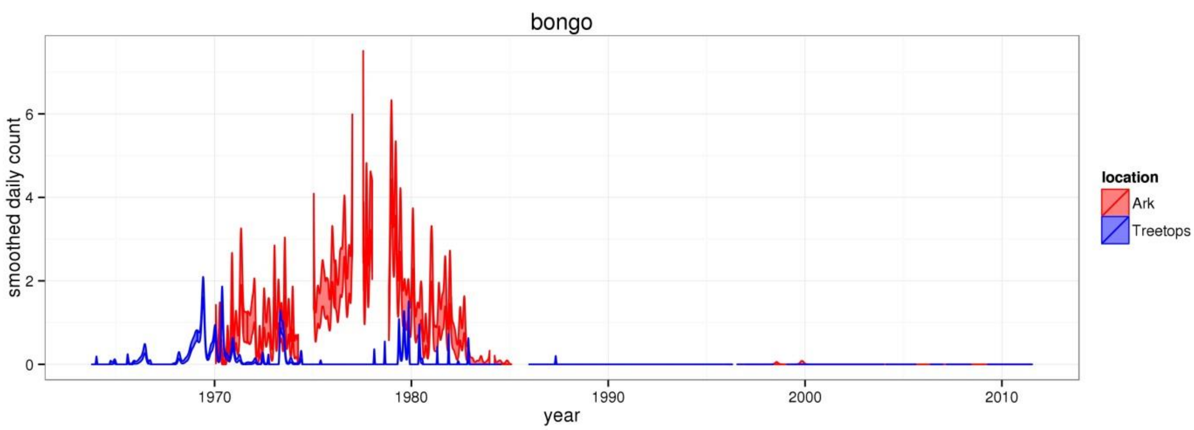
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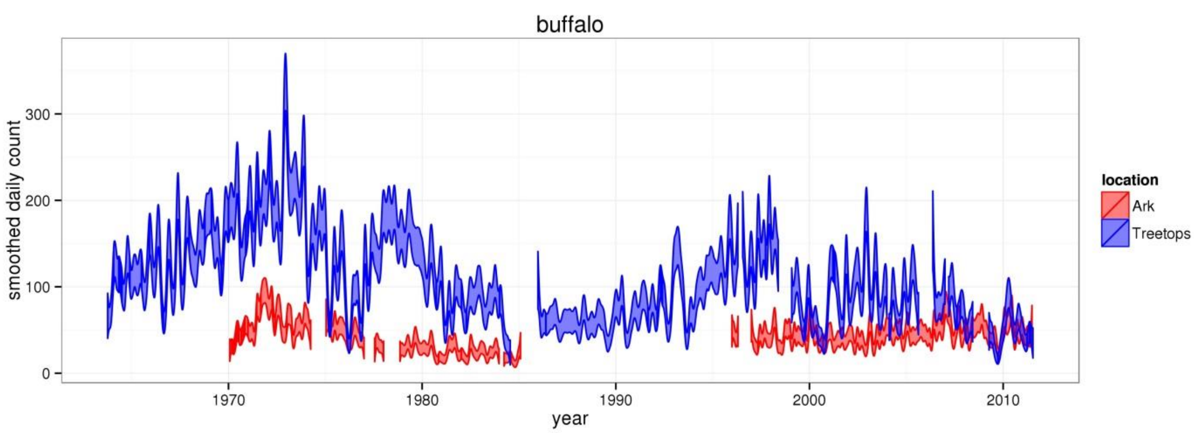
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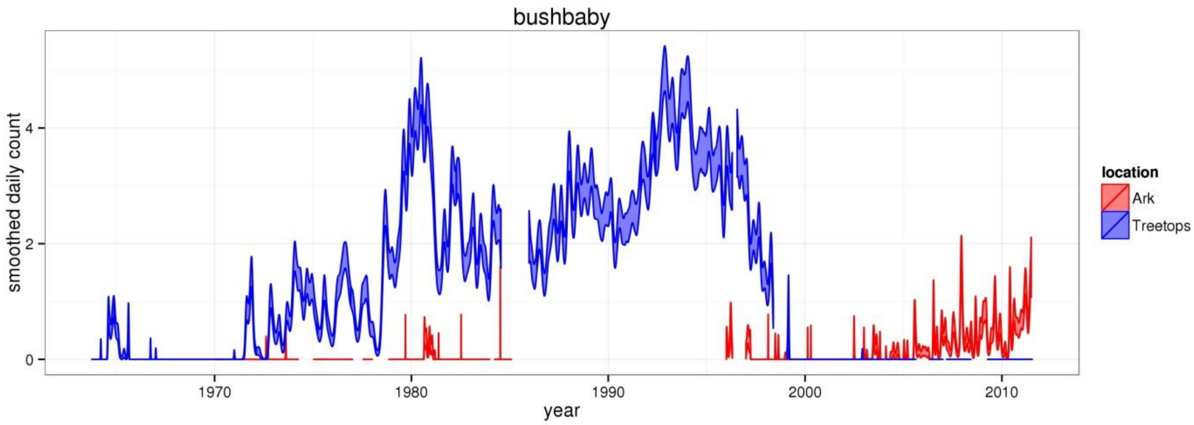
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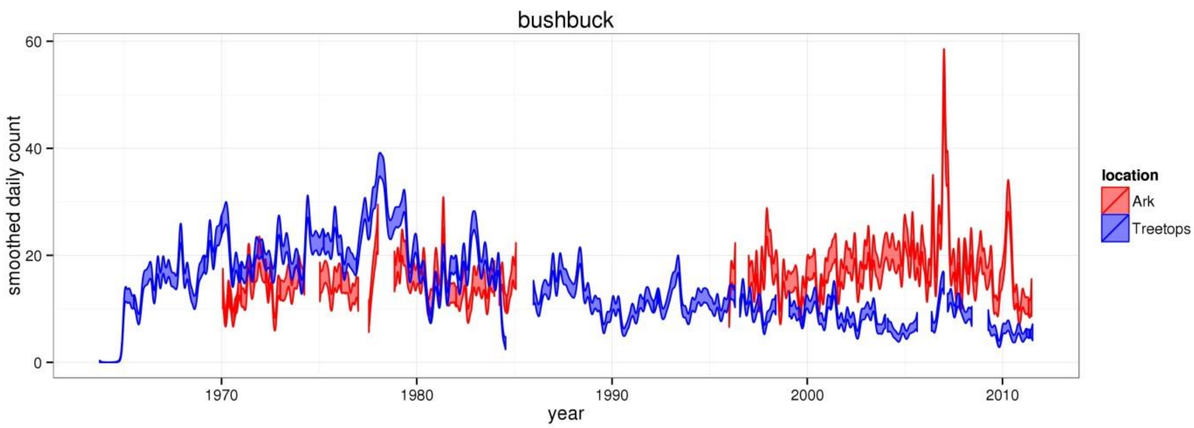
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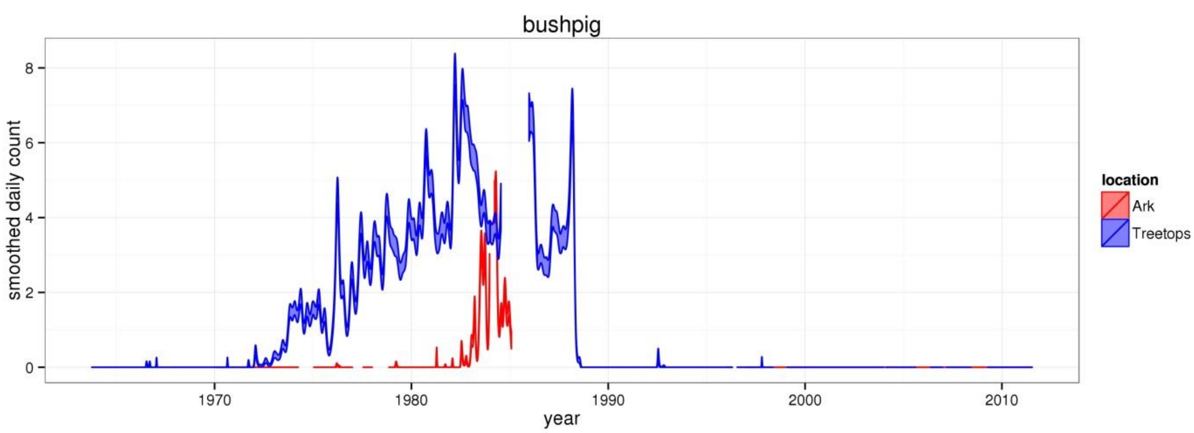
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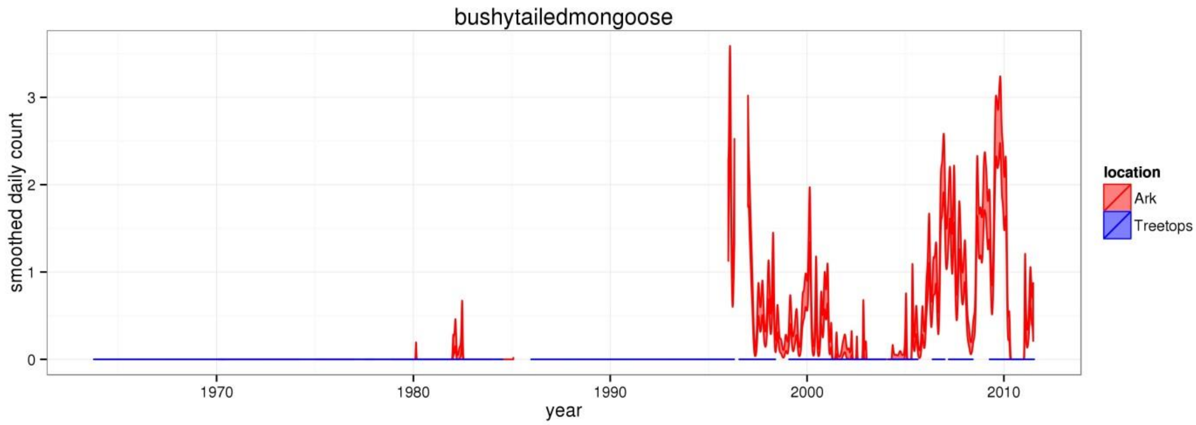
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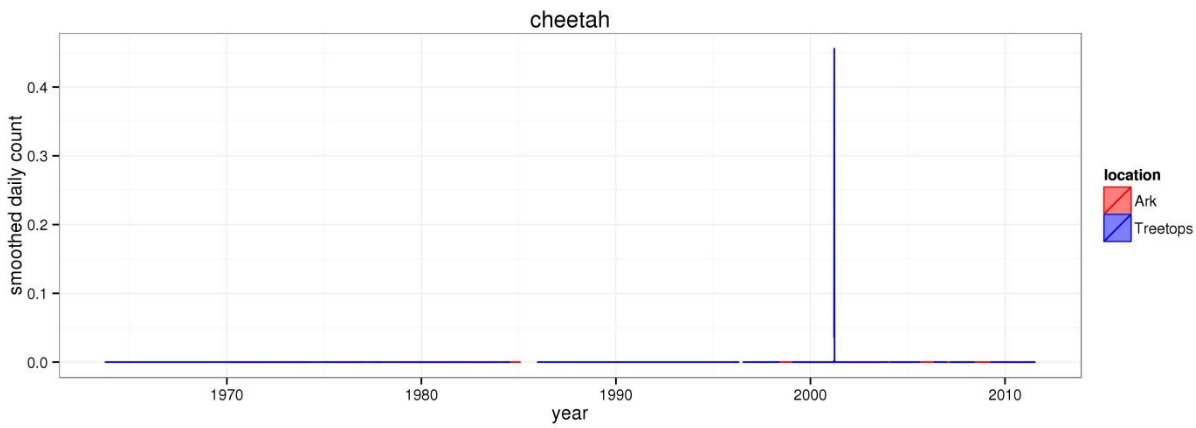
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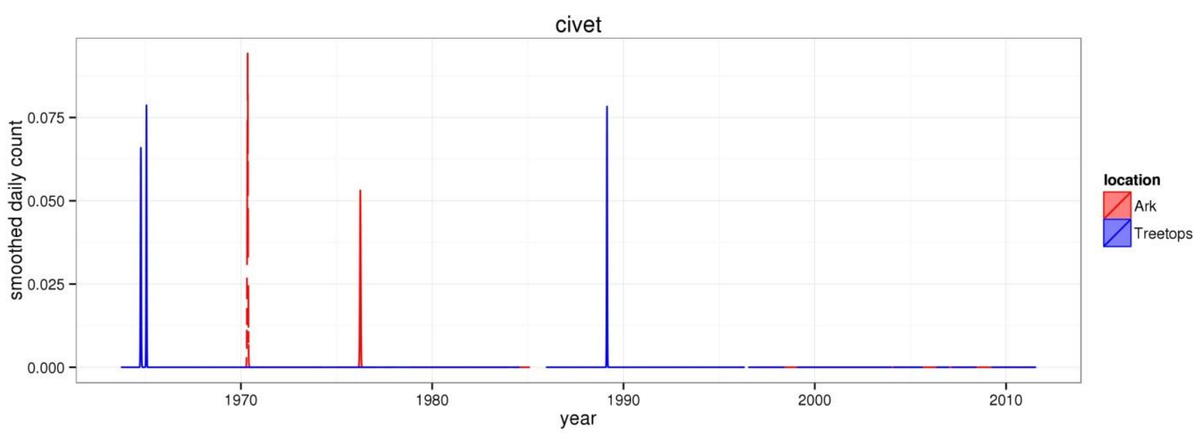
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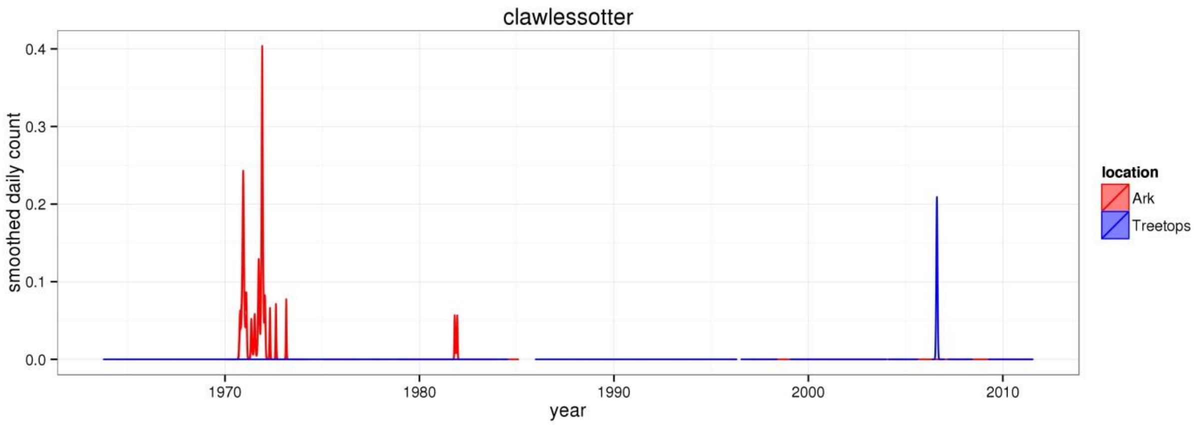
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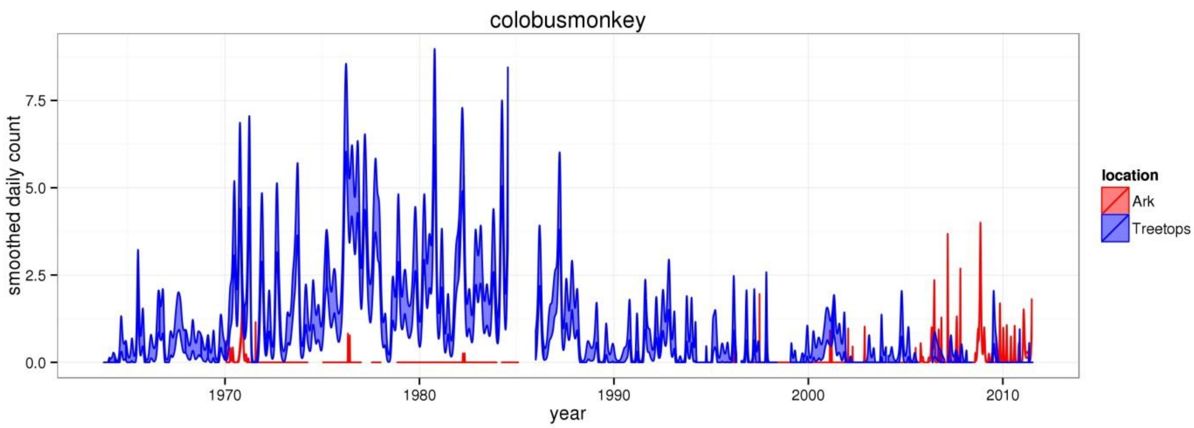
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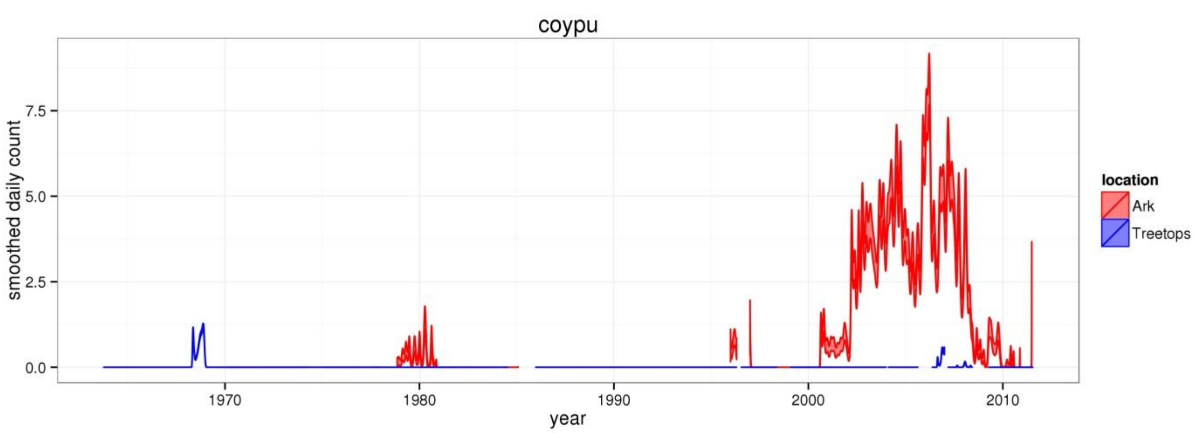
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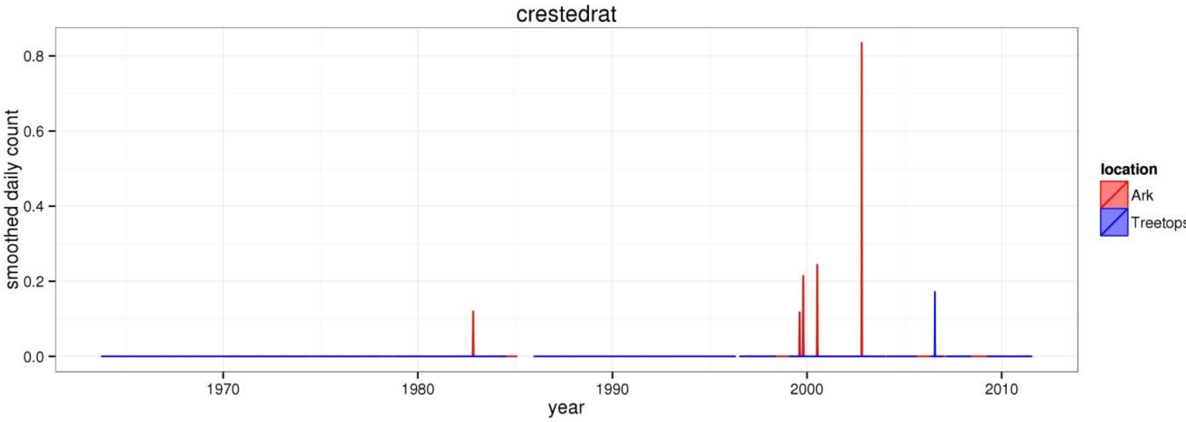
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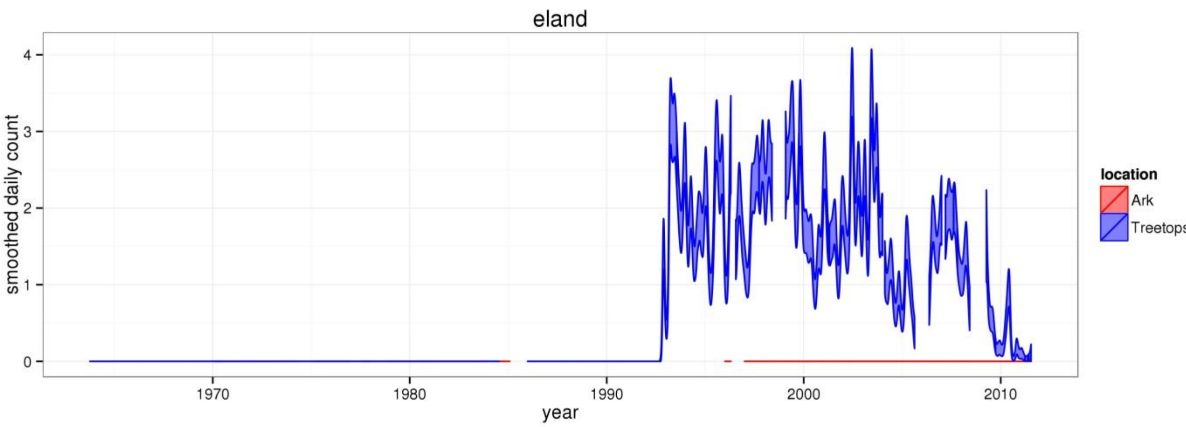
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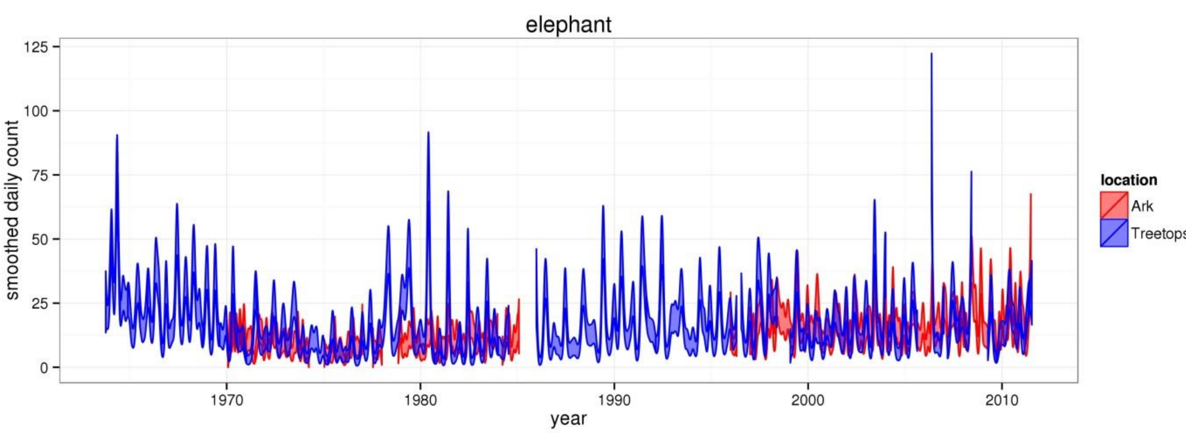
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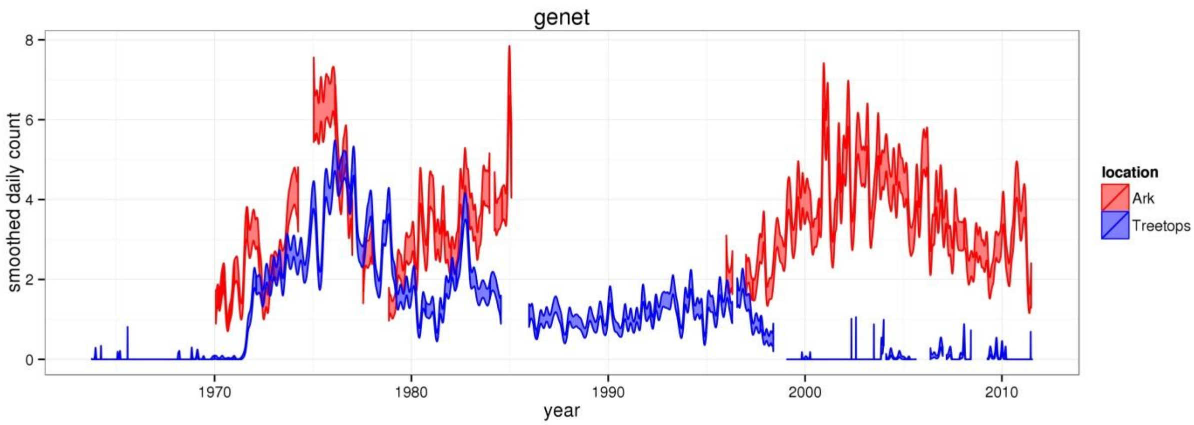
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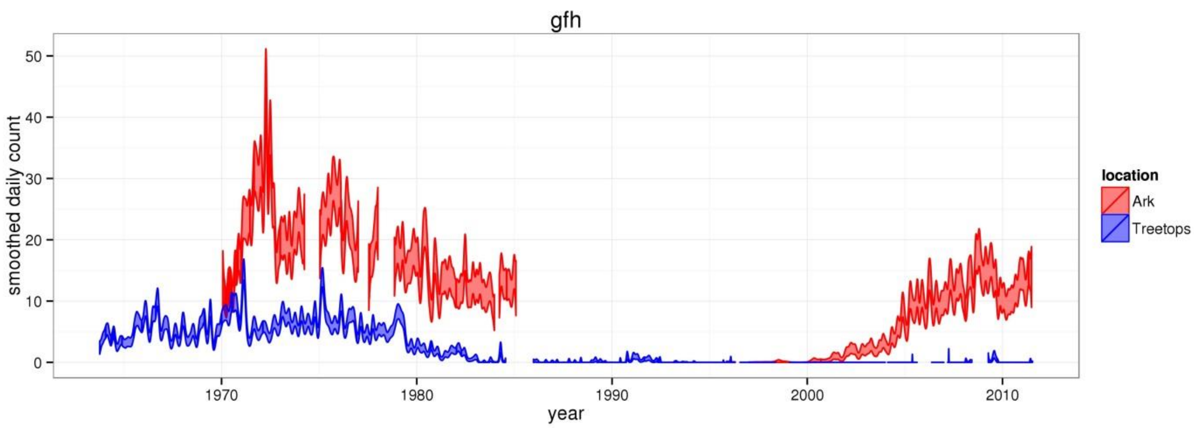
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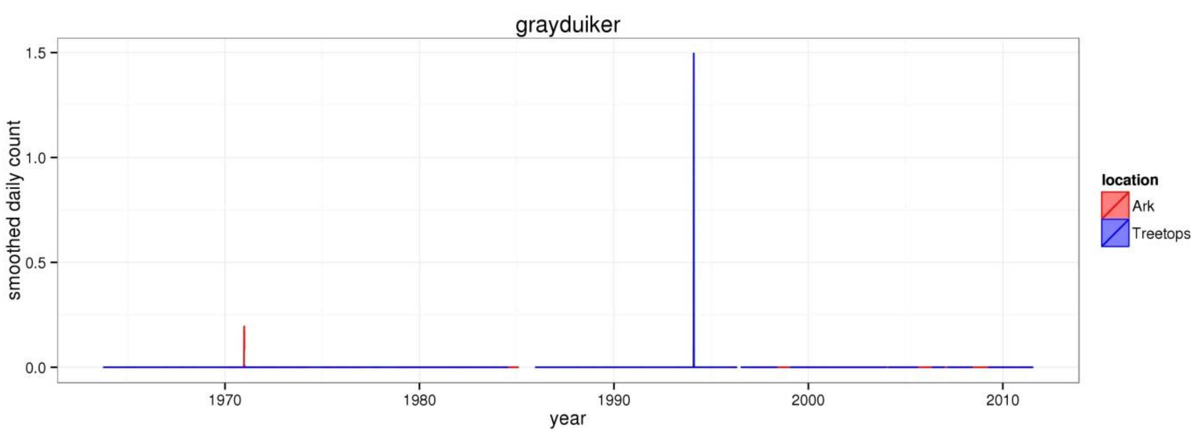
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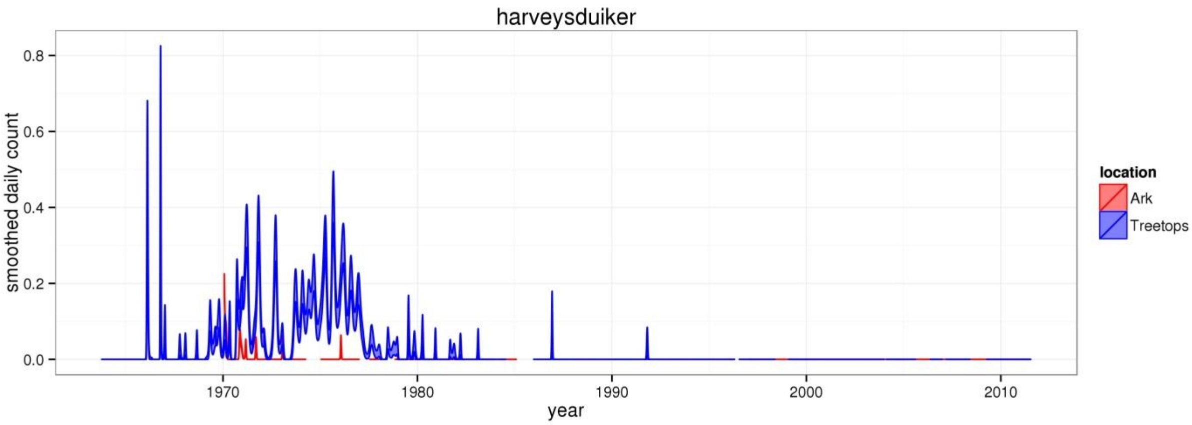
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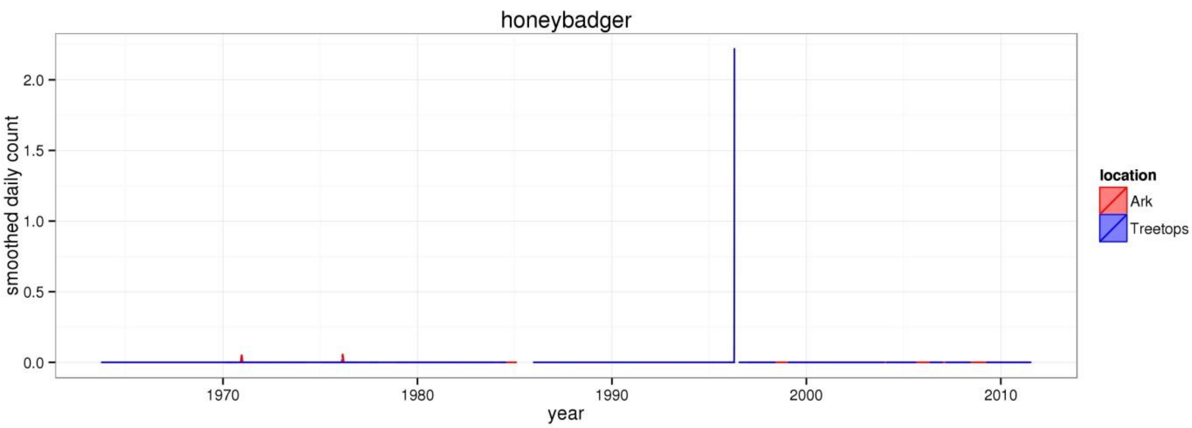
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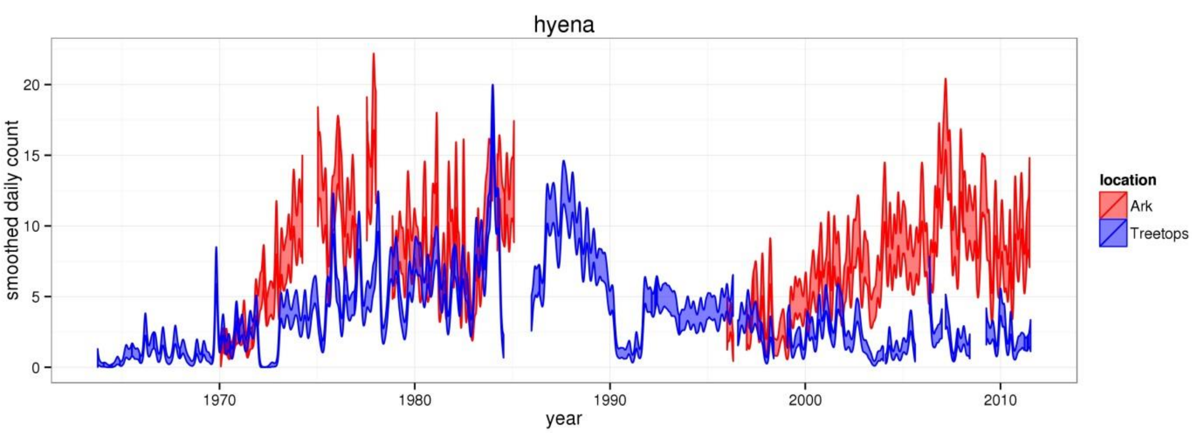
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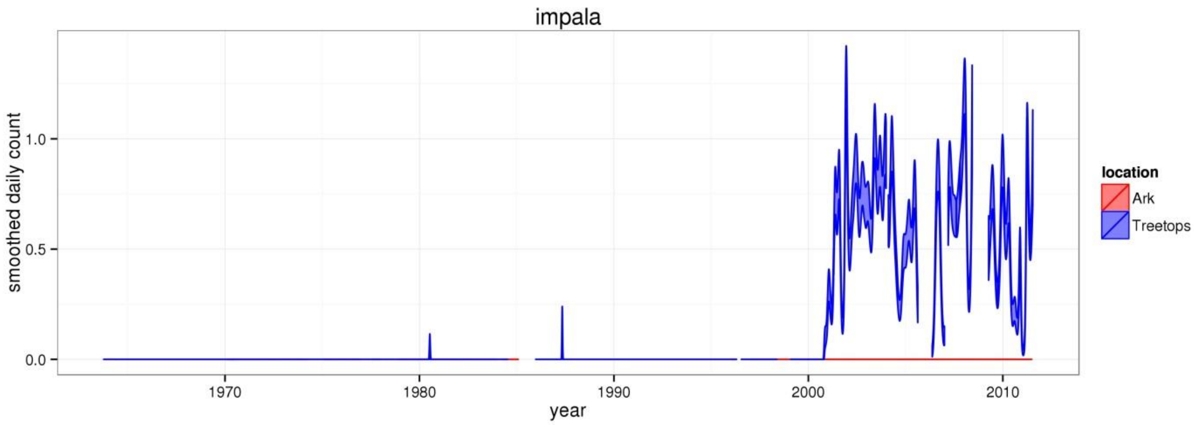
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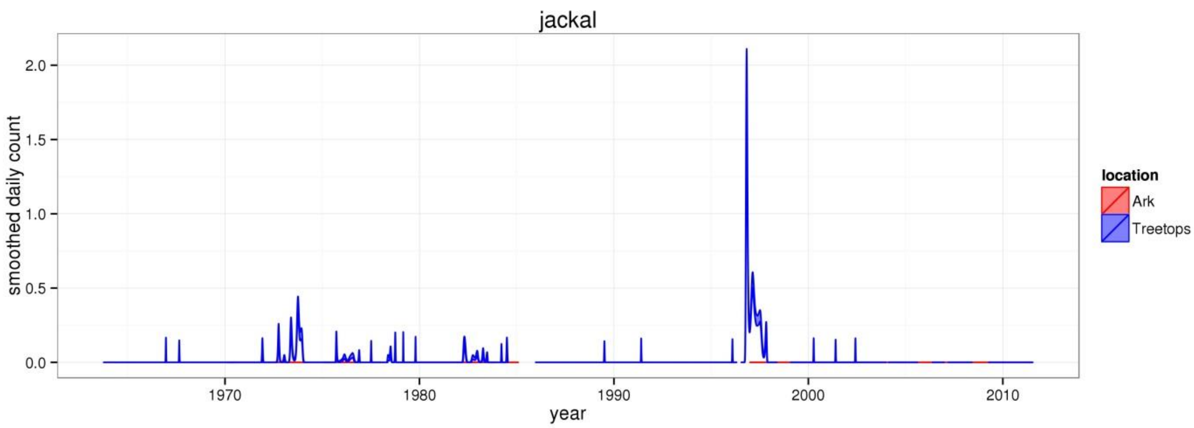
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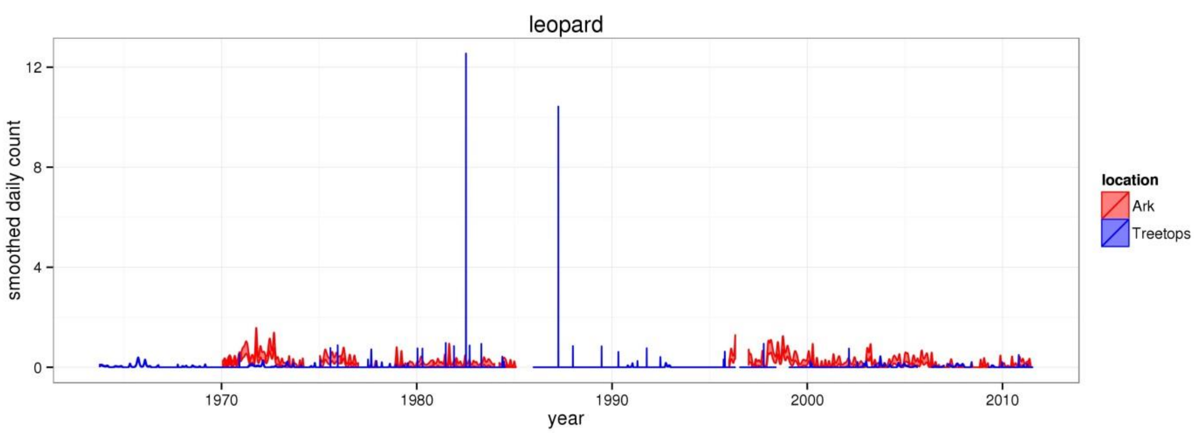
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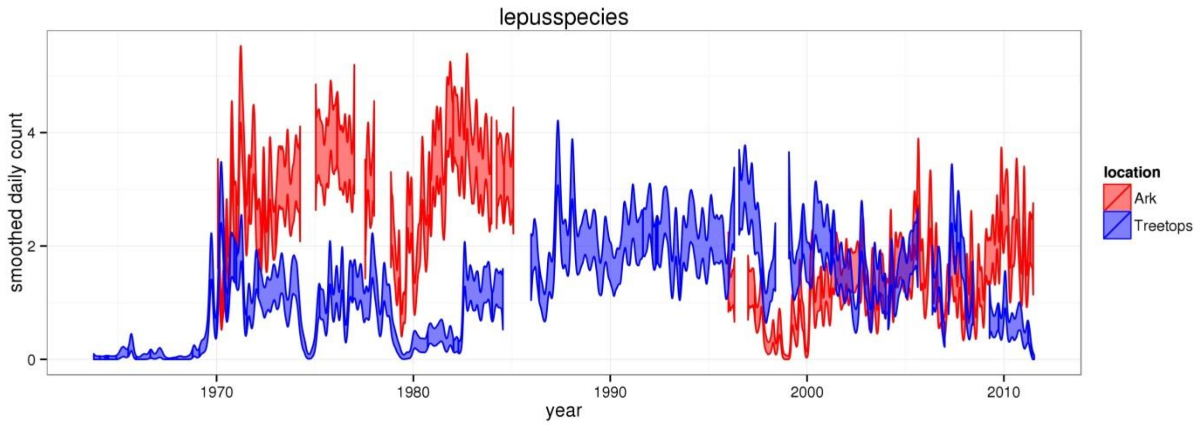
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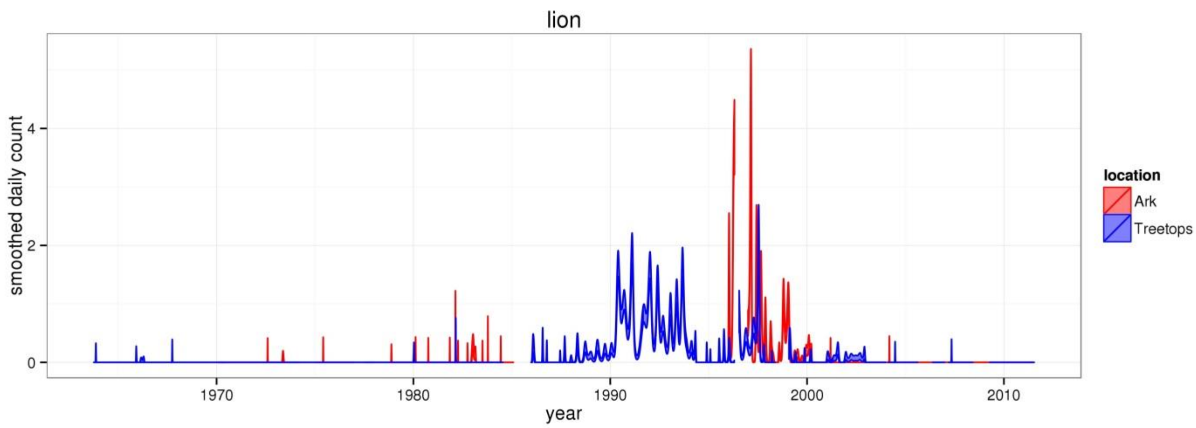
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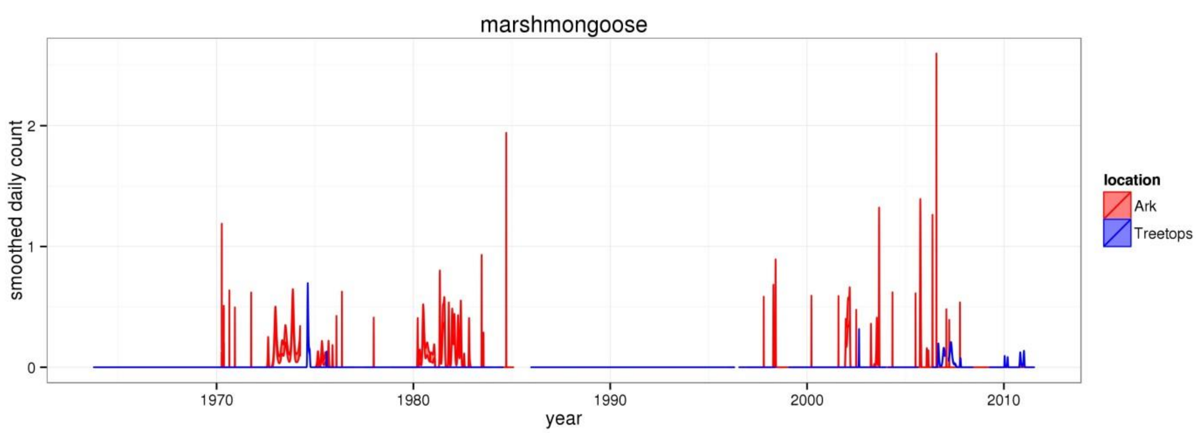
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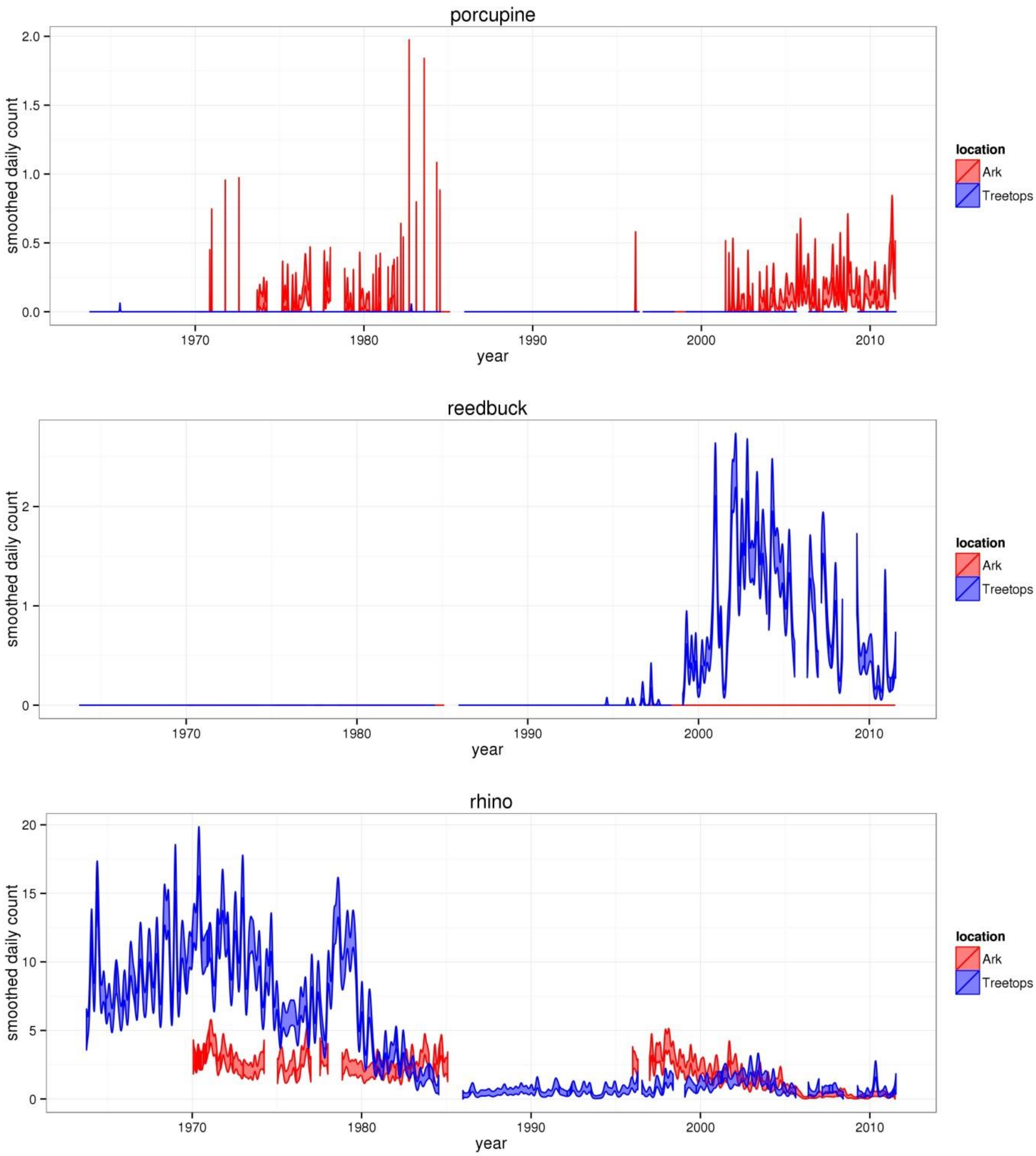
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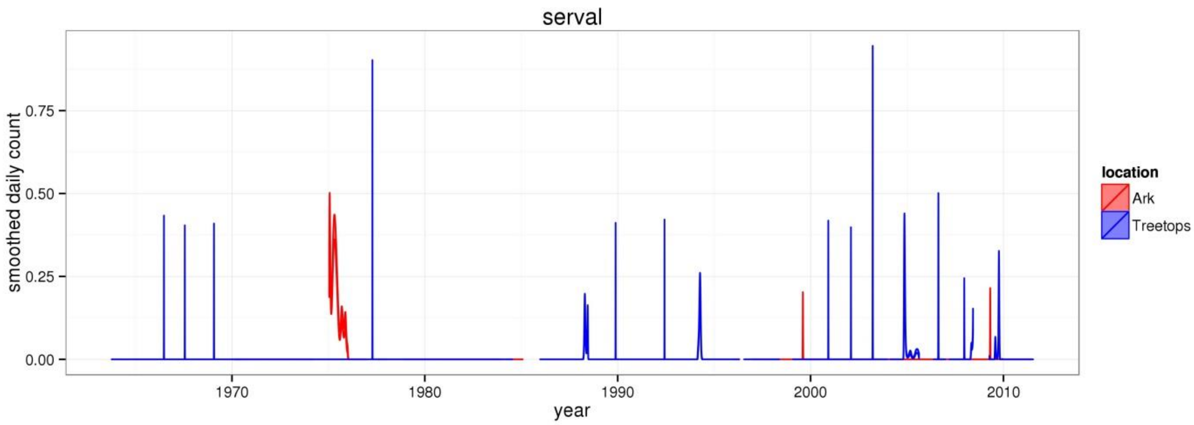
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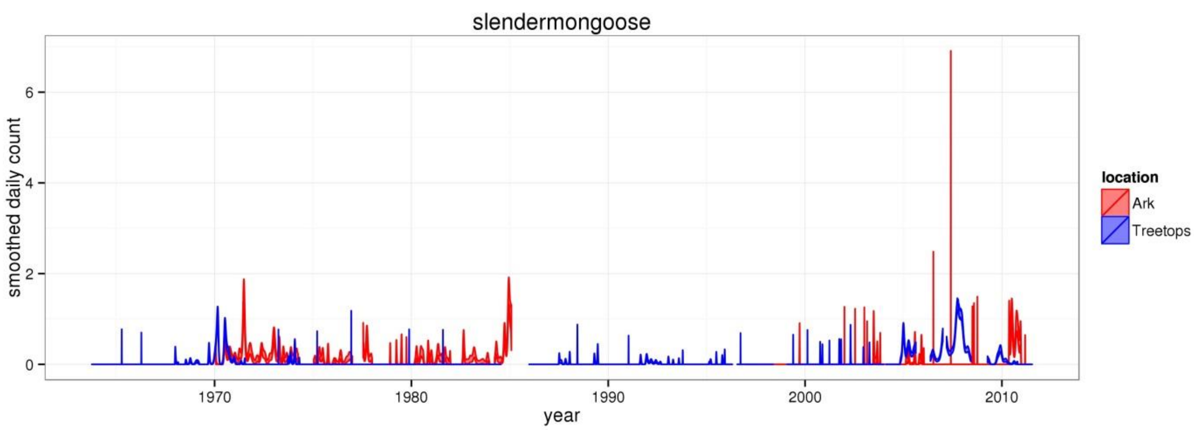
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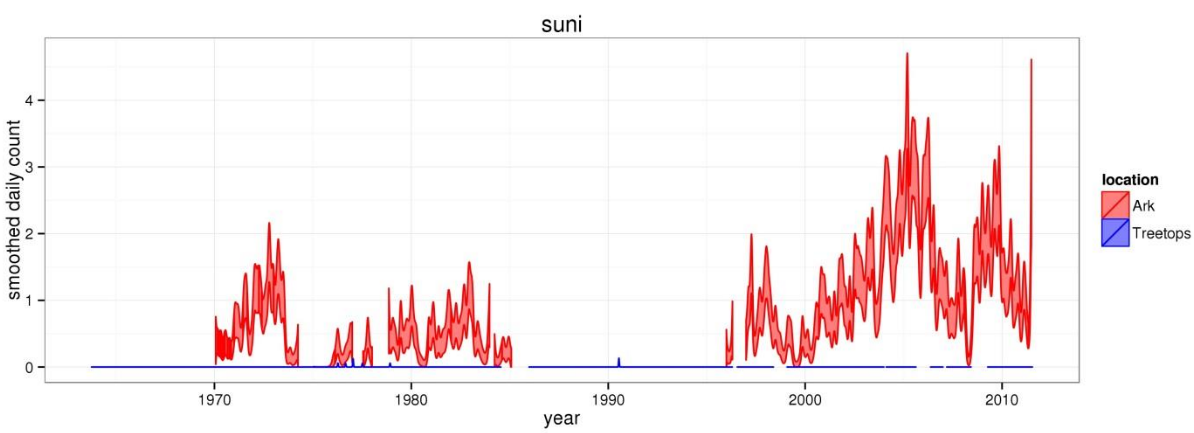
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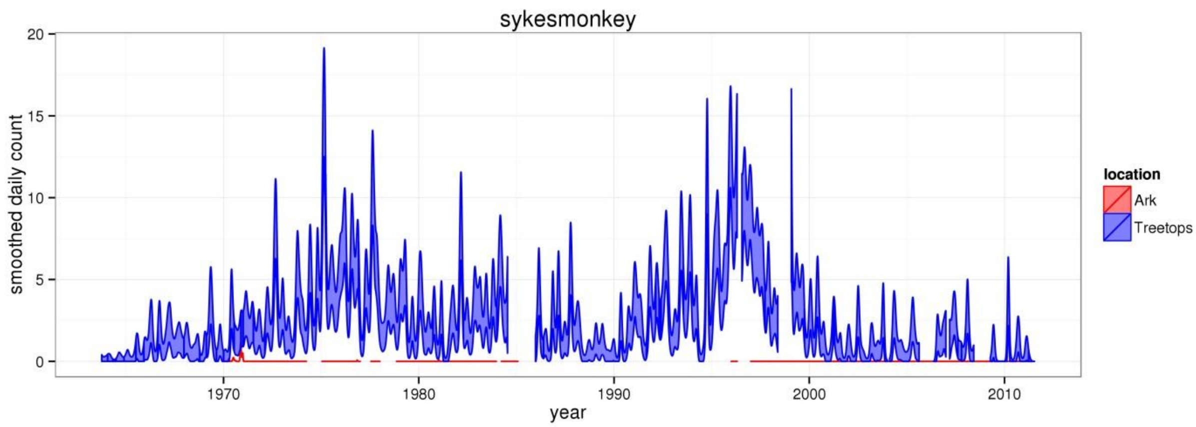
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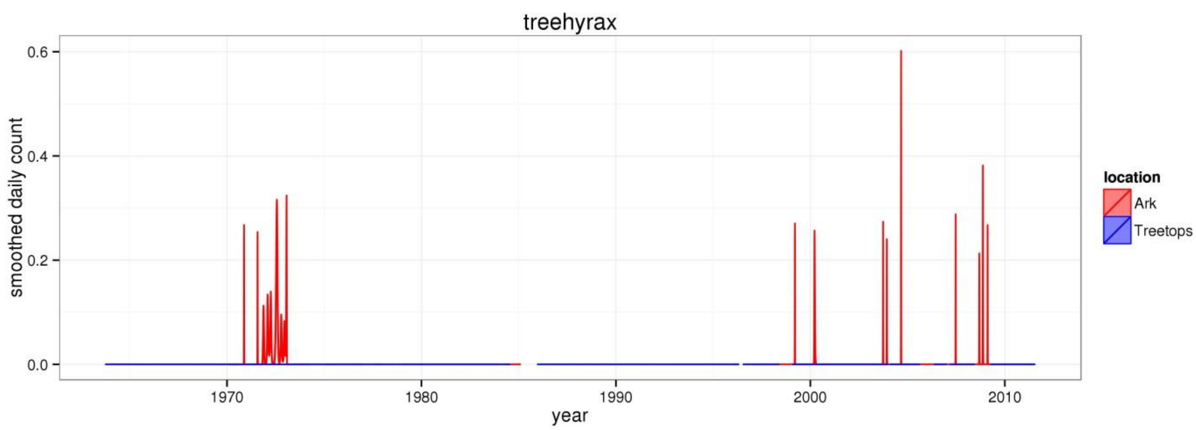
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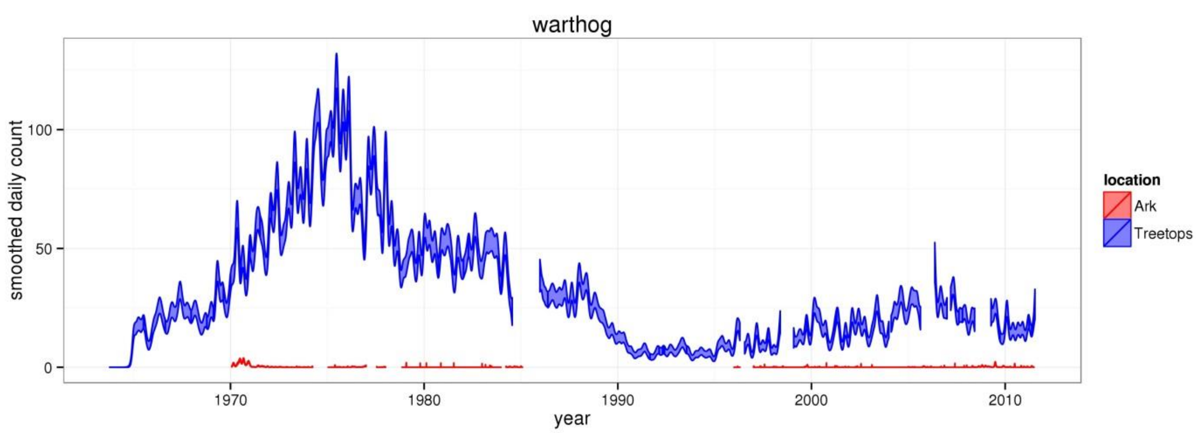
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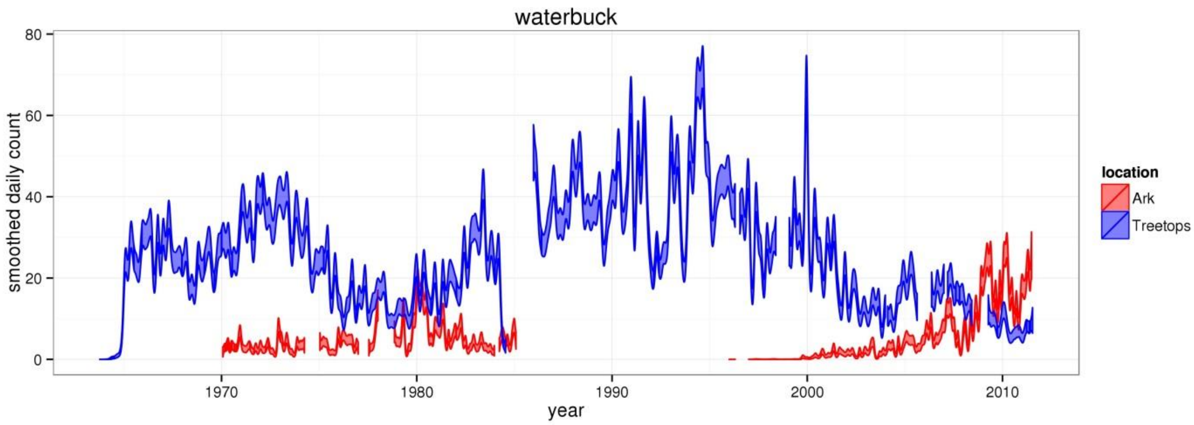
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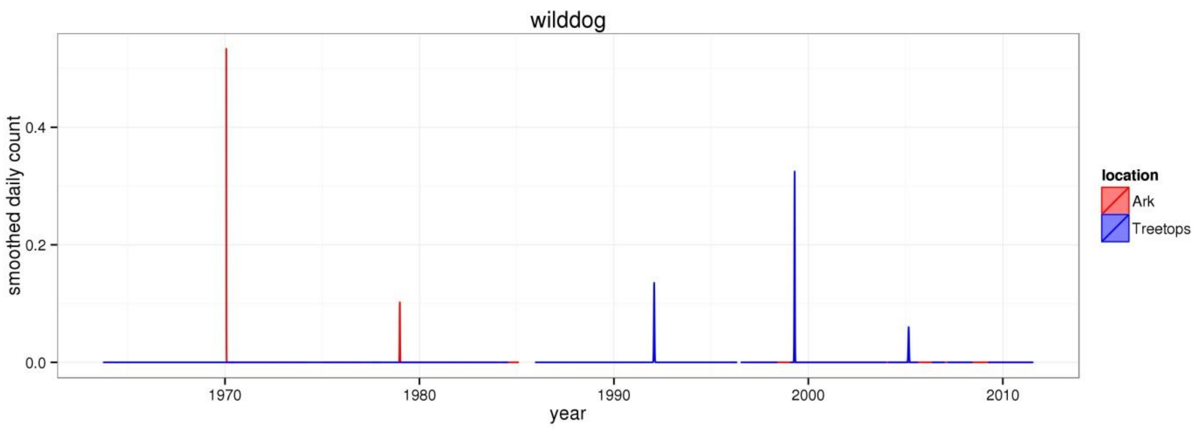
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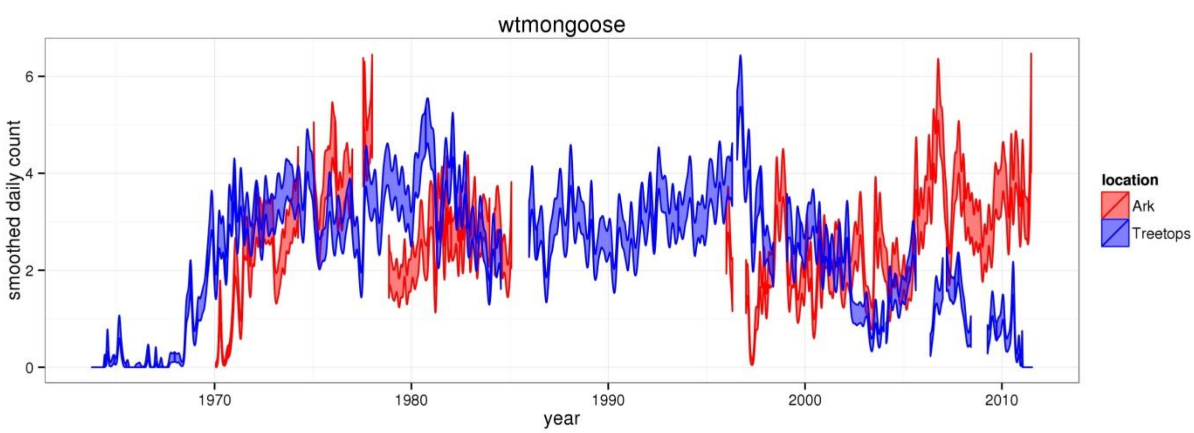
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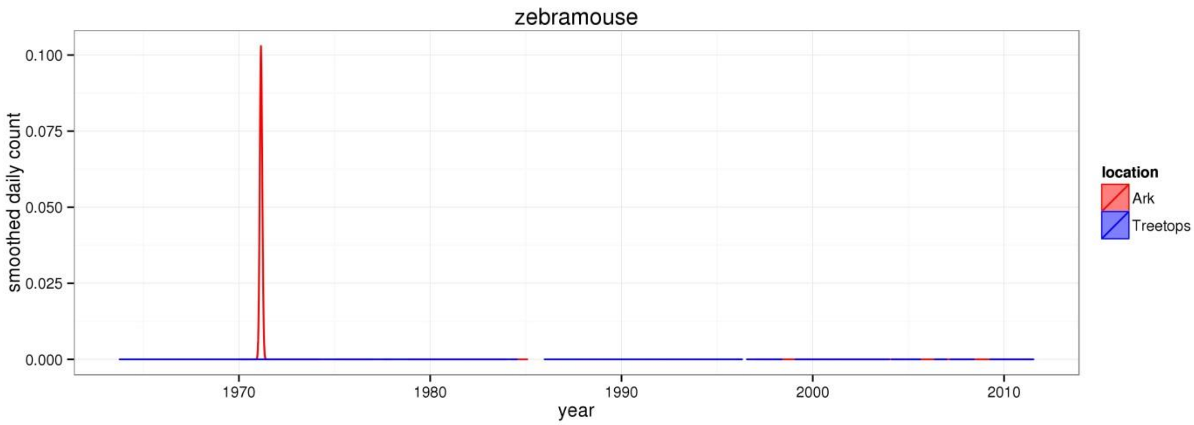
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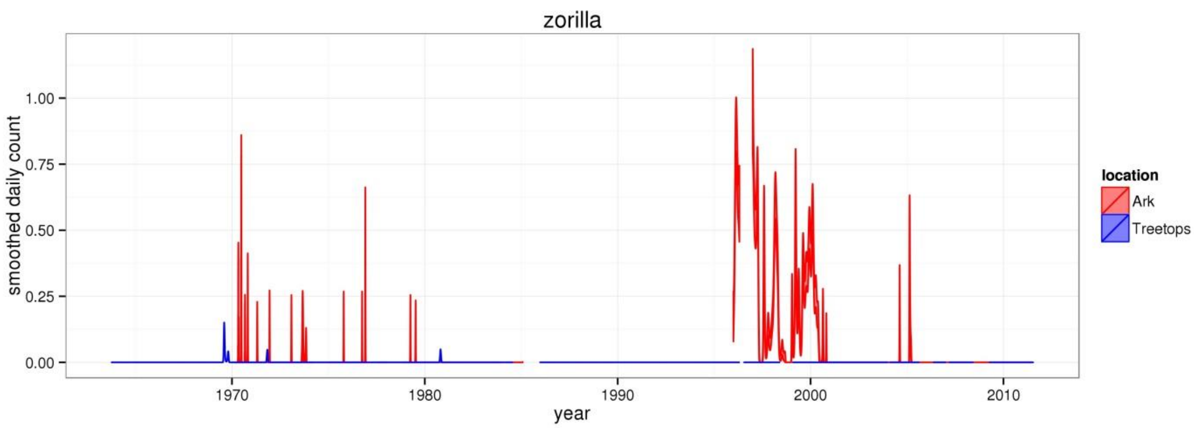
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0.75
0.50
0.25
0.00
1970
1980
1990
2000
2010
year
location
Ark
Treetops

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